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FOOD AND OTHER RESOURCES OF THE WILD RABBIT *Oryctolagus cuniculus* (L.)

by

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requirements for the Degree of
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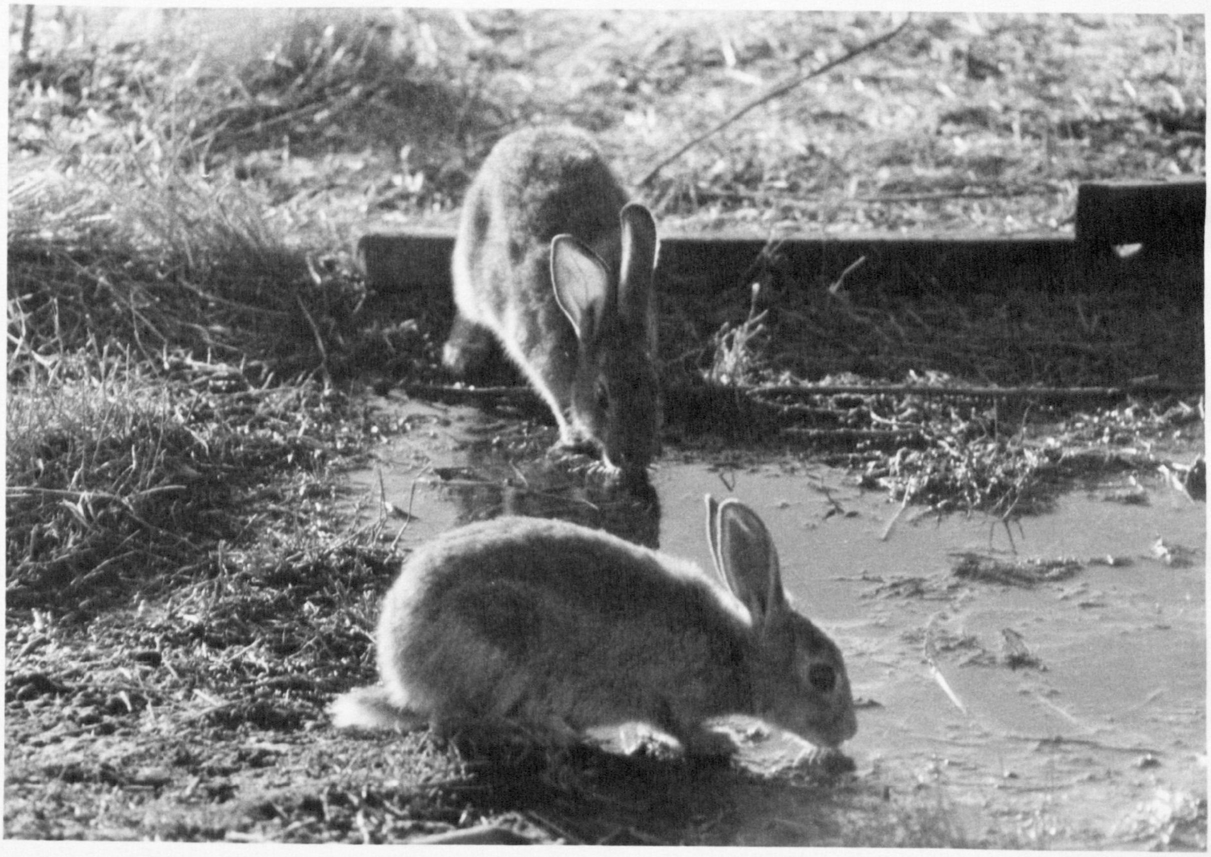

PLATE 1 Rabbits drinking water from a leaking tank at Witchitie in January 1970.

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SUMMARY

The numbers of rabbits in a natural population in an arid part of South Australia were recorded over a period of six years. During the first two years, the population increased rapidly but a crash followed in which over ninety-percent of the rabbits died. As the population fell, rabbits sought water at bores and ate atypical foods such as twigs from shrubs. Any of three factors, namely, the numbers of rabbits and shortages of food or water, could therefore have caused the population crash.

It became apparent however that the crash was not an outcome of the social friction which results from crowding. Instead it seemed that rabbits were simply too numerous for a resource such as food or water.

Field experiments in which supplementary water was provided for the rabbits showed that the additional water could substantially reduce the loss of weight shown by many rabbits during the drought which followed the population crash. However, it seems that the crash was not caused by shortage of water alone because at the time of the crash the rabbits were forced to eat indigestible, perennial vegetation to obtain their water and as a result they had a low intake of energy. The advantage of supplementary water apparently lay in enabling the rabbits to eat more of the dry, marginally better annual vegetation than they could when they had to obtain their water from coarse vegetation.

To further investigate the importance of environmental factors such as the weather and grazing on the availability of water for the rabbit, the moisture content of the more common species of plants was determined at regular intervals. In addition a soil-moisture model was developed to estimate periods when growth of plants might occur and drought prevail. Since this model proved useful in predicting the water content of ungrazed or lightly-grazed plants it could be ascertained that, at the time of the initial population crash, sufficient water for the rabbits should have been available in the pastures if they had not been heavily over-grazed.

A survey of the literature showed that plants likely to be useful to the rabbit were those which contained less than forty-percent fibre. Consequently, chemical analyses of plants from the study area showed which species were potentially useful to the rabbit and these results were supported because the major concentrations of rabbits were found where such plants grew most densely.

Changes in the abundance of vegetation were recorded by photographing clearly defined quadrats at regular intervals. The index of abundance of vegetation so obtained was then divided according to the fibre contents of the pasture species to provide an index of the abundance of food for the rabbit as distinct from the abundance of vegetation in general.

Between 1969 and 1972 there were three periods when food was in short supply. The first corresponded to the major crash in the rabbit population and was almost certainly caused because the unusually large numbers of rabbits ate most of the available food. The second food shortage occurred when the larvae of the moth *Loxostege affinitalis* ate most of the soft plants in the pasture. Drought and heavy grazing by sheep caused the third period of food shortage. The number of rabbits in the population fell whenever food became scarce and rose some time after food became more plentiful again.

By analysing the contents of rabbits' stomachs it was ascertained that the food eaten by rabbits always contained adequate nitrogen but fibre appeared to be limiting. A strong correlation found between the quality of food eaten and the amount of food available to the rabbit was compared with similar data obtained from studies on sheep. The comparison produced some evidence that shortage of food prevented rabbits from reaching their full potential of reproduction and growth in most seasons.

Multiple regression analyses showed that the availability of food and water could explain much of the variability observed in the weights of the rabbits' gonads. Furthermore, because gonad weights could be readily related to function, the availability of food and water was obviously related to reproductive success. The influence of water was thought to be indirect however and probably acted by influencing the growth of plants rather than by limiting the supply of water for the rabbits.

To complete successful reproduction a continued supply of food for weaned kittens was necessary because growth rates of the young were strongly correlated with the availability of food.

Although these results show that food shortage probably limited the capacity of the rabbit population to increase, one major short-coming of the study is that the causes of death of the rabbits remain unknown. Except in unusual circumstances, starvation was not observed but it is possible that predators or disease could cull rabbits debilitated by food shortage.

In general, the influence which other species of

animals have upon the rabbit population, by competing for limited supplies of food or through their predatory or pathogenic actions, remains the greatest obstacle to a full understanding of the dynamics of populations of wild rabbits.

DECLARATION

This thesis contains no material which has been accepted for any other degree or diploma at any university and to the best of my knowledge contains no material previously written or published by another person except where due reference is made in the text of the thesis.

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1. INTRODUCTION

Several studies of the wild rabbit in Australia have shown food to be a resource which can have an important effect on the size of populations (e.g. Poole, 1961; Stodart and Myers, 1966; Myers and Poole, 1963a, 1963b).

Mostly the quality of food has been considered, as for instance when Poole (1961) suggested that the rabbit only bred successfully when pastures were actively growing. In fact, Poole's ideas were verified experimentally when Stodart and Myers (1966) compared reproduction and the survival of young in groups of rabbits given either growing pastures, with or without supplements, or dry hay and grain only. The results showed that green, growing vegetation was indeed essential for breeding and also for the survival and health of the young.

In addition to limiting the duration of the breeding season shortage of food of adequate quality also appeared to have some influence on fecundity although much of the evidence for this was indirect and subject to more than one interpretation. For example, the seasonal variations in fecundity observed by many authors may be at least partly explained in terms of availability of food because ovulation rates reach a peak in late spring or early summer when pastures are most abundant. However, Mykytowycz (1960) and Lloyd (1963, 1967) proposed that the variations in fecundity could be largely explained in terms of crowding and social friction because at high densities of rabbits relatively few young are born.

Yet, as I have commented before (Cooke, 1970) the idea that crowding reduces fecundity does not explain why some of the mature does in the enclosures maintained by Mykytowycz

(1960) began to breed only in spring about the time that young rabbits born earlier in the breeding season were also beginning to breed. An alternative hypothesis was obvious; the rabbits could have caused deterioration of the pasture by overgrazing whenever they reached high densities and it was poor diet rather than social friction that reduced the fecundity of the does.

Indeed, there was some evidence to support this idea. The numbers of rabbits in the enclosures maintained by Mykytowycz (1960) were close to the estimated carrying capacity of the pastures and, in the case of Lloyd's (1967) population on Skokholm island, the pastures were described as 'impoverished'. Finally, Myers (1964) showed that crowding had very little effect on fertility and fecundity, even among rabbits kept at extremely high densities of 500/ha, provided all rabbits could obtain ample food.

The enclosure studies of Myers and Poole (1963a, 1963b) showed that rabbits could readily increase to levels where they ate most of the available food. They provided the first evidence that food shortage could limit the size of populations of wild rabbits.

However, the rather ayptical environment of the enclosures made it unwise to apply the results uncritically to free-living populations of rabbits. In contrast to wild populations the enclosed populations maintained by Myers and Poole were provided with troughs of drinking water and were also free of the major predators such as cats (Myers and Schneider, 1964) and foxes which can dig nestling rabbits from the burrows (Myers and Parker, 1965). On the other hand the rabbits in the enclosures did not have to compete with other grazing herbivores which might have eaten some of the available food. There was a further serious objection in that the enclosures could prevent the dispersal of young or subordinate animals and food shortage might be an abnormal consequence of the inhibition of social mechanisms for limiting population density. A mechanism of this type has been suggested to explain the high numbers reached by enclosed vole populations (Krebs, Keller and Tamarin, 1969; Krebs, 1971).

While acknowledging the dangers of extrapolating from an enclosure to the field I was nevertheless greatly impressed by certain similarities between the crashes observed in the populations studied by Myers and Poole and the population which I had followed at Witchitie. As shown in figure 1, the population of rabbits at Witchitie increased to relatively high numbers in 1968, rose higher in mid-1969 then crashed dramatically in the late-spring. The sequence of the population changes - lactation failure and death of nestlings, then death of juveniles followed by death of adult rabbits - and the severity and timing of the crash, which coincided with the maturation of the annual pastures, were quite similar to those which Myers and Poole recorded for the enclosed populations at Albury.

This pattern of mortality, it could be argued, would also result from other causes such as predation but at Witchitie only the occasional fox was seen on the study area at that time and besides most adult rabbits suffered severe weight losses during the crash. The weight losses of the adults made it more likely that food shortage rather than predation was the cause of the crash. Furthermore, rabbits at both Witchitie and Albury were observed to eat coarse

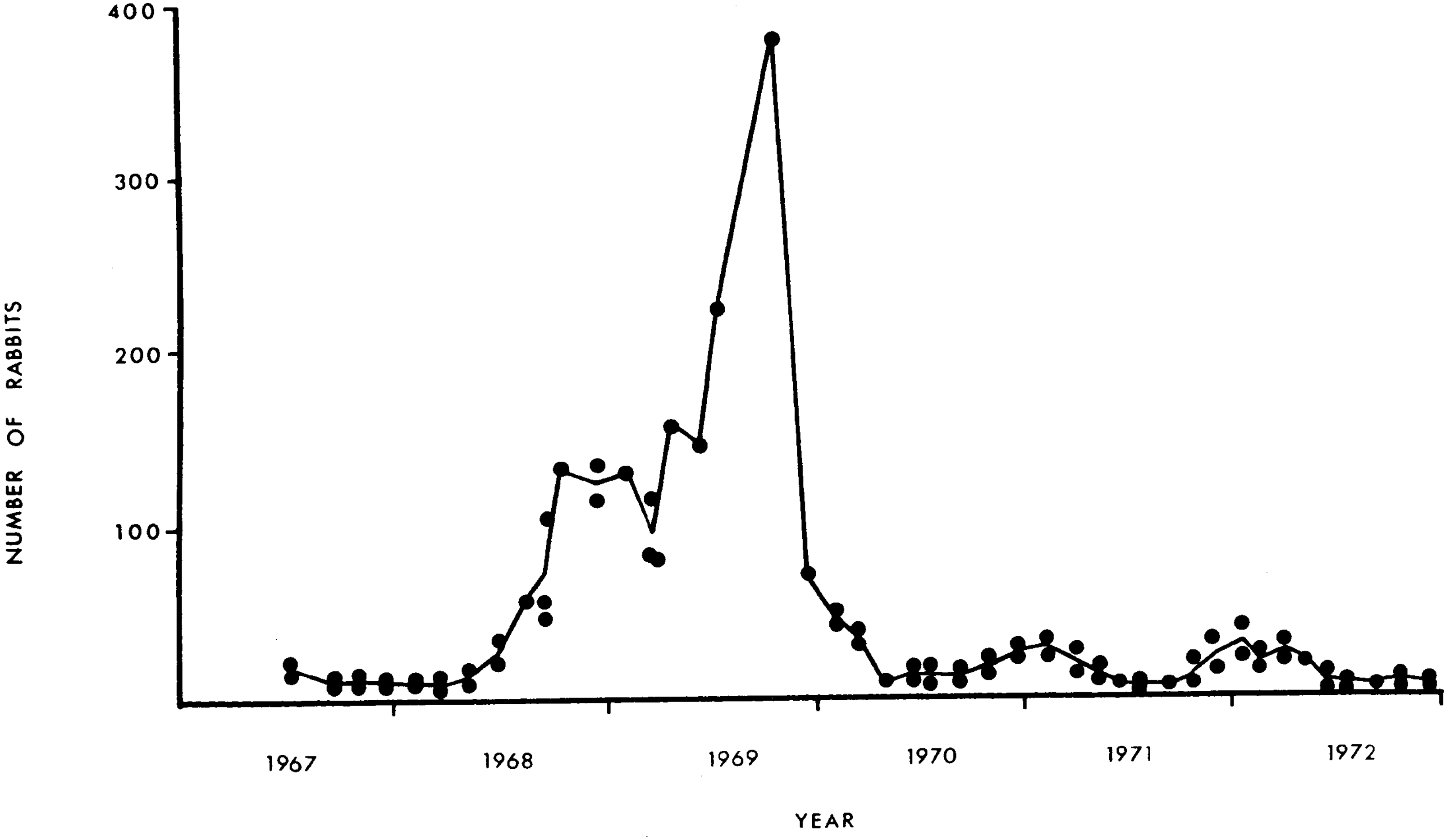

Fig. 1 The number of rabbits counted on spotlight transect at Witchitie, 1967 - 72.

vegetation such as *Echium plantagineum* just before the crash, and, since this plant was not normally eaten, here was additional evidence that food was becoming scarce.

It therefore seemed from the agreement between the two population studies that the free-living population at Witchitie had been affected by shortage of food. Yet several problems remained. For instance, although it was clear that stress associated with high numbers of rabbits could not limit reproduction sufficiently to prevent the rabbits from increasing excessively it was nevertheless possible that behavioural changes which might occur if rabbits were abundant could cause a population crash (Chitty, 1952; Krebs, 1971).

Furthermore, the availability of water was implicated in the population crash because some rabbits began moving to water at a mill located some 200 m off the main study area as the ephemeral vegetation began to dry off. The attraction that this water held for the rabbits was pointedly demonstrated when a commercial rabbit trapper set nets around the mill and caught many rabbits including forty-three tagged rabbits from the study area.

It should be emphasized at this point that the trapper's efforts had little to do with the population crash because 69% of the 1200 or so rabbits on the study area had been tagged by the time he began trapping in late November 1969. At most he might have accounted for 5% of the rabbits from the study area.

Beyond these general observations little more could be said about the role of water in causing the population crash. Its importance could only be decided from further empirical data or experimental evidence. There was however some advantage in reconsidering certain aspects of the crash in detail to test my supposition that food shortage rather than social behaviour had caused the population crash.

Theoretically, aggressive social behaviour could influence the size of a population if rabbits became too numerous for specific resources such as burrows, food or space. However, the consequences of shortages of each resource might differ considerably and although the net result of each kind of shortage would be a reduction in the size of the population, the events associated with the population crash might be indicative of the particular resource in short supply. For instance, if it was argued that space was short, as Chitty (1952) and Krebs (1971) have done for populations of voles, then dispersal as a consequence of increased aggressiveness might be apparent. On the other hand, if food was short, dispersal might not necessarily be associated with aggression.

Now, in a field study, the consequences of a shortage of resources are seldom observed directly but they can be implied from abnormal physiology or behaviour. For example, body-weight can be used as an index of physical well-being. More reliably, loss of weight, or in the young, low growth rates can be used to indicate stress. Normally, young rabbits at Witchitie grew at rates of at least 10 g/day. Abnormally wide-ranging movements or shifts in home-range can also indicate stress because rabbits normally have a well defined home-range which, I have found, rarely exceeds 600 m in diameter. Figure 2 shows the home-ranges of rabbits caught on the study area at Witchitie. Each of these rabbits was caught at least five times so that a good idea of their range was obtained.

Bearing these ideas in mind, it was useful to review

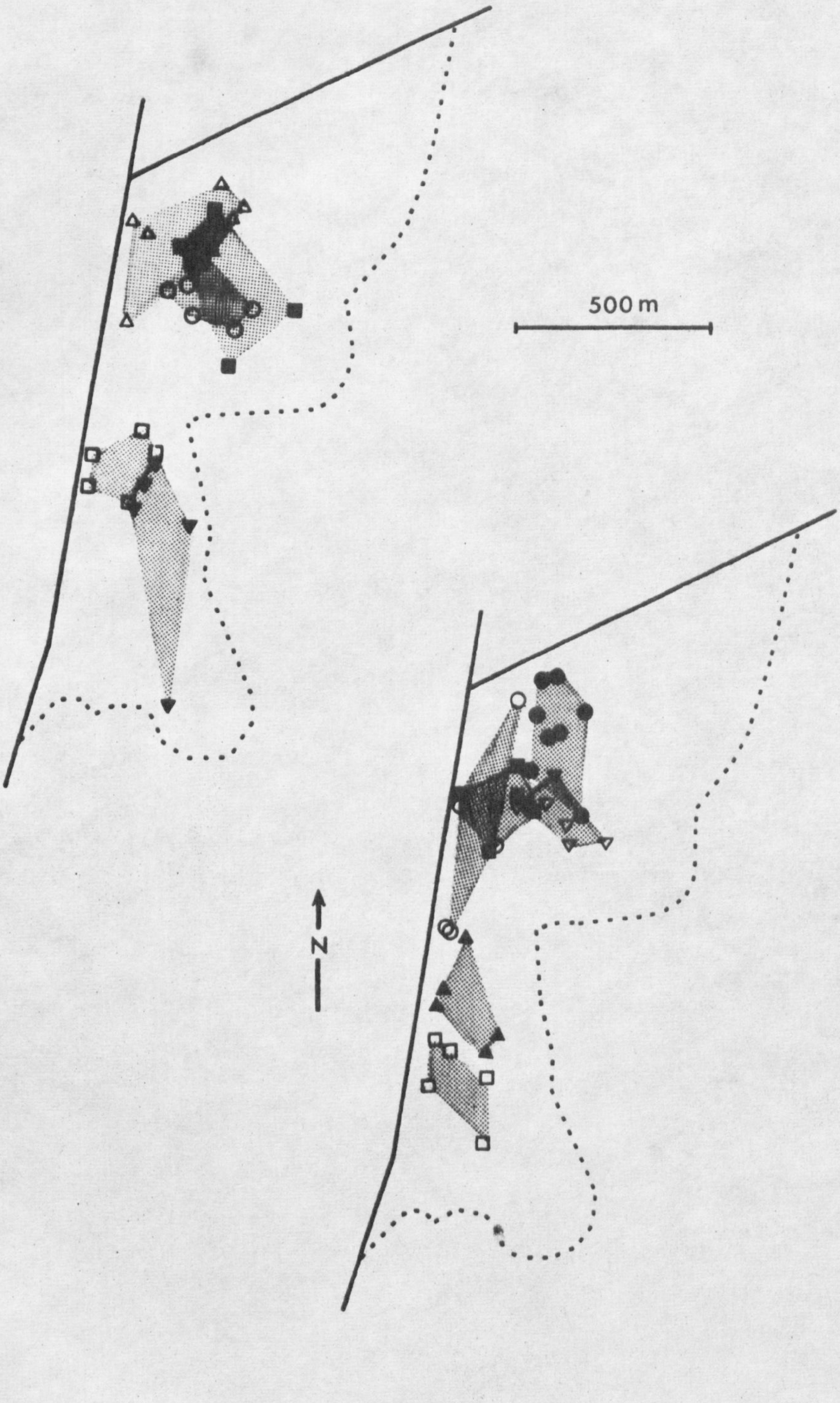

Fig. 2 The home ranges of rabbits on the study area. Each rabbit was caught at least five times during 1969–70.

some of the observations made at the time of the population crash and attempt to determine the most likely causes of the decline by investigating each resource in turn.

a) Burrows.

Burrows seemed to be in short supply just before the crash because all the warrens were occupied, extensions were made to existing warrens and some breeding stops were dug away from the main warrens. However, it was difficult to see how a shortage of burrows could lead to a population crash. Although the shortage may have slowed the rate at which the population increased because some does were forced to breed in shallow, insecure stops it was not so acute that subordinate rabbits were prevented from finding shelter during the heat of the day. Furthermore, the shortage did not last long because the rabbit population began to fall soon after the breeding stops were dug.

One fact could be stated conclusively however. Because the soils at Witchitie were heavy, unused warrens persisted for many years and so the number of warrens there probably reflected the maximum number of rabbits during population peaks of the past. It could be concluded therefore that in 1969 the rabbits had again reached the maximum numbers the area would support.

b) Food.

Although at the time of the crash there was little direct evidence to show that food was short, the weight and behavioural changes observed in the rabbits were nevertheless compatible with most aspects of food shortage. On the most crowded part of the study area for example, female rabbits ceased breeding a month earlier than in less crowded areas.

These does were apparently unable to maintain lactation because newly emerged nestlings were either grossly underweight or emerged precociously. Some of these nestlings weighed only 150-175 g instead of the usual 225 g recorded for most of the nestlings caught at Witchitie.

Older kittens had a hard time too. Those which weighed less than 1200 g either died or left the crowded part of the study area soon after the females ceased breeding. Two of the youngsters which wandered were later recaptured and their weight on recapture showed that they had grown slowly at only 5 and 7 g/day instead of the more normal rates of 10-15 g/day. It was significant too that the sub-adults which survived during the initial stages of the crash had all passed the age of about four months when rabbits reach sexual maturity and begin to lay down reserves of fat (see fig. 3).

Even though there was nothing inconsistent with the idea that a shortage of food had caused the population crash, or that the high numbers of rabbits were partly responsible for the shortage, it remained possible that the observations as recounted might also be explained by other hypotheses. For instance, the density of the population might have a strong influence on the behaviour and physiology of these rabbits as suggested by Christian (1950) for rodents and later by Mykytowycz (1959, 1960) and Lloyd (1963, 1967) in the case of rabbits.

Yet, although social interactions could conceivably supress lactation in wild rabbits there are several observations which do not support the idea that social pressures caused the young rabbits to wander. These will be considered presently.

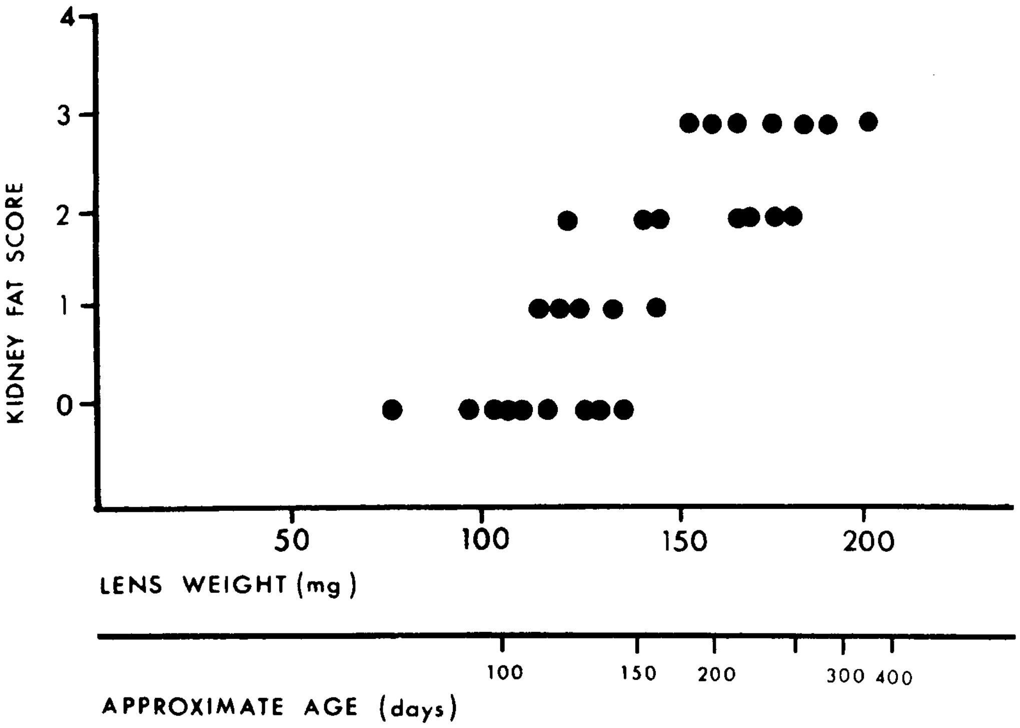

Fig. 3 The relationship between age and the amount of fat around the kidneys of young rabbits at Witchitie, 1969. The amount of fat is given here as a relative score, 0 = no fat, 4 = kidneys covered with fat. Rabbits had no reserves of kidney fat before 120 days of age.

c) Space.

It was known from trap records that even though rabbits were fairly evenly distributed among the warrens they were nevertheless more numerous on some parts of the study area than others. This arose because the warrens were clumped in favourable areas.

Consequently, to illustrate the density of rabbits on different parts of the study area I divided the area into arbitrary sub-units of roughly 1 ha each. Then, assuming that on average a rabbit moves 300 m from its burrow (half the diameter of a home-range) I calculated from the records of the trapped rabbits, the number of rabbits which might be expected to reach each arbitrary area to feed or interact socially. These results are given in figure 4.

With this picture of rabbit distribution in mind it is useful to return to consideration of the importance of social interactions, or shortage of space, in causing the crash. In particular, reference must be made to the dispersal of young rabbits.

As already mentioned, young rabbits weighing less than 1200 g began to disappear from the most crowded part of the study area before their numbers began to fall in the less crowded areas. The sub-adults stayed on in the crowded area however - at least during the initial stages of the population crash.

Most of the kittens, if they dispersed, must have died soon after leaving their birth places because no tagged rabbits of any age were caught more than 600 m from the study area despite extensive trapping at distances of up to 3 km from the boundaries. The only hint of dispersal was the

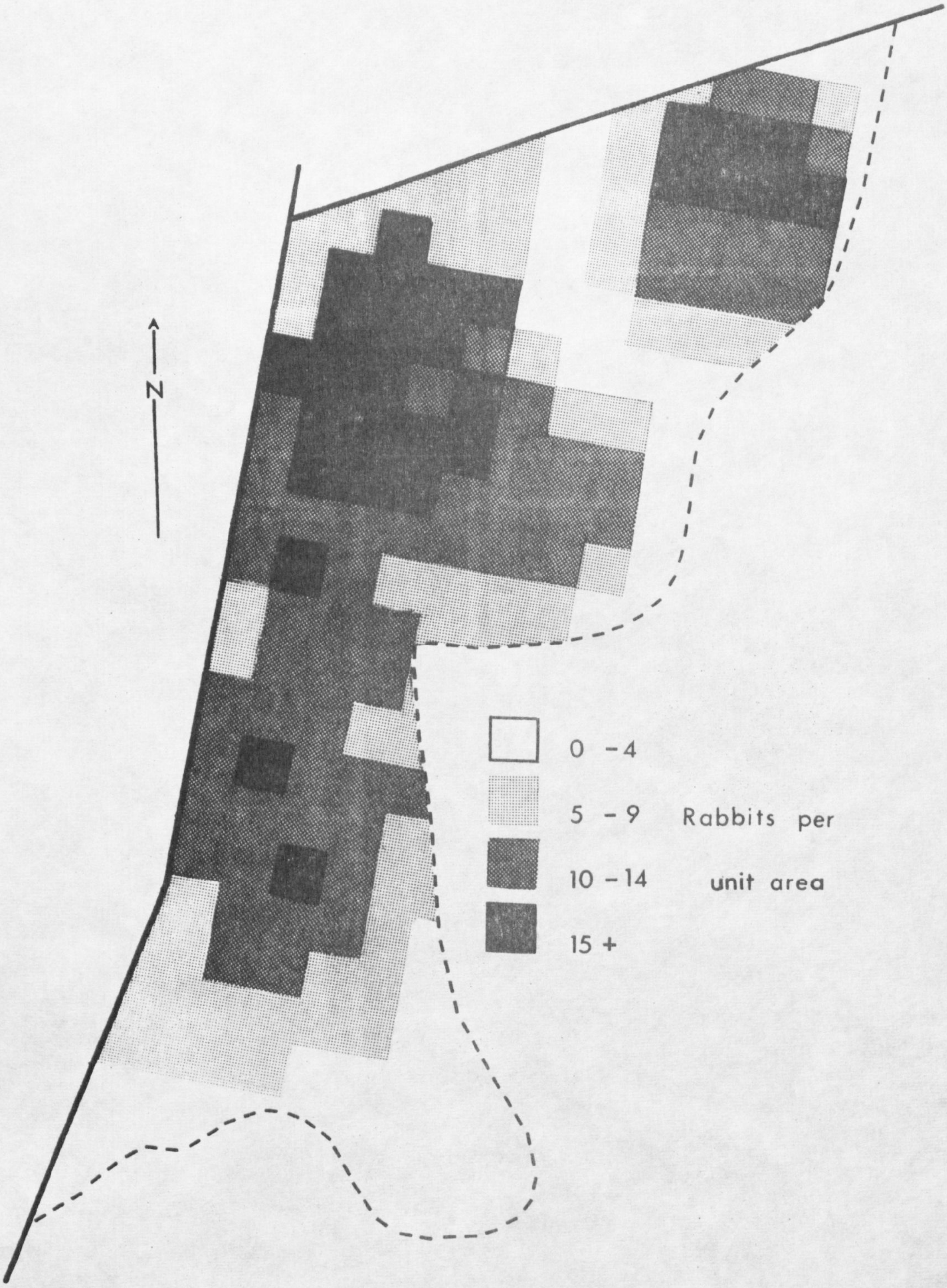

Fig.4. The relative density of rabbits on the study area. Densities represent the number of rabbits which might feed or interact on any given area rather than the number of rabbits per hectare.

recapture of the two young rabbits which had moved from the most crowded part of the study area to establish themselves in an area where there were fewer rabbits.

Now it would be expected from the observations of Mykytowycz (1959, 1960) that when adults in a crowded population acted aggressively toward youngsters such actions would usually be directed at sub-adults over three months of age or towards younger rabbits from strange territories. It therefore follows that the aggressive behaviour of adults cannot explain why the young rabbits disappeared from the study area at Witchitie yet the sub-adult rabbits remained. Neither can it explain why two young rabbits left their home warrens at a time when the adults were no longer breeding, yet were able to establish themselves in equally crowded warrens where breeding was still in progress and territories were, presumably, well defended.

Thus it seems that some factor which acted most severely on the young ultimately caused the crash in the rabbit population. This factor also caused dispersion of young despite social forces which would oppose the movement of kittens to new warrens.

The most likely cause of the crash was of course shortage of food, as suggested earlier. In this context Mykytowycz (1960) also concluded from his studies on enclosed populations of rabbits that a primary cause of dispersal of young was lack of food. He observed that the youngsters which dispersed came mainly from large, heavily populated warrens which had small feeding areas. He noted too that dispersal occurred despite territorial defence by the does which lived in the areas to which the young moved. Many of the young were actually injured in the skirmishes which ensued.

From such considerations, there seemed to be little point in continued investigations of the burrows or space available to the rabbits. On the other hand, food was a resource which warranted examination in much more detail.

To take this idea further, it seemed that the obvious problems in investigating the food of free-living populations of rabbits lay in defining the basic requirements for maintenance of the rabbit then in finding out how food might influence the size of a rabbit population. It would be essential to measure the quality and quantity of food available and the frequency with which dietary deficiencies or food shortages occurred.

The causes of dietary deficiencies would also be important. Some, such as the influence of weather on the quality of plants could be anticipated from the work done on other grazing herbivores such as sheep. Donald and Allden (1959) had shown for instance that in South Australia the mediterranean-type pastures are seasonally deficient in energy and nitrogen for weaner sheep and it would also be expected that young rabbits would not be able to cope with dry, mature pastures. Other causes of food shortage such as over-grazing were also apparent from the earlier work at Witchitie and it would be interesting to see how often the rabbits might exceed their resources of food.

These anticipated effects of food on the rabbit population and associated problems such as the importance of water, which is a normal component of the food, determined the course of my study.

For convenience the results of the experiments and measurements made during this study have been presented in three parts. The first deals with water, the second with the quality and abundance of food. In the third and final part the effects of food and water supplies on the performance of the rabbits have been considered.

2. DESCRIPTION OF THE STUDY AREA

The general study area of about 10,000 ha is part of "Witchitie" sheep station which lies to the east of the Flinders Ranges about 380 km north of Adelaide. Within this area lies a small valley ringed by stony hills (plate 2) in which a small population of rabbits was studied intensively.

Witchitie has a low erratic rainfall and although the mean annual rainfall is said to be 190 mm, annual totals have varied between 49 mm and 387 mm during the course of this study which began in 1967.

Osborne, Wood and Paltridge (1935) described the general climate of "Koonamore" station which abuts the eastern boundary of Witchitie. They provided a table showing the monthly distribution of rainfall (see table 1) which approximates that on Witchitie. More recently Hall, Specht and Eardley (1964) showed that there has been a shift toward greater summer rainfall in this area. (Fig. 5).

There has been a similar trend toward good summer rains and poor spring rains at Witchitie over the last six years (Table 1).

Other climatic data obtained by Osborne et al. (1935) are presented in Table 2. Although figures for saturation deficit given by Osborne et al. (1935) provide some indication of the drying power of the atmosphere they are based on only three to five years records; consequently I have included estimated evaporation rates published by Trumble (1948). These data are for Johnburg, now a deserted township, some 30 km from Witchitie. Trumble's figures are based on the general correlation between evaporation and saturation deficit which he estimated for each month from mean temperature and

PLATE 2 General view of the study area showing the stony hills which surround it. Each warren was permanently marked with a numbered metal plate on a post as shown.

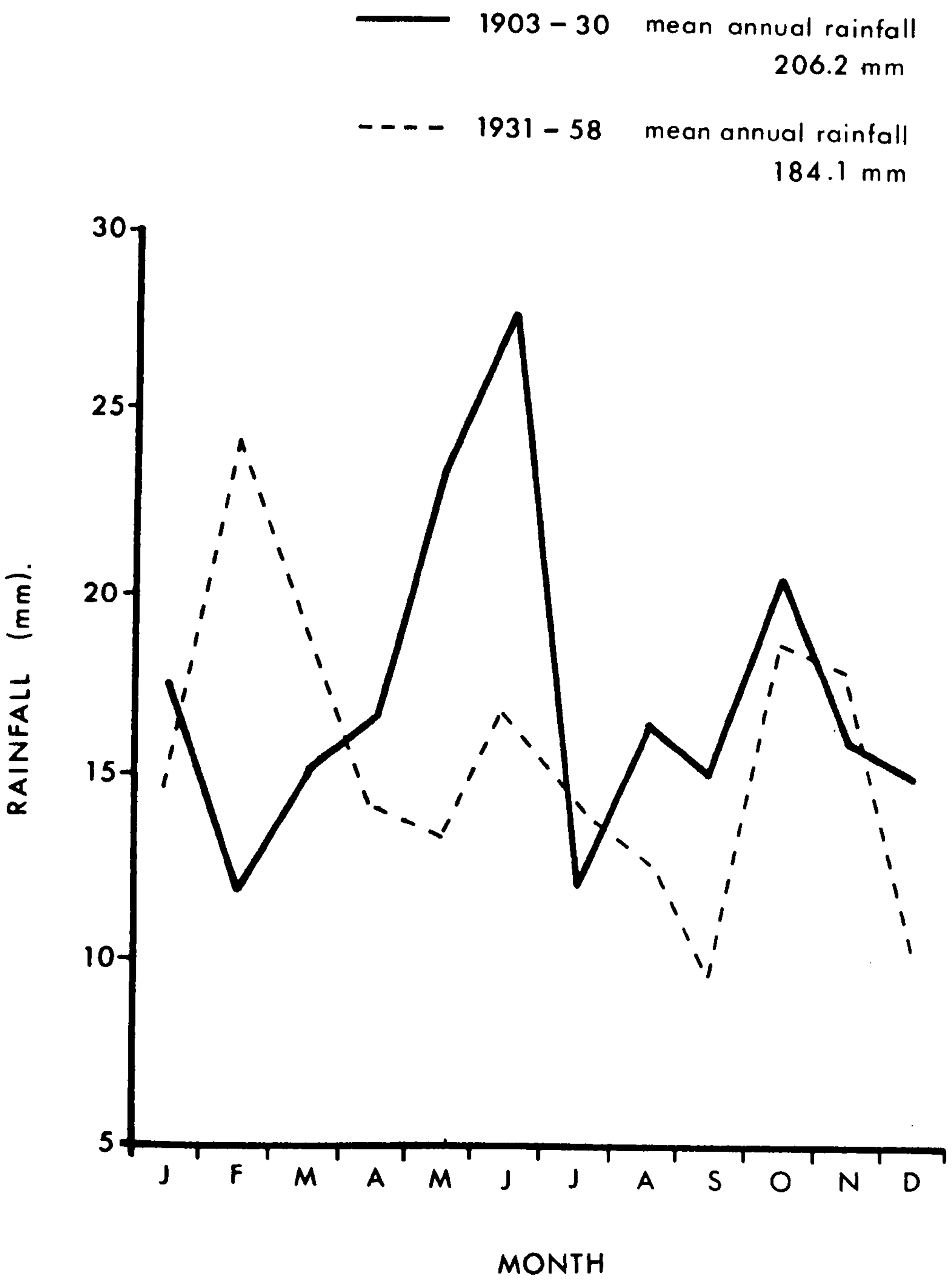

Fig. 5. The monthly distribution of rainfall at Koonamore which approximates the pattern of rainfall at Witchitie. Data from Osborne et al., 1935 and Hall et al., 1964.

TABLE 1. Rainfall data for Witchitie and an adjoining station Koonamore.

		Month											
		Jan	Feb	Mar	Apr	May	June	Jul	Aug	Sep	Oct	Nov	Dec
Monthly rainfall at Witchitie 1966-72 (mm)	1966	2	39	4	0	15	42	8	3	7	0	17	56
	1967	11	14	0	0	0	0	1	15	3	5	1	0
	1968	127	22	4	63	34	63	37	7	5	1	21	3
	1969	31	36	51	17	17	22	28	7	10	17	3	0
	1970	3	1	3	51	1	4	3	29	41	8	47	8
	1971	0	4	53	24	3	19	26	12	19	0	28	31
	1972	114	5	0	2	0	7	6	38	8	17	3	2
Average monthly rainfall at Koonamore 1903-30 (Osborne et al. 1935)		17.8	11.4	15.5	16.3	23.6	27.4	11.7	16.0	14.7	20.6	16.3	15.0
1926-62 (Hall et al. 1963)		15.2	30.5	11.7	10.4	13.4	16.2	12.4	10.4	12.4	18.0	14.7	12.4

TABLE 2. Temperature, relative humidity and evaporation.

		MONTH											
		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC
Temperature* (°C)	mean max	33.6	32.7	28.5	27.8	17.4	16.6	15.2	18.7	19.8	26.7	29.0	30.4
	mean min	14.3	16.3	12.8	8.1	3.7	2.1	1.4	2.1	2.7	7.4	12.1	13.0
	mean	23.9	24.6	20.6	17.9	10.5	9.3	8.3	10.4	11.2	17.1	21.0	21.9
Relative* humidity (per cent)	mean max	93	82	83	87	87	91	91	87	87	81	80	84
	mean min	37	35	34	39	43	51	47	42	37	35	31	35
	mean	65	58	59	63	65	71	68	64	62	58	55	59
Saturation* deficit (mm Hg.)		7.87	10.16	7.62	5.58	3.30	2.54	2.54	3.56	3.81	6.10	8.89	8.89
Evaporation** (mm/month)		343	292	211	150	79	53	53	81	137	229	284	338
No. of hours/day when humidity is above 80% or less than 40%*	>80%	n.r.	3.9	4.5	7.2	9.6	8.7	8.1	6.2	4.7	3.8	3.8	3.1
	<40%	5.5	6.9	5.9	3.1	2.4	1.0	1.8	4.1	6.0	6.9	8.9	7.6

* after Osborne et al. (1935) - data for Koonamore

** after Trumble (1948) - data for Johnburg

9 a.m. relative humidity records.

On the hills of the study area, soils are generally shallow, grey loams with exposed parent rocks such as laminated shales, siltstones and minor sandstones. The lower hill slopes and low-angle slope deposits are red-brown clay loam containing much weathered shale and these soils grade into the heavier red-brown clays of the drainage channels and flood plains.

With this pattern of soils there is a corresponding distribution of vegetation. The hills are vegetated by tough grasses such as *Triodia, Stipa* and *Enneopogon* and other hardy vegetation such as *Sida* spp. The intermediate soils of the low angle slope deposits support mainly chaenopods such as *Bassia* spp. and *Atriplex*. The heavier clay soils of the flood plains support *Stipa* almost exclusively as the dominant species.

Along the creeks which drain the area grow the red gum, *Eucalyptus camaldulensis* Denh. (1932), mallees, *E. odorata* Behr et Schlechtd., native pine, *Callitris glauca* R. Br. and the bullock bush, *Heterodendron oleifolium* Desf. The mulga, *Acacia aneura* F.v.M. grows over much of the hilly country and another acacia, *A. Victoriae* Benth. (1848) grows densely along some sections of the major water courses.

3. GENERAL METHODS

Since the aim of the study was to assess the importance of food and water to a rabbit population the data to be collected fell into two main categories. On the one hand, numerical and physiological changes in the rabbit population had to be recorded, and on the other, changes in the availability and quality of food were to be noted and the important factors which caused these changes had to be assessed.

To answer specific questions, experiments were carried out both in the field and in the laboratory but I have presented the methods used in detail in the appropriate sections of the thesis. However, the general methods used to gather information in the field were as follows.

On each visit to the study area, usually at six to eight week intervals, rabbits on the main study area were counted by means of spot-light transect counts (Cooke, 1970) and supplementary evidence of changes in the population was obtained by using baited cage-traps. From the rabbits captured, additional information, such as the age structure of the population and the use of warrens, was obtained.

Even though the numerical changes in the rabbit population provided data on successful breeding and mortality it was also necessary to shoot rabbits to obtain detailed information on their reproductive state and general physical condition. A sample of ingesta was taken from the fore-stomach of each rabbit and analysed for fibre and nitrogen after the methods of van Soest (1963) and Conway (1962). Blood samples were also collected for myxomatosis antibody tests (Sobey, Conelly and Adams, 1966) even though the earlier studies (Cooke, 1970) had shown that myxomatosis did not appear to affect the rabbit population greatly.

The quality of vegetation available to the rabbits was estimated from samples of plants collected from the study area. These were assessed in terms of the water, energy and nitrogen they contained. The abundance of useful vegetation was estimated from photographs of pastures on permanently marked quadrats, which were taken on each visit to the study area.

Finally, rainfall records were obtained from the homesteads situated close to the study area.

4. RESULTS

4.1 Water

4.11 Shortage of water in the field

4.111 Introduction

As already stated, the dramatic crash in the rabbit population at Witchitie appeared to be at least partly caused by a shortage of water. As the ephemeral pastures matured and drought began the rabbits not only began moving to water at the mill but they also began gnawing bark from exposed tree roots and twigs and frequently climbed into the branches of trees and shrubs to reach young leaves and stems.

These observations strongly suggested that a shortage of water in the vegetation probably had a role in the population crash even though some rabbits, especially the young, had begun to disappear two or three weeks before the pastures became quite dry.

If shortage of water decreased the rabbits' ability to survive then I could test this experimentally by providing supplementary water and comparing their performance with that of rabbits without access to water. The performance of the rabbits could be measured in terms of loss of weight and survival.

4.112 Methods

Two areas were chosen on the southern half of the main study area. On one area two watering points were provided, each consisting of a small trough fed from two drums of water which together held 450 l. The water level in the trough was maintained by a float valve. In the netting fence which surrounded each point were small gates through which the rabbits could push. The gates only opened inwards so that rabbits coming to water were readily trapped, but the gates could be tied open if it was not necessary to capture the rabbits.

The second area, which was the control, lay too far from the artificial watering points for the rabbits to go to drink. The limits of movement of rabbits to a water source had been fairly well defined using the information from rabbits caught by the commercial trapper. Most of the rabbits he took had been caught at the mill although he also shot a few along the north-eastern boundary of the study area. Figure 6 shows the locations at which the rabbits he took were initially marked. It was clear that the rabbits were almost invariably moving less than 600 m to water. In my experiment therefore the control area could be defined as that area which lay more than 600 m from water. Subsequent observations showed that this decision was justified (see part 4.113).

Since there was a lower density of rabbits on the control area than on the experimental area (see fig. 4) and the rabbits in the control area were generally heavier and in better condition than the experimental rabbits it seemed that significant differences in weight loss or survival shown by the experiment would be real differences i.e. the errors would tend to reduce the likelihood of showing significant differences between treatments.

The watering points were completed and the experiment began on 20th December 1969.

To begin with I had hoped to record the survival of rabbits on each area by counting them as I walked along set transects in the late afternoon. Initially I counted about thirty rabbits on each area but as the experiment progressed

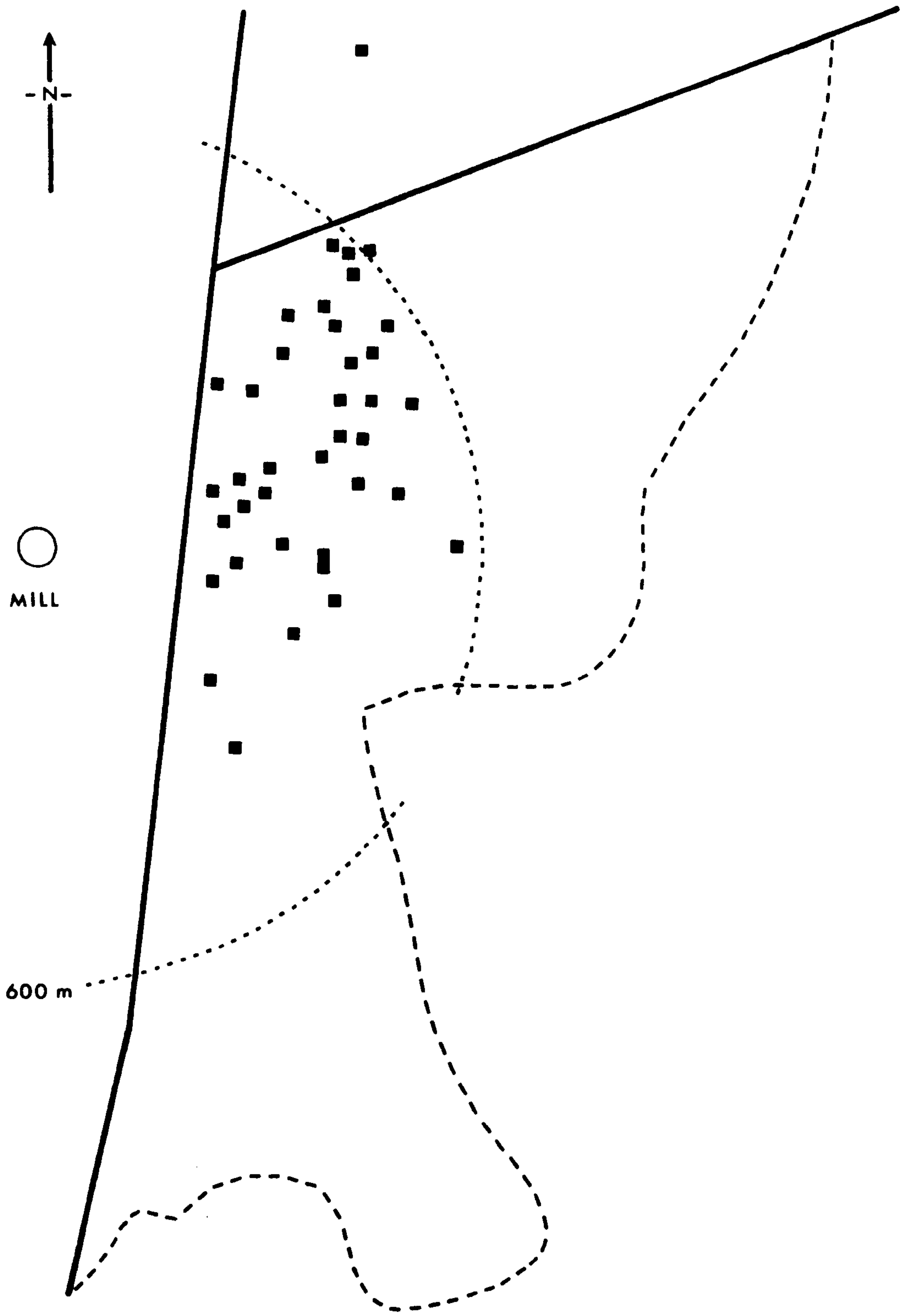

Fig. 6 The distance from the mill to the previous site of capture of the tagged rabbits caught by the trapper. Most of the rabbits came from within 600 meters of the mill.

the numbers of rabbits declined to about half on each area and I began to notice differences in the behaviour of the rabbits too. On the control area the rabbits were usually seen sitting in groups of up to six rabbits in the shade of trees. In contrast the rabbits on the experimental area were generally more active and ran to the burrows as I approached. Vagaries of weather added further variability to the counts and I abandoned them as useless.

Towards the end of summer however, when rabbits from the entire study area were again caught in cage traps some interesting results were obtained. The survival of rabbits on the experimental and control areas could be compared because most of the rabbits present on these areas had been trapped in late November 1969 just before the experiment began and were trapped again in March 1970. Information obtained from these rabbits included movements and changes in body weight as presented in table 3. It is advantageous to consider these movements and changes of weight first because they are relevant to the interpretation of the results on survival.

4.113 Results

a) Movements of rabbits to water.

The rabbits which entered the yards to drink were captured and their tag numbers, sex and body weight recorded. Trapping was carried out on four consecutive nights once each month. Several nights were required to enable shy or infrequent drinkers to come to water but a limit of four nights had to be set because some rabbits which were captured night after night lost up to 10% of their body weight when they were first trapped. Rabbits caught at the watering

TABLE 3. Change in weights of rabbits during the population crash at Witchitie in the summer of 1969-70.

No.	Sex	Weight (g)		% weight change	Dist. from water(m)	Notes
		Nov.'69	Feb.'70			
1	F	1425	1375	- 4	100	D*
2	M	1750	1200	-31	300	
3	M	1550	1525	- 2	50	D
4	M	1650	1575	- 5	100	D
5	M	1700	1625	- 4	200	D
6	M	1700	1400	-18	300	
7	F	1625	1200	-26	150	
8	M	1375	1300	- 5	50	D
9	F	1675	1625	- 3	50	D
10	M	1600	1600	0	100	D
11	M	1500	1300	-13	150	
12	M	1900	1625	-14	200	D
13	M	1625	1575	- 3	100	D
14	F	1650	1550	- 6	50	D
15	M	1350	1325	- 2	50	D
16	M	1650	1600	- 3	200	D
17	M	1600	1550	- 3	300	
18	M	1675	1325	-21	250	D
19	M	1475	1225	-17	150	D
20	F	1325	1350	+ 2	250	D
21	F	1525	1425	- 7	50	
22	M	1600	1275	-20	450	
23	M	1875	1825	- 3	450	
24	M	2025	1800	-11	450	
25	M	1775	1425	-20	500	
26	F	1800	1625	-10	500	
27	F	1450	1425	- 2	350	
28	M	1775	1325	-25	500	
29	M	1625	1325	-18	450	
30	M	1775	1625	- 8	350	
31	M	1700	1350	-21	650	
32	F	1925	1650	-14	350	
33	F	1900	1325	-30	750	
34	M	2025	1325	-35	900	
35	M	1850	1400	-24	850	
36	M	1825	1025	-44	700	
37	F	1500	1300	-13	900	
38	M	1625	1050	-35	950	
39	F	1600	1200	-25	950	
40	F	1600	1175	-27	1300	
41	M	2000	1325	-34	1300	
42	F	1425	1025	-28	1100	

* D = rabbits which were caught at the watering points and presumably drank.

points were assumed to have gone there to drink whereas rabbits which were never caught at the water I regarded as 'non-drinkers'.

Figure 7 shows the distance the rabbits moved to the watering points. Each symbol which represents a rabbit has been placed at the centre of the rabbits known home range, excluding known movements to water.

Of seventeen rabbits captured at the watering points and for which some information on home range was available not one lived more than 550 m from water. This confirmed the earlier assumption (see part 4.112) that 600 m was a useful arbitrary figure to define the limits of the distance rabbits will move to water.

Since the maximum diameter of the rabbits' home-ranges was found to be 650 m and since some rabbits which lived within 200 m of watering points did not go to drink it seems that rabbits may not be able to sense small sources of water at a distance, but only find water when it occurs on their normal home range. The obvious advantages in obtaining supplementary water, presently to be discussed, also indicated that the rabbits which did not drink were those which failed to find water rather than rabbits which refrained from drinking.

b) Weight changes.

Table 4 shows that rabbits on the control area lost significantly more weight during the summer than those which drank the supplementary water.

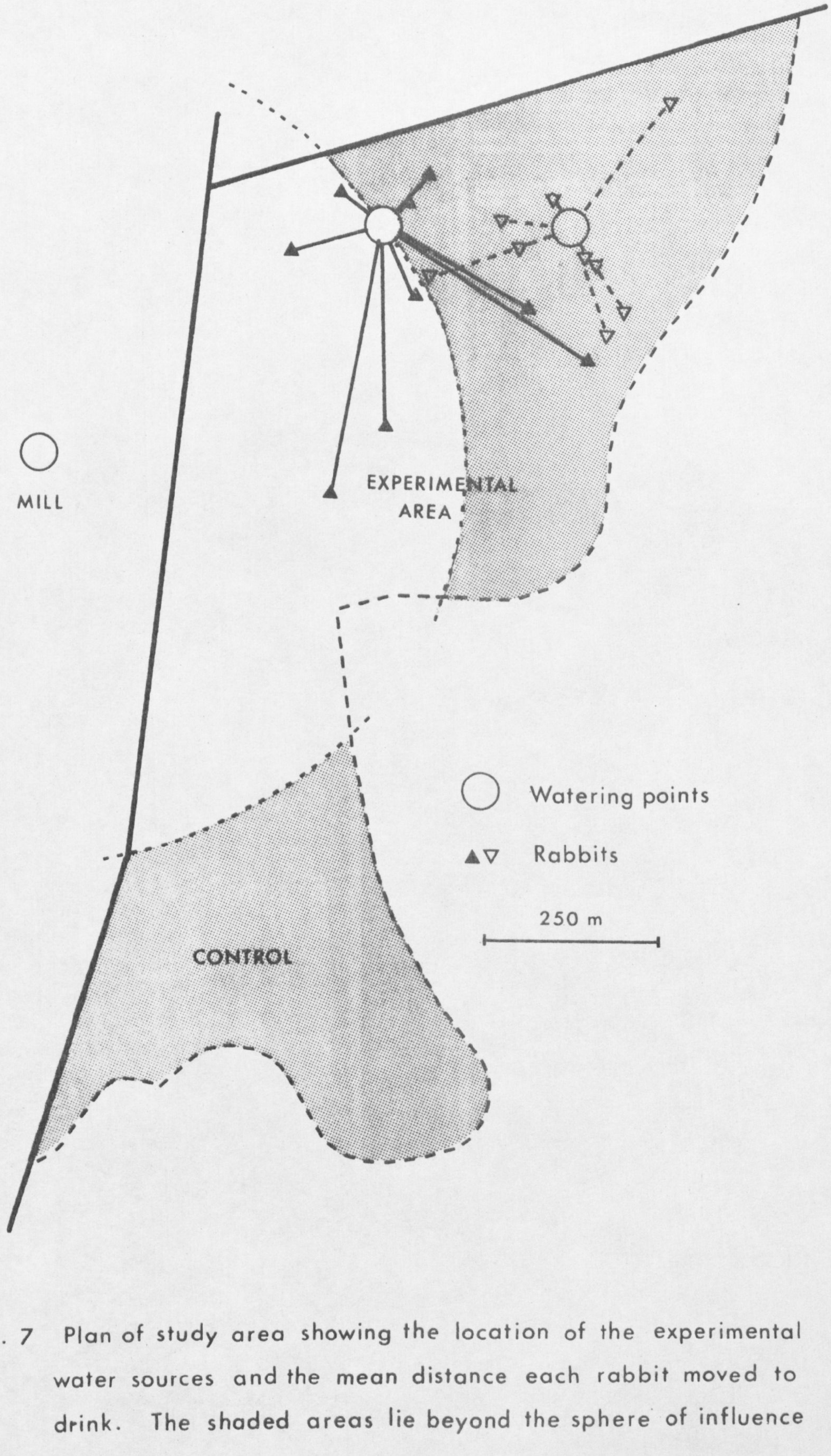

Fig. 7 Plan of study area showing the location of the experimental water sources and the mean distance each rabbit moved to drink. The shaded areas lie beyond the sphere of influence of the mill.

TABLE 4. Loss of weight of rabbits during the summer. (data from rabbits caught in cage traps)

	Treatment	
	Water supplied	Control
Sample size	15	11
Mean weight (g) before summer	1575.0 ± 157.6	1731.8 ± 201.0
Mean weight (g) after summer	1480.0 ± 144.0	1227.3 ± 139.8
Mean percentage weight loss	5.8 ± 6.4	28.7 ± 8.3

$t_{24} = 7.96, P < 0.001$

Although these results seemed conclusive enough, I was by no means entirely satisfied that the control area and the experimental area differed only in the availability of water. In fact differences in the vegetation on each area became apparent in later studies as we shall see in part 4.25, Fig.14.

To test this point I decided to look at the weight losses of rabbits from the control area and compare them with the weight losses of a number of rabbits on the experimental area which were never observed to drink. The results appear in the following table.

TABLE 5. Loss of weight of rabbits which did not drink. (data from rabbits caught in cage traps)

	Area	
	Experimental	Control
Sample size	16	11
Mean weight (g) before summer	1732.8 ± 155.7	1731.8 ± 201.0
Mean weight (g) after summer	1481.3 ± 196.7	1227.3 ± 139.8
Mean percentage weight loss	14.3 ± 8.8	28.7 ± 8.3

$t_{25} = 4.29, P < 0.001$

Clearly, even among non-drinking rabbits there were significant differences in the performance of rabbits from each area. This seriously affected the experimental results because the effects of water shortage and some other factor, such as the quality of food, were obviously superimposed. It was fortunate that many of the rabbits on the experimental area did not drink because this enabled me to conclude that, even apart from the availability of water, the control area was less favourable for rabbits than the experimental area. It also enabled me to decide quite simply whether the provision of supplementary water really did help the rabbits. Instead of comparing rabbits from the control and experimental areas, the drinkers and non-drinkers which lived within 600 m of water were compared. Presumably these rabbits foraged over quite similar areas so they would use essentially the same resources.

From table 6 it can be seen that the rabbits which drank did not lose as much weight as the non-drinkers. Thus, the availability of water had a considerable influence on the weight changes of the rabbits.

TABLE 6. Loss of weight of rabbits on the experimental area. (data from rabbits caught in cage traps)

	Drinkers	Non-drinkers
Sample size	15	16
Mean weight (g) before summer	1575.0 ± 157.6	1732.8 ± 155.7
Mean weight (g) after summer	1480.0 ± 144.0	1481.3 ± 196.9
Mean percentage weight loss	5.8 ± 6.4	14.3 ± 8.8

$t_{29} = 3.27,\ 0.01 > P > 0.001$

c) Survival of rabbits.

Because it had been shown that weight losses of rabbits on the control area did not result from lack of supplementary water alone, valid comparisons of the survival of rabbits on the control and experimental areas were precluded.

Of twenty-eight rabbits caught on that part of the experimental area that lay beyond the sphere of influence of the mill, nine were trapped again after the summer. In comparison only nine out of fifty-four rabbits were trapped on the control area. The proportion of the rabbit population which survived on each area did not differ significantly ($\chi^2 = 2.57$, $P > 0.1$) which was a little surprising because the rabbits on the control area apparently had to contend with very poor quality food as well as shortage of water.

There were, however, at least three weaknesses in the experimental design which might have accounted for this.

Firstly, the estimated survival rate of rabbits on the experimental area was the product of survival of both drinkers and non-drinkers and was therefore an underestimate.

Secondly, there were problems in the method of assessing the number of rabbits which survived on each area which led me to suspect that the number of survivors on the experimental area was under-estimated. To start with it had to be assumed that rabbits on each area were equally likely to be trapped so that results would be quite comparable. Yet from previous difficulties I had had when trapping rabbits while pastures were abundant I knew that some rabbits in good condition were quite difficult to trap. Consequently, it seemed possible that the rabbits which drank and maintained good physical condition would be less readily trapped than the rabbits on the control area. Although this idea could not be tested, I did find however that among the rabbits caught at water were some which could not be caught in cage-traps. As shown in figure 8 these rabbits had been heavier than their fellows when last captured at the watering-points ($t_{27} = 2.37$, $0.05 > P > 0.01$) so it was possible that their relatively good physical condition reduced the likelihood that they would enter cage-traps. If the ability to trap rabbits was indeed influenced by the physical condition of the rabbits as these data suggest, then the number of survivors on the experimental area was almost certainly under-estimated.

The third problem arose because the rabbits on the control area were, on average, heavier than those on the experimental area at the beginning of the experiment and may have been able to tolerate a proportionally larger weight loss (Hayward, 1961).

It was apparent that the limitations of my experimental methods could have masked real differences between the treatments and to remedy this I attempted to repeat the experiment, with certain modifications, in the summers which followed. To allow for the affects of differences in vegetation I increased the size of the study area considerably, providing in all four replicates of each treatment. However, although these watering-points were maintained throughout the summers of 1970-71, 1971-72, and 1972-73 the rabbits did not seek supplementary water again because none could be caught in the yards.

4.114 Summary and conclusions

It was clear that provision of supplementary water had enabled the rabbits to maintain their body weights far better

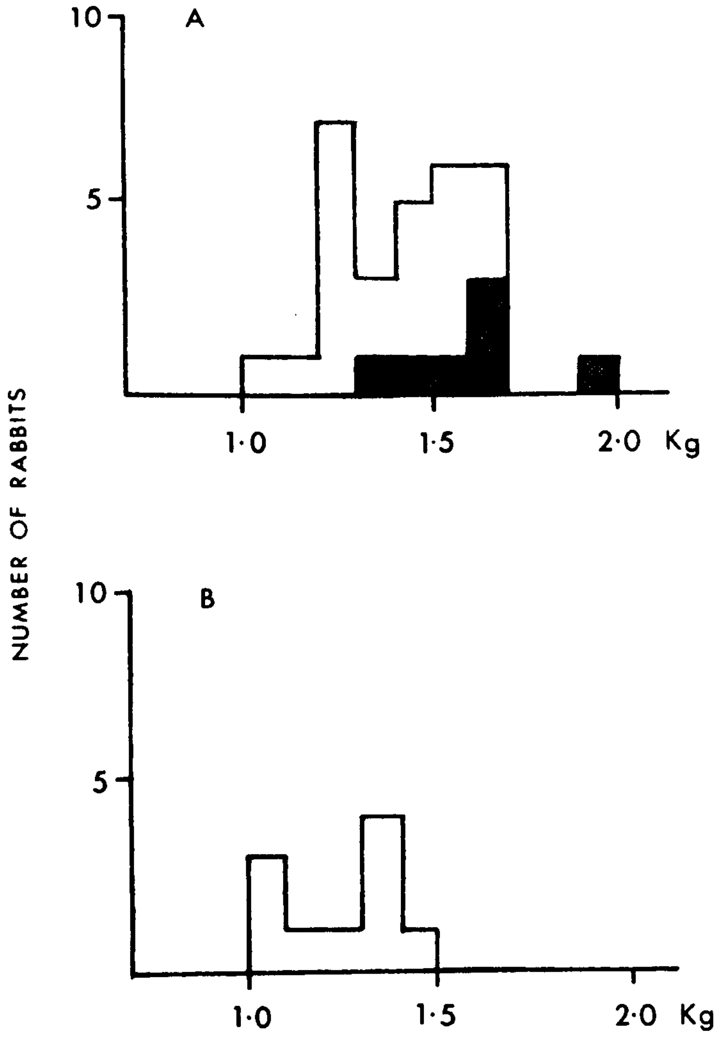

Fig. 8 Weight distribution of rabbits in the yards of the experimental watering-points (A) and those caught in cage-traps on the control area (B). Some rabbits (shading) could not be caught in cage-traps at the end of the summer.

than rabbits which had no supply of water. It seemed likely also that the supplementary water enabled the rabbits to survive better although I was unable to demonstrate this. Presumably the supplementary water enabled the rabbits to eat more or better food than the rabbits which did not drink.

To investigate the way in which water influenced the rabbits I began to study the physiological effects of water shortage on rabbits. First of all I compared a sample of rabbits which had been shot just before the harsh summer of 1969-70 began with another which was taken near the summer's end.

4.12 Physical changes observed in the rabbits during the population crash.

A sample of fifteen adult male rabbits shot on 22nd October 1969 on an area adjacent to the main study area was compared with another similar sample of sixteen males taken on 17th March, 1970. Females from the same samples could also have been compared except that the pregnant, lactating does shot in October were not readily comparable with the anoestrous does of March.

Table 7 gives the mean weights, standard deviations and the percentage change observed in weights of organs, including eyelenses, taken from each sample.

The absolute weights of organs - not weights relative to body size or corrected for age - have been compared because the rabbits shot in March were clearly representatives of the same group of males as sampled the previous October. Earlier observations (Cooke, 1970) had shown that those rabbits which had not reached maturity by October 1969 died during the early stages of the population crash.

TABLE 7. Weights of organs from male rabbits shot prior to the population crash in comparison to those shot after the crash.

	October 1969	March 1970	% diff.	P
Eye lens weight (mg)	171.7 ± 24.1	186.3 ± 29.7	+ 8.5	0.2>P>0.1
Whole body weight (g)	1646.7 ± 99.9	1279.9 ± 198.6	-22.3	P<0.001
Stomach weight (g) (with contents)	86.0 ± 12.5	76.4 ± 12.2	-11.2	0.1>P>0.05
Whole Gut (g) (with contents)	358.7 ± 35.7	334.6 ± 63.3	- 6.7	0.3>P>0.2
Kidney weight (g)	12.8 ± 1.5	10.4 ± 1.2	-19.3	P<0.001
Kidney fat (mean index)	1.67	0.19	-88.6	P<0.001*
Spleen weight (mg)	426.8 ± 76.4	181.1 ± 51.1	-57.6	P<0.001
Liver weight (g)	43.0 ± 4.9	26.9 ± 4.8	-37.4	P<0.001
Testes weight (g)	2.48 ± 1.18	0.57 ± 0.67	-77.1	P<0.001

* Kolmogorov-Smirnov two sample test

Table 7 suggests that rabbits, on average, lost 22.3% of their body weight, quite similar to the losses observed among non-drinking rabbits on the main study area (20.2%). Much of the rabbit's perirenal fat had gone by March, and all organs had decreased significantly in weight except for the stomach and gut and the eyelens.

A slight increase in the mean weight of the eyelenses might have been expected because Dudzinski and Mykytowycz (1961) had shown that the lens weight increases with age, and this of course was the purpose of recording lens weights. On the other hand, the absence of marked changes in the weight of the gut with contents was somewhat unexpected because, from the work of Hayward (1963), I had anticipated that the weight of the rabbits' guts would have been greatly reduced during the population crash. My reasoning was as follows. Hayward kept rabbits in an enclosure of dry pasture, but gave them no supplementary water. The rabbits gradually lost weight, many of them losing about 50% of their initial weight before they died. Further, it could be demonstrated that their loss of weight was caused partly by loss of tissue and partly by the loss of gut contents. For instance, a rabbit which initially weighed 1.4 kg lost 0.5 kg in two months. However, after it was given water its body weight increased from 0.9 kg to 1.1 kg overnight then continued to increase, though at a very much slower rate. The weight lost by the rabbit therefore had two components. The first, which was rapidly replaced when water became available, I assumed to arise from loss of gut fill or, to a lesser extent, loss of water from the tissues because of dehydration. The second component, slow to be replaced, almost certainly resulted from depletion of body tissues such as fat or muscle.

Since the weight lost from the gut apparently amounted to 200 g, yet the gut, including contents, of a wild rabbit normally weighs only about 360 g (table 8), then a rabbit which had been deprived of water could be expected to have a gut which was greatly reduced in weight. Actually, it was possible that Hayward's rabbits had very little digesta in their guts because I have found that the guts of wild rabbits, after removal of all digesta, weigh only about 180 g, although the equivalent organs of a starving rabbit would probably weigh even less.

The situation in Hayward's enclosure therefore contrasted strongly with that of the free-living rabbits at Witchitie. As shown in table 7 there was no indication that the rabbits at Witchitie showed symptoms of severe water deprivation in the way that Hayward's rabbits did. I was therefore faced with two conflicting ideas. On the one hand, experimental evidence suggested that water was essential for the rabbits at Witchitie yet on the other there was no indication that the water shortage had drastically reduced the food intake of the rabbits as seemed to be the case in Hayward's enclosure study. Before going on to explore this problem further however, one more comparison between the rabbits at Witchitie and those maintained by Hayward was of interest.

Among rabbits trapped at Witchitie the greatest weight loss observed was 44% of the initial body weight, yet those rabbits which lost 30% of their body weight were extremely weak and emaciated. Certainly no rabbits showed a weight loss of 50% as observed in Hayward's rabbits and the weights of rabbits trapped at Witchitie did not fall below 1.0 kg although Hayward found that many of his rabbits weighed only 0.8 - 0.9 kg at death. From this evidence it seemed that the rabbits on my study area usually died if they had lost about 30% of their body weight. Such a conclusion contrasted with Hayward's observations but the two sets of data could be reconciled. The feature they had in common was that an adult rabbit could survive a depletion of body tissues amounting to 30% of its weight. The two groups of rabbits differed only in the amounts of digesta they had in their guts.

This hypothesis implied a complex interaction between shortage of water and some other factor such as the quality or quantity of the available food. At Witchitie, water shortage did not simply act by severely reducing the food intake of the rabbits.

We can now consider the results of one further experiment which was designed to investigate the response of rabbits to a shortage of water. This experiment verified certain assumptions I had made in interpreting Hayward's (1961) data and also provided further information on the water requirements of rabbits which was important for an understanding of data on the availability of water in the field.

4.13 The effects of water deprivation on the rabbit

4.131 Methods

Fifteen wild, adult male rabbits were assigned to three experimental groups and placed in individual metabolism cages. According to their group, rabbits were given 20 ml, 50 ml or ad lib water daily. Temperatures were low, averaging about 13°C and the relative humidity averaged 65% so that the rabbits were not subjected to severely dehydrating conditions.

Food given to the rabbits during the experimental period consisted of commercial stock pellets (Kangaroo pellets from Whiting and Chambers, Adelaide). Food intake, and for the control group of rabbits, water intake was measured daily. The rabbits deprived of water always drank their ration as soon as it was given to them.

Faeces were collected under oil and their moisture content determined gravimetrically after drying them in an oven at 105°C. Urine was collected, also under oil, the volume was recorded and the concentration of nitrogen was determined using the method of Conway (1957). Measurement of the osmoconcentration of urine samples was kindly arranged by Dr P. Baverstock, Institute of Medical and Veterinary Science.

A preliminary trial showed that the body weight and the food intake of rabbits at first fell rapidly if their supply of water was restricted but after five days their rates of food intake and weight loss remained constant. In the main experiment therefore the rabbits were weighed on the first day, the sixth day and again when they were killed on the eleventh day.

As the rabbits were killed, the gut was dissected out and weighed, complete with digesta. A sample of digesta from the hind gut was then collected to be dried so that its water content could be determined. A sample of skin from the back of each rabbit and the large muscle mass from one hind leg were also dissected out and dried at 105°C to determine the water contents. It was essential to know the water content of skin and muscle because these provided a measure of the importance of dehydration of tissues in the recorded weight losses of the rabbits. Flemister (1941) showed that in dehydrated rabbits water was lost from the skin in substantial quantities before fluid began to disappear from other tissues such as the muscles. In severely dehydrated rabbits Flemister found that up to 18% of the water contained in the skin had been lost. A small loss of cutaneous water would therefore imply a negligible loss of water from other tissues and an insignificant amount of tissue dehydration.

4.132 Results

The experimental results are presented in table 8.

Some of the results justified the assumptions I had made in interpreting Hayward's (1961) data. For instance, I had assumed that a rabbit deprived of water would have a reduced intake of dry food which would result in a reduction in the weight of the gut. The experiment showed that there was indeed a reduction in food intake and the weight of the gut when water was limited. Moreover, since there was no corresponding reduction in the water content of the digesta or tissues, with the exception of a small loss from the skin, it seemed that the weight of the gut could only have fallen because the gut contained less digesta.

Since the loss of water from the skin was small, i.e. less than 10% of the total water content, and there was no evidence of dehydration of the muscles it seems that dehydration did not contribute appreciably to the weight losses of the rabbits. This meant that after changes in the gut fill, catabolism of tissues must have accounted for the remaining weight loss. In fact the observed losses agree well with published data on the energy requirements of rabbits. For example, one rabbit which initially weighed 1.965 kg lost 20.2 g daily during the final five days of the experiment.

TABLE 8. The effects of water deprivation on rabbits.

	Daily water intake			F	P
	20 ml	50 ml	ad.lib.		
Food intake (g/kg, initial weight$^{0.75}$)	12.92 ± 3.00	24.15 ± 3.00	56.28 ± 3.00	56.31	* * *
Water/Total food and water intake (% by weight)	63.32 ± 2.53	68.84 ± 2.53	63.98 ± 2.53	1.32	n.s.
Water in faeces (% wet weight)	48.34 ± 1.59	50.43 ± 1.59	50.30 ± 1.59	0.71	n.s.
Nitrogen in urine gN/100 ml	5.21 ± 0.39	3.70 ± 0.39	2.66 ± 0.39	10.55	* * *
Osmolarity of urine (mosm/ℓ)	1899.0 ± 128.1	1810.0 ± 114.6	1863.0 ± 114.6	0.14	n.s.
Urine volume (ml/kg initial weight $^{0.75}$)	15.27 ± 2.90	23.50 ± 2.90	40.69 ± 3.24	17.40	* * *
Gut weight (g/kg initial weight$^{0.75}$)	104.67 ± 5.68	129.11 ± 5.68	138.61 ± 5.68	9.52	* * *
Water in digesta (% wet weight)	73.64 ± 0.05	73.18 ± 0.05	72.66 ± 0.05	0.24	n.s.
Water in skin (% wet wt.)	54.11 ± 1.04	54.28 ± 1.04	58.98 ± 1.04	4.74	* *
Water in muscle (% wet wt.)	71.45 ± 1.97	69.81 ± 1.97	73.58 ± 1.97	0.85	n.s.
Weight change (g/kg initial weight $^{0.75}$)	-12.93 ± 1.15	-7.47 ± 1.15	-7.00 ± 1.15	7.91	* *
Digestibility of dry matter	71.90 ± 1.83	67.97 ± 1.83	61.36 ± 2.05	7.40	* *

(n.s. not significant) (* * 1% level) (* * * 0.1% level)

Because food intake and presumably gut weight were constant during this time it can be assumed that the loss represented catabolised tissue. This would yield 77.4 cal daily because Hellberg (1949) showed that 3.83 cal are produced for every g of tissue used. In addition, 67.3 cal were derived daily from food the rabbit ate because the rabbit's intake was 22.2 g pellets daily and the pellets had a dry-matter digestibility of 73.0% and yielded about 4.15 cal/g digestible matter. The calculated metabolic rate of the rabbit was therefore 144.7 cal/day, quite close to the expected maintenance metabolic rate of rabbits of this size, e.g. 153 cal (Crampton and Lloyd, 1959) or 164 cal (Krasnianski and Nessonowa, 1934).

Apart from justifying my earlier assumptions, the experiment gave further interesting results. The rabbits which were given only 20 ml water daily had greatly reduced their urinary and faecal losses. Urine volumes dropped sharply and the concentrations of urinary nitrogen rose to 5.2 g N/100 ml urine, roughly equivalent to 1.86 M urea. This was similar to the concentrations of urea, 1.5 - 2.0 M urea, found by Hayward (1961) for rabbits deprived of water. Oddly enough however, there was no corresponding increase in the osmotic concentration of the urine, (see 5.1 Discussion).

The percentage of water in the faeces was not significantly reduced by shortage of water, but the total faecal water loss was small because less food was eaten and the digestibility of dry-matter was increased so that the total mass of faeces produced daily was quite small.

Despite the substantial reductions in the urinary and faecal water loss, the rabbits apparently maintained fairly normal metabolic rates so the respiratory-cutaneous water losses would have remained unchanged.

One further observation was that if the daily intake of dry food is considered in relation to the intake of water, including the free-water contained in the pellets, it can be seen that among rabbits given only 20 ml water daily, the dry-matter intake amounted to only 36.7% by weight of the total intake of food and water. Conversely, water amounted to over 60% of the nutrients ingested and this proportion of water in the daily diet was constant for all three groups of rabbits irrespective of the amount of water they could obtain. This suggested that the wild rabbit has high requirements of water when compared with other species of mammals such as the desert-dwelling kangaroo-rat, *Dipodomys*, which can get all the water it needs from seeds which contain only 10% water (Schmidt-Nielsen, 1964).

4.133 Conclusions

The responses of wild rabbits to shortage of water showed two main features. Firstly, an absolute shortage of water reduces the food intake of rabbits and the amount of digesta held in the gut. Secondly, water must comprise about 60% of the rabbit's dietary intake. When a rabbit has access to water it can eat dry foods, but in the field where there is often no supplementary water it would need to find foods which contained about 60% water.

Quite clearly, the rabbits studied by Hayward (1961) could not find sufficient succulent vegetation to meet their water requirements and as a consequence they had to eat much less food than normal. At Witchitie however, the problem appears to have been quite different. The rabbits apparently found enough water-bearing vegetation but I wondered if it had such poor nutritive properties as to be useless to them. Apparently, in the experiments at Witchitie the value of supplementary water lay in the fact that it enabled the rabbits to eat more of the dry, annual vegetation than they could when they obtained all their water from coarse vegetation of poor quality.

We can return to consider the nutritional quality of the plants the rabbits ate during the population crash (part 4.24) after considering the availability of water in the field.

4.14 Measurement of the water available in the field

4.141 Water in plants

On each visit to the study area large samples of the more common species of plants were collected, sealed in tough plastic bags and transported to the laboratory in a car-refrigerator. The plants were collected in the early morning, soon after sunrise, to ensure that they contained maximal amounts of water. This precaution was necessary because the plants often wilted during the day but regained their water during the night when the humidity rose (table 2).

In the laboratory samples of 150-200 g were dried in an oven at 105°C to estimate the amount of water each plant species contained. The variations in the water content of several species of plants are shown in figure 10 and table 9 for the two years 1971 and 1972.

The water content of the plants generally reflected the effects of weather, especially rain and drought, but was also influenced by herbivorous insects and mammals which selectively grazed leaves and other plant organs which contained a high proportion of the water in the plants. To gain

TABLE 9. Water content of four plant species from study area at Witchitie.

Date	Soil moisture or drought[1]	Bassia patenticuspis[2]	Bassia lanicuspis[2]	Stipa variabilis[2]	Atriplex eardleyi[2]
29.11.70	+ 5	80.1*	84.6*	43.3*	73.1*
19.12.70	- 32	64.7*	79.9*	37.6*	57.6*
14. 2.71	-140	38.7*	63.2*	8.0*	25.0*
19. 3.71	+ 40	78.4	86.7	39.9	73.3
30. 4.71	+ 23	29.4[†]	69.7[†]	54.0	23.0[†]
25. 5.71	+ 4	76.3*	78.7*	42.6	14.6[†]
23. 7.71	+ 15	76.0*	72.5*	63.0*	-
22. 9.71	+ 28	70.9	80.6*	55.9	75.9
26.10.71	- 11	51.6[†]	45.5	36.4*	52.3*
10.12.71	+ 50	12.2	77.3	31.3	80.5
21. 1.72	+103	84.7	79.9	56.9	77.0
17. 2.72	+ 43	79.3	79.9	51.1	67.5
29. 3.72	- 25	73.3*	70.4*	32.1*	53.7*
5. 5.72	- 61	73.8*	60.9*	24.5*	34.5*
22. 6.72	- 64	54.8*	43.5[†]	21.4*	26.2
13. 7.72	+ 7	60.8[†]	50.7[†]	23.9	31.8[†]
4. 8.72	+ 6	-	59.8[†]	28.1	31.1[†]
14. 9.72	+ 8	70.2[†]	62.9[†]	37.0	54.3
26.10.72	+ 5	68.8*	65.9*	28.4	68.7*
15.12.72	- 87	51.0*	60.8*	15.6*	48.1*
25. 1.73	-165	23.0*	55.0*	11.0	39.0*

* Data used to calculate relationship between plant moisture and the severity of drought.

[†] Data on plant moisture influenced by grazing of plants by sheep or insects.

[1] Data in mm

[2] percentage wet weight

a good understanding of the effects of climate on the water content of the plants I therefore followed the response of ungrazed or lightly-grazed plants to the weather and discounted those samples comprised of heavily grazed plants.

4.142 Soil Moisture model

The effects of climate, particularly rainfall and evaporation, are readily combined in a model of soil moisture. Slatyer (1962) developed a simple model to determine from rainfall and evaporation the duration of periods of plant growth. This model was extended by Newsome (1965) to provide a method for estimating the severity of drought. Basically the model depends on two premises;

(a) the soil must be moist for at least two weeks to enable germination and significant plant production

(b) the rate of evaporation and transpiration of water from the soil is about one-fifth the rate of evaporation from a free water surface (E_w = mm/week).

It follows that rains which exceed 0.4 E_w would cause germination of annuals and growth of perennials.

Because Trumble (1948) had published tables of evaporation rates for a site near Witchitie (part 2.0) the approximate weekly evaporation could be calculated and used in conjunction with the recorded rainfall to estimate the availability of moisture in the soil at Witchitie. To facilitate calculations each year was divided into fifty-two arbitrary weeks and the rains treated as though they fell in the middle of each week. The model was built up as follows.

When, say after a period of drought, enough rain fell to cause a response in the pasture, the soil moisture was set equal to the rainfall and then the weekly evaporation from the soil was subtracted until the soil moisture reached zero. Any rains which fell while the soil remained damp were added to the calculated soil moisture and so reduced the rate of drying of the soil. As Newsome (1965) showed, it was also useful to accumulate the estimated evaporation after the soil had dried out, for although these negative values had no meaning in terms of soil moisture they nevertheless provided an index of the drying power of the climate on the vegetation. Small rains which caused no response in the vegetation slowed the rate at which the index of severity of drought increased. When useful rains again fell, the soil moisture level was again equated to the rainfall.

A computer program was written to calculate the weekly soil moisture levels and the index of drought for the study area at Witchitie during the years 1968-1972. The results are given in table 10.

The basic assumptions of the soil moisture model had been tested for the Witchitie study area and at Belton which lies 32 km to the west (Cooke, 1970). The data collected since that time also demonstrate a good correlation between the levels of soil moisture and the periods when growing plants were available. These results are presented in figure 9.

4.143 Severity of drought and the amount of water in plants

When the soil was moist, plants were usually fully hydrated and the rabbits had plenty of water in their food. During drought, however, the amount of water in the plants gradually fell until many species contained only about 10% moisture.

For some of the more common plants on the study area a

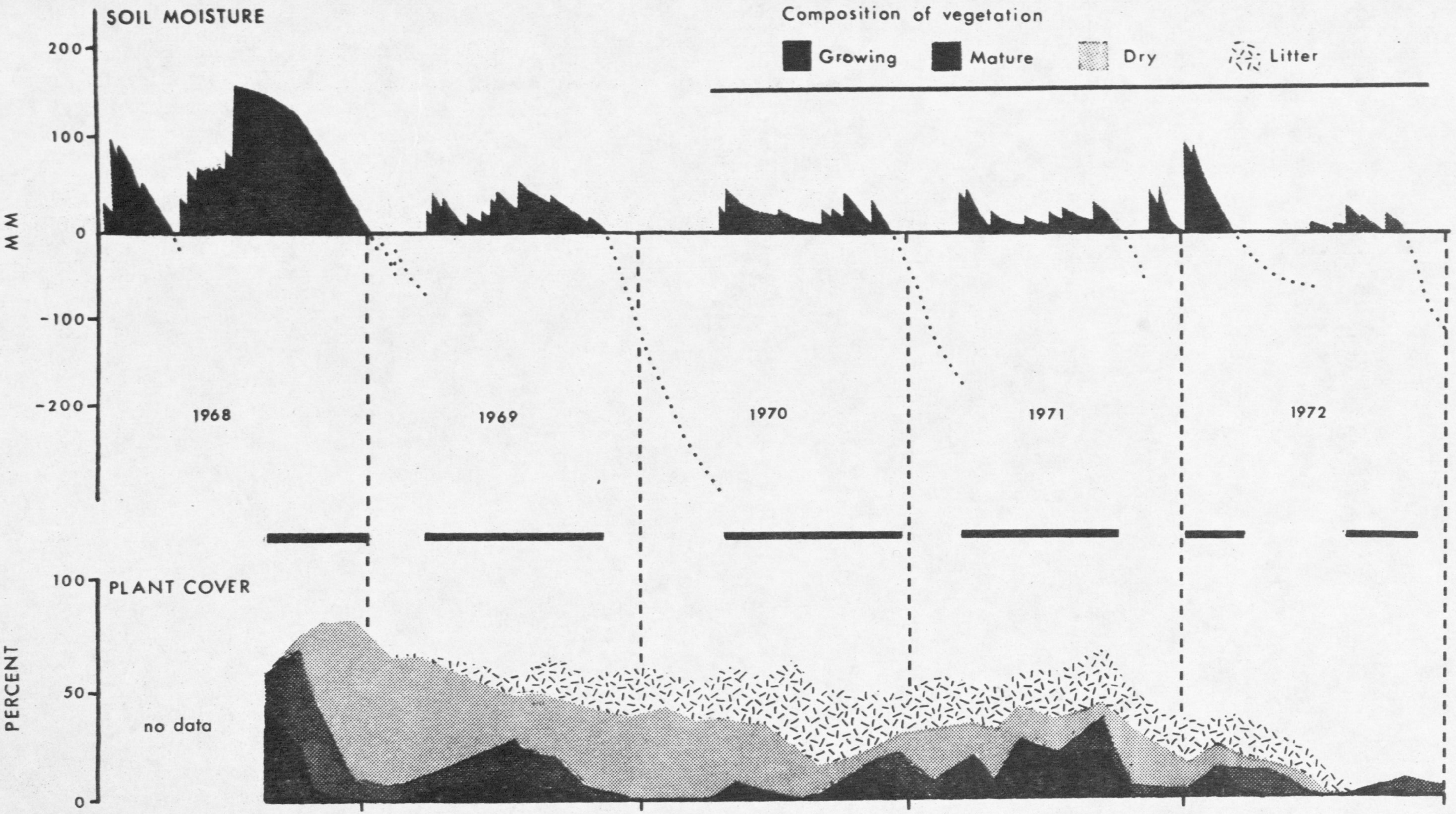

Fig. 9 The relationship between soil moisture and pasture production. Periods of plant growth are shown thus ▬.

TABLE 10. Values of soil moisture and the severity of drought estimated from rainfall recorded at Witchitie 1968-1972 and evaporation data from Trumble (1948).

WEEK	1968	1969	1970	1971	1972
1	9.40	-31.24	-147.57	-66.29	-13.21
2	-6.35	-19.05	-163.32	-82.04	102.87
3	98.55	-34.54	-178.82	-97.54	100.08
4	86.61	-48.26	-194.06	-112.78	84.84
5	71.63	-61.98	-209.04	-127.76	69.85
6	56.90	-51.05	-223.27	-142.49	55.12
7	42.67	-65.28	-236.73	-156.72	45.97
8	51.82	-69.60	-249.94	-166.12	32.77
9	43.18	-82.04	-262.38	-178.56	20.32
10	31.75	-93.47	-273.81	40.13	8.89
11	21.84	-84.07	-281.18	40.89	-1.02
12	12.95	31.50	-290.07	32.51	-9.91
13	4.83	23.37	-298.20	24.38	-18.03
14	-2.54	16.00	-305.56	17.02	-25.40
15	-9.14	22.86	-312.17	10.41	-30.99
16	26.16	20.07	19.81	27.43	-35.81
17	57.15	14.73	46.48	23.11	-41.15
18	52.58	10.16	41.91	18.54	-45.72
19	68.07	8.89	37.85	14.48	-49.78
20	68.58	5.33	34.29	10.92	-53.34
21	75.69	8.89	31.24	11.18	-56.39
22	72.90	15.49	30.48	12.70	-59.18
23	72.39	20.83	27.94	24.38	-61.72
24	76.20	24.38	26.92	21.84	-64.26
25	90.42	28.45	24.89	19.56	-66.04
26	165.10	26.16	23.11	17.27	6.35
27	163.83	24.13	22.86	14.99	7.62
28	161.29	46.99	20.32	22.10	6.60
29	161.04	46.74	18.54	22.10	4.83
30	160.27	43.94	15.75	29.21	2.03
31	157.23	42.93	19.05	32.00	6.35
32	156.21	40.89	15.49	28.96	8.89
33	153.16	36.83	11.43	30.48	26.92
34	150.37	32.26	6.86	25.91	22.35
35	147.07	33.02	23.88	24.64	20.57
36	141.22	28.70	18.03	29.97	14.73
37	134.87	24.89	18.80	31.75	8.38
38	127.76	21.84	20.07	24.64	1.27
39	125.22	14.22	38.10	17.02	1.52
40	118.11	5.84	29.72	8.64	-6.86
41	108.71	-3.05	22.10	-.76	-14.48
42	98.30	-11.94	11.68	-11.18	-9.14
43	87.12	-8.64	6.86	-22.35	-20.32
44	85.85	-18.80	-3.05	-34.29	-32.26
45	80.77	-30.73	40.64	-46.99	-44.45
46	67.31	-44.20	28.96	-60.45	-57.15
47	55.88	-58.17	17.53	48.26	-71.12
48	42.16	-72.64	3.05	33.78	-83.31
49	27.94	-87.63	-11.68	49.28	-98.30
50	12.70	-102.87	-19.30	34.04	-113.54
51	-1.02	-118.36	-34.80	18.54	-129.03
52	-16.76	-134.11	-50.29	2.79	-142.49

strong correlation was found between the amount of water they contained and the estimates of the severity of drought (see figure 10). The data were analysed as follows. Exponential curves were fitted to the transformed data by assuming a linear relationship of the type

$$\log_e Y = \log_e C + bX \qquad \ldots\ldots\ldots\ldots \quad (1)$$

where Y is the water content of whole plants (% wet weight) and X is the severity of drought (mm).

On taking anti-logs (1) becomes

$$Y = Ce^{bX} \qquad \ldots\ldots\ldots\ldots \quad (2)$$

the confidence limits of the estimates of Y are given by

$$Y = Ce^{bX}.e^{\pm SE\ \log_e Y} \qquad \ldots\ldots\ldots\ldots \quad (3)$$

Table 11 lists details of these analyses viz; sample size, regression coefficients, slopes and the probabilities that the regressions are significant.

The relationships are also illustrated in figs. 11 a-d for the four most common plant species, *Atriplex eardleyi, Bassia lanicuspis, Bassia patenticuspis* and *Stipa variabilis*.

These formulae enabled calculation of the potential water content of plants for each week of the study between 1968 and 1972, and so gave a greater insight into events in the field than could be obtained by relying solely upon information obtained from samples of plants collected every six weeks or so. In addition it was known (part 4.13) that the rabbits had high water requirements because even those rabbits with a restricted supply of water needed 60-65 percent water in their diet. Consequently, by using this value to define the rabbits' minimum requirements, it was possible to discover how frequently the rabbits were likely to be short of water.

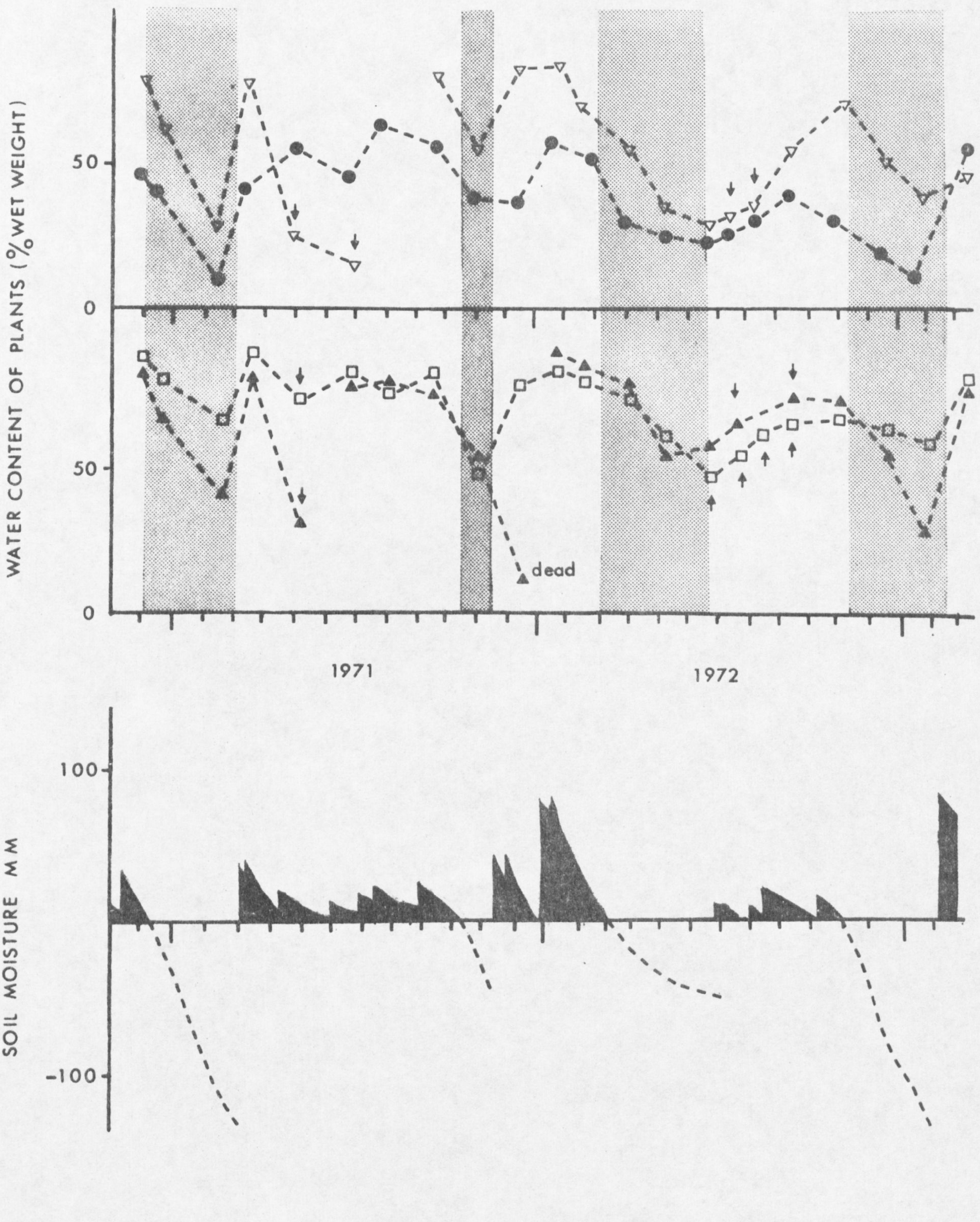

Fig. 10 The water content of plants in relation to soil moisture and drought.

▽ Atriplex eardleyi, ● Stipa variabilis, □ Bassia lanicuspis, ▲ Bassia patenticuspis. The shaded bands indicate periods of drought, the arrows (↓) show when plants were severely over-grazed.

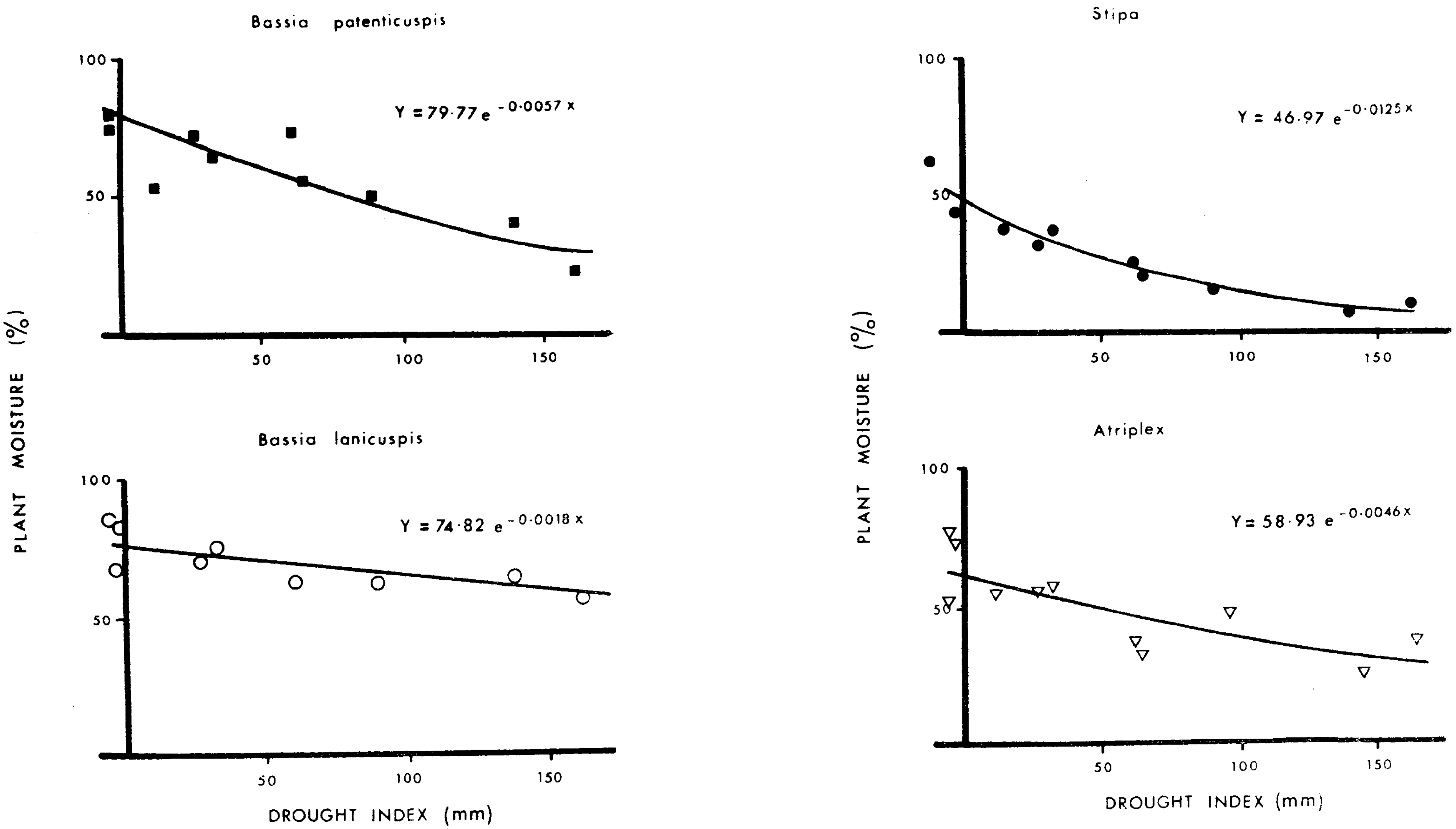

Fig.11 Water content of plants in relation to the severity of drought.

TABLE 11. Water content of pasture species during drought.

Species	N	r	b	$S_{\log_e Y}$	C	P
Atriplex eardleyi	10	-0.7072	-0.0046	0.2830	58.93	$0.02>P>0.01$
Bassia lanicuspis	11	-0.7775	-0.0018	0.0964	74.82	$0.01>P>0.001$
Bassia patenticuspis	14	-0.8162	-0.0057	0.2461	79.77	$P<0.001$
Stipa variabilis	9	-0.9842	-0.0125	0.1161	46.97	$P<0.001$

Formulae:

Atriplex eardleyi $Y = 58.92\ e^{-0.0046X}$

Bassia lanicuspis $Y = 74.82\ e^{-0.0018X}$

Bassia patenticuspis $Y = 79.77\ e^{-0.0057X}$

Stipa variabilis $Y = 46.97\ e^{-0.0125X}$

In the summers since the major population crash it was found that only one summer was particularly dry i.e. 1970-71, yet it was also known that the rabbits were not really short of water because they did not drink at the artificial watering points. It was noticed, however, that rabbits were grazing heavily upon the leaves of *B. lanicuspis* and this offered an explanation for the rabbits' lack of interest in the supplementary water. From the preceding equations (Table 11) it was calculated that during the driest part of the 1970-71 summer *B. lanicuspis* should have contained 53.8% water on average. However, the leaves of this species contained a higher proportion of water, usually about 10% more than the plants as a whole. Moreover, I have found that by examining plants closely, then picking only the greenest tips it is possible to select leaves containing up to 15% more water than the whole plant. For instance, a sample of *B. lanicuspis* collected in December 1973 gave the following values

Stems	48.9% water
Leaves	62.4% "
Selected tips	67.0% "
Whole plants	54.1% "

By eating the leaves of this species of *Bassia* the rabbits would have eaten food containing at least 65% water throughout the summer of 1970-71.

If this method of calculating the availability of moisture for the rabbit is to be tested further it will be necessary to wait until a really dry summer enables observations of the response of rabbits to supplementary water as the drought intensifies. Although the rabbits sought supplementary water during the summer drought of 1969-70, the observations were complicated by the fact that the rabbits were unusually numerous. Nevertheless, calculations of the percentage of water expected in *B. lanicuspis* at the time of the population crash demonstrated that the crash could not have been caused by drought alone. Most of the rabbits on the study area died before the end of December 1969 yet even in mid-January 1970 any *B. lanicuspis* remaining ungrazed should have contained 56.2% water and the leaves more than 65% water. Most probably the rabbits' need for supplementary water and the population crash resulted from the fact that the rabbits had eaten out much of the water-bearing vegetation (see part 4.28).

4.144 The frequency of drought which might affect the rabbit's supply of water

Although there was no drought of sufficient intensity to deprive the rabbits of water between 1969 and 1972, records nevertheless showed that very severe droughts occurred on the study area from time to time. Again I used the soil-moisture model to determine how often such droughts had occurred, although, because I was unable to obtain long-term records of rainfall from Witchitie station I had to use those from Koonamore station which lies some 20 km from Witchitie and has an annual average rainfall of about 190 mm. The rainfall records from Koonamore for the years 1926 to 1953 were kindly supplied by Miss Constance Eardley of the Botany Department of the University of Adelaide.

These records were used in the soil-moisture model to calculate the severity of drought for each week from 1926 to 1953 inclusive. The water content of the leaves of the most common, drought-resistant pasture species (*Bassia lanicuspis*) was also calculated, again for each week. These calculations were made using the known relationship between the moisture content of plants and the severity of drought after assuming that leaves contained 10% more water than the plants as a whole (see part 4.143).

The proportion of years in which water was probably adequate for the rabbits could then be calculated for each arbitrary week of the year as shown in Table 12 and Figure 12.

The most interesting aspect of this exercise was the illustration that sufficient water was available in drought-resistant plants for a much greater part of the year than might be expected from consideration of rainfall or soil moisture levels alone.

Table 12 shows that during the hottest month of the year, January, soil moisture was adequate for growth of plants only one year in five, but the leaves of *B. lanicuspis* contained sufficient water for the rabbits in most years because the weather was severe enough to dry up the plants only one year in every five. The most critical time for the rabbit was apparently in late April when the ephemeral vegetation had a good chance of drying-off completely before the winter rains began. Only rarely, one year in ten, were the pastures too dry to support the rabbits during the spring months.

This type of analysis provides of course only very general information. At times, such as during the autumn, the shortage of water may be more acute than predicted by the model if the pastures were very heavily grazed. On the other hand, patches of moister vegetation might persist in hollows and gutters even though the pastures were generally dry.

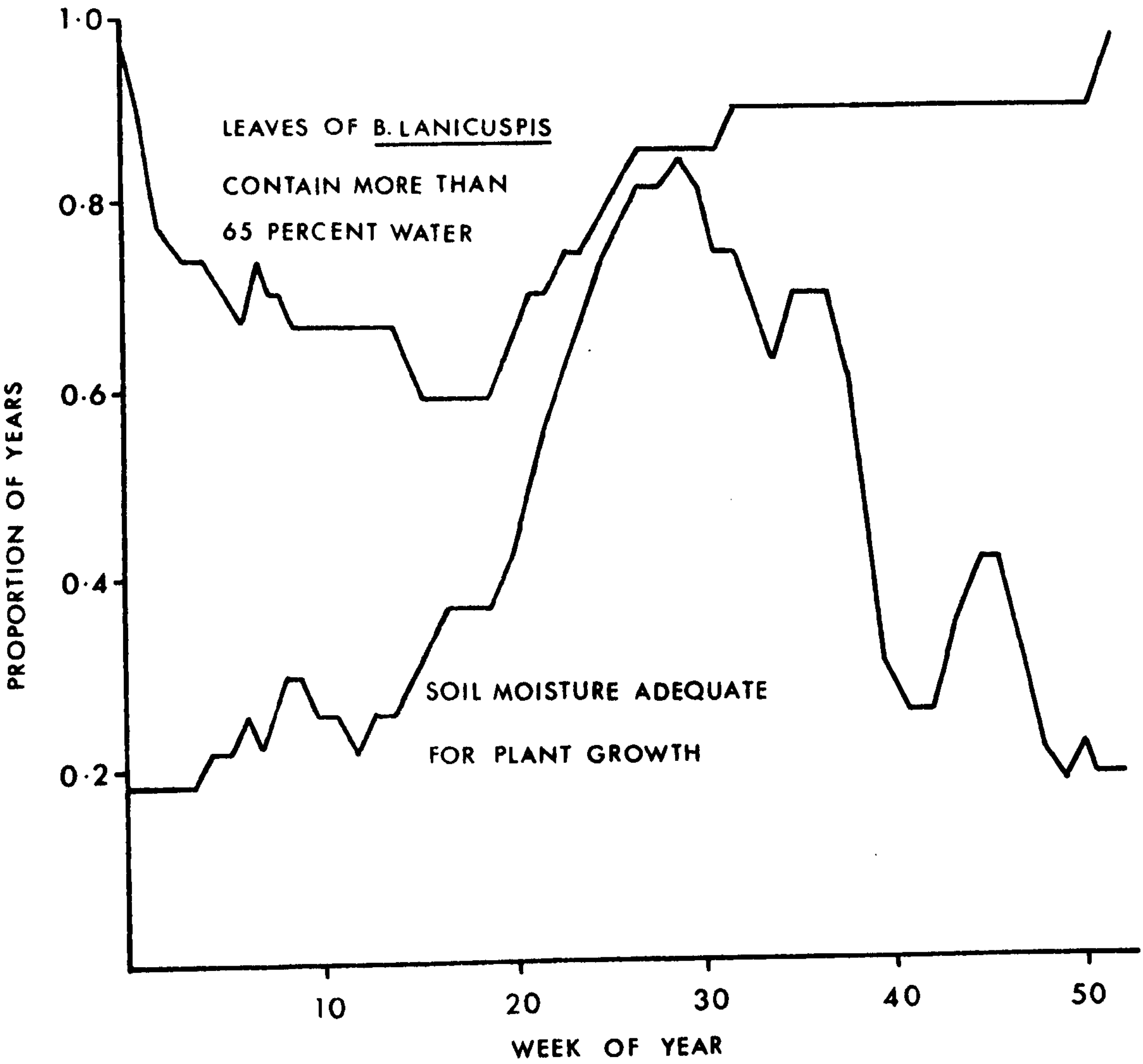

Fig.12 Estimates of the seasonal availability of water in the soil and the leaves of B. lanicuspis ; based on rainfall at Koonamore between 1926 and 1953. Although the soil was often dry in summer, plants usually contained enough water for the rabbits.

TABLE 12. The proportion of years between 1926 and 1953 when soil moisture was adequate for plant growth and plants contained enough water for the rabbits.

Week	Proportion of years when soil moisture was adequate for growth	Proportion of years when the leaves of *B. lanicuspis* contained 65% water or more
1	.19	.89
2	.19	.78
3	.19	.74
4	.22	.74
5	.22	.70
6	.26	.67
7	.22	.74
8	.30	.70
9	.30	.67
10	.26	.67
11	.26	.67
12	.22	.67
13	.26	.67
14	.26	.67
15	.30	.63
16	.33	.59
17	.37	.59
18	.37	.59
19	.37	.59
20	.44	.63
21	.48	.70
22	.56	.70
23	.63	.74
24	.67	.74
25	.74	.78
26	.78	.81
27	.81	.85
28	.81	.85
29	.85	.85
30	.81	.85
31	.74	.85
32	.74	.89
33	.67	.89
34	.63	.89
35	.70	.89
36	.70	.89
37	.70	.89
38	.63	.89
39	.41	.89
40	.30	.89
41	.26	.89
42	.26	.89
43	.33	.89
44	.37	.89
45	.41	.89
46	.41	.89
47	.30	.89
48	.22	.89
49	.19	.89
50	.22	.89
51	.19	.89
52	.19	.96

Nevertheless the data are useful in showing when the rabbits living on the marginal, better drained parts of the study area might have been affected by water shortage.

4.2 Food

4.21 Introduction

To assess the influence of the abundance of food on a population of wild rabbits it is necessary first of all to define precisely what we mean by 'food' and measure its availability. Secondly it is necessary to determine how efficiently the rabbits may use the available food. If the results show that food is sometimes scarce and the rabbits are not eating foods of sufficient quality to meet their needs then it can be argued that food shortages may be affecting the population.

Basically the concept is simple yet there are several major problems which arise mainly because of the rabbits' reliance on coprophagy as a normal part of digestion (e.g. Thacker and Brandt, 1955) and their ability to recycle urea which is apparently used by bacteria in the gut to synthesize amino-acids (e.g. Houpt, 1963; Yoshida, Pleasants, Reddy and Wostman, 1968).

For instance, Thacker and Brandt (1955) argued that coprophagy greatly facilitated the digestion of foods and Myers (1955) showed that the proportion of food which was recycled varied according to the quality of the pastures. It would follow that if coprophagy had a powerful influence on the digestibility of foods then it might be difficult to define the rabbit's basic requirements of energy and nitrogen from one season to the next.

However, a survey of the literature, given in detail in the Appendix (part 6.1), showed that coprophagy has a very small influence upon the amount of dry-matter digested and consequently upon the energy obtained from the food. Its role in the digestion of protein was less clear because as mentioned previously, new amino-acids may be synthesized from urea. Nevertheless it could be stated with certainty that coprophagy could not greatly offset shortages of digestible energy or protein in the rabbit's diet. (Voris, Marcy, Thacker and Waino, 1940; Crampton, 1934; Cassidy, Damon and Suitor, 1963).

The conclusions drawn from the survey meant that data published on the rabbit's requirements of energy and nitrogen could be used to define the quality of food necessary to maintain a population of rabbits irrespective of the seasonal changes which might be expected in the reingestion of soft faeces. The basic nutritional requirements of the rabbit are discussed shortly in parts 4.22 and 4.23.

A further potential problem arising from the rabbits reliance on coprophagy was the fact that soft faeces in the stomach could mingle with recently ingested food and cause fermentation thus making difficult the accurate measurement of the quality of food eaten. A similar problem is well known for ruminants such as deer in which rumen samples do not reflect the quality of food eaten (e.g. Bissell, 1959). Yet the rabbit has a simple stomach and although Griffiths and Davies (1963) have shown that soft faeces may promote considerable fermentation there, Myers and Bults (unpublished data) have shown that the quality of food can be predicted from the quality of recently ingested food in the anterior part of the stomach. Their data are presented in table 6.2 of the Appendix.

I therefore used chemical analyses of ingesta from the forestomach to assess shortages of food for the rabbits at Witchitie instead of resorting to more detailed procedures such as the microscopic examination of plant particles in the ingesta. Although it would be interesting to determine precisely which plants the rabbits were eating, and samples of stomach contents have been stored for this purpose, the procedures were so time consuming as to lie beyond the scope of a Ph.D. study. Furthermore, the results obtained from microscopic examination are difficult to interpret because not all plant particles can be identified and it is necessary to use a correction factor according to the proportion of particles which can be identified in pure samples of each of the plant species eaten (Griffiths and Barker, 1966).

The major problems which arise in the use of such correction factors are (a) the questionable assumption that the plant samples used to derive correction factors are equivalent to the parts of the plants grazed by the rabbits, (b) the fact that correction factors are likely to alter according to the stage of growth of each plant species and a full range of plants would need to be collected to derive new correction factors on each visit to the study area (Griffiths, CSIRO, Division of Wildlife Research, pers. comm.).

In my survey of the literature (Appendix, 6.1), I had considered four components of the rabbit's diet, namely, energy, the quantity and quality of protein and the water-soluble vitamins. Of these only energy and protein seemed worth following up in a field study. The energy available to the rabbit was the more interesting of these not only because of the ease with which the results could be interpreted (i.e.

there were no real complications arising from the effects of coprophagy on the digestibility of food) but also because it was necessary for a rabbit to have an ample supply of energy to maintain itself in nitrogen balance (Hellberg, 1949).

The quality of protein and the availability of B-vitamins in pastures were not studied largely because the biochemical procedures necessary for such studies were too complicated or too expensive for use in an extensive field study.

Before turning to the field studies, however, it is necessary to know the rabbits' minimum requirements of energy and nitrogen and to consider briefly the ways in which these dietary components may be measured.

4.22 The relationship between fibre and the energy available in the foods of the rabbit

Voris, Waino, Thacker and Marcy (1940) found that the amount of fibre in food had a very important effect on the energy intake of domestic rabbits. As fibre increased, both the ability to digest food and the voluntary food intake were reduced so that highly fibrous plants usually proved unsatisfactory as food because the rabbits could not eat enough to meet their energy requirements. In general, plants which provided the rabbit with sufficient energy contained at least 47% digestible dry-matter.

Bailey (1969) similarly showed that young cotton-tails (*Sylvilagus*) were only able to maintain themselves if the food they ate contained more than 2.0 cal of digestible energy/g dry-matter. Since each g digestible matter contains about 4.15 cal, the minimum digestibility of useful foods would have been about 48%, quite close to the value obtained for

Oryctolagus.

From the data of Voris et al. (1940) I derived a function which expressed the digestibility of foods in terms of the amount of fibre they contained. In the function

$$Y = 104.05\ e^{-0.0265X} \qquad \ldots\ldots\ldots\ldots \quad (4)$$

Y = digestibility of dry matter (%), X = fibre content (%). The 95% confidence limits are given by multiplying (4) by

$$e^{\pm 0.2029}$$

From the foregoing equation it could be argued that foods containing more than 30% fibre would usually be too indigestible to meet the energy requirements of the rabbit. However, this limit only applies to caged rabbits because in natural populations rabbits have a wide choice of foods, and, from foods of a given fibre content could select the most digestible components. If rabbits were highly selective, as the work of Myers and Poole (1963) suggests, the relationship between the digestibility and the fibre content of foods eaten by free-living rabbits might be best approximated by the upper 95% confidence limit of equation (4) rather than the equation itself. A further reason for using this upper limit arises in part 4.42 when I argue that at certain periods during the study the food available was too fibrous for the rabbits.

It can be calculated from the equation to the 95% confidence limit that foods containing more than 40% fibre would be less than 47% digestible and therefore useless to the rabbits (see fig. 13).

For my field studies I decided to simply measure the fibre content of the rabbit's food and, when necessary, calculate the energy available to the rabbit. I had the

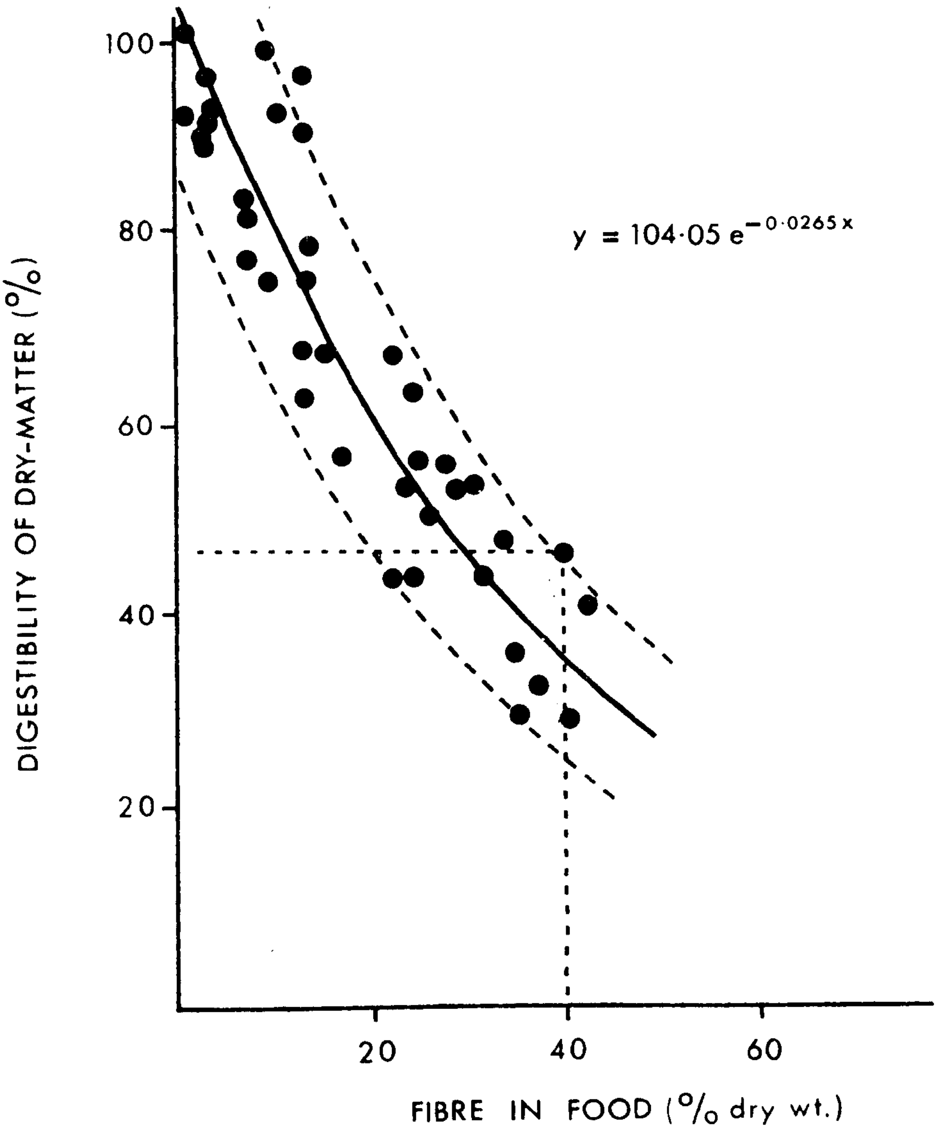

Fig. 13 The relationship between the fibre content and the digestibility of food, derived from the data of Voris et al., 1940. The broken lines on either side of the curve are 95 % confidence limits.

choice of estimating fibre by using either the method of Voris et al. (1940) or one developed more recently by Van Soest (1963).

The newer method for estimating fibre had several major advantages. Firstly, it was a very simple procedure. Secondly, it gave better correlations between fibre and digestibility; mainly because indigestible lignin was retained in the fibre fraction whereas during earlier alkali extraction procedures it was dissolved. Thirdly, and perhaps most importantly, when my studies began, the newer technique for estimating fibre was being used in studies of the food of the wild rabbit at CSIRO, Division of Wildlife Research, and it was advantageous to collect results which could be readily compared.

The only disadvantage in using Van Soest's method was that the results I obtained would not be strictly comparable to those of Voris et al. At first this seemed an important obstacle because my arguments depended upon a reasonably accurate definition of the limit of fibre which the rabbit could tolerate. However, on careful consideration it seemed that the general relationship between fibre content and digestibility of food would remain irrespective of the method used to estimate fibre. There was no reason to expect that the total yield of fibre would differ greatly from one extraction procedure to the next. In the case of acid-detergents for example, lignin was retained but more hemicellulose was dissolved than in the alkali extraction method. Since lignin and hemicellulose make up only a small proportion of the total plant fibre and losses of hemicellulose counteract to some extent the gain of lignin, the differences in the estimates of fibre should be small.

I therefore used Van Soest's method for estimating fibre during my studies, but retained the value of 40% fibre derived from the data of Voris et al. (1940) to delimit the proportion of fibre which the rabbits could tolerate in their food.

4.23 Nitrogen in the rabbit's diet

The nitrogen requirements of rabbits have been investigated by a number of authors, e.g. Hellberg, 1949; Richet and Minet, 1926. The most careful study, that of Hellberg (1949), showed that rabbits of 1.75 kg, about the size of a mature wild rabbit, would need 5.1 g protein daily. This value agreed closely with an estimate of 5.0 g/day calculated from principles outlined by Brody (1940) and modified by Crampton and Lloyd (1959). However, some other authors have obtained higher values of up to 7.7 g protein/day for a 1.75 kg rabbit (Coles and McDonald, 1963).

If the most extreme nitrogen requirements listed in the literature are taken, i.e. 7.7 g protein/day, and it is assumed that in poor quality food the digestibility of protein is only 60% (see Voris et al., 1940), it can be calculated that a rabbit weighing 1.75 kg which eats, say, 100 g food daily will need foods containing 13% protein.

During my field studies, nitrogen in the rabbits food was estimated using the method outlined by Conway (1962). Crude protein could be estimated by multiplying the nitrogen content of the foods by 6.25. It follows that foods which contain slightly more than 2% nitrogen should enable a rabbit to maintain nitrogen balance.

Once the minimum food requirements of the rabbit had been defined I could consider the availability of foods in the field. In doing so, I concentrated mainly upon the availability of energy, although as we shall see in part 4.32, plants which are low enough in fibre to be of use to the rabbit generally provide the rabbit with enough protein too.

One of the first tasks was to analyse the most common species of plants on the study area to find those which might be most useful to the rabbit.

4.24 The quality of pasture species

Samples of twenty-four species of plants were collected and analysed for fibre content using the method of Van Soest (1963). For the ephemeral grasses and forbs, fibre was estimated from samples of whole plants. This was done partly because of the plants' small size but also because the rabbits ate stems as well as the leaves of many species. For the woody perennials however, only leaves and twigs equivalent to those eaten by the rabbits were analysed.

The samples of ephemeral species were made up of young plants collected during periods of good plant growth and so the fibre contents were representative of plants in their most digestible stages of growth. Plants which contained more than 40% fibre were considered most unlikely to be an important source of food for the rabbit even if they included a few digestible components such as buds or reproductive organs.

Tables 13 a and b list the fibre content of each species analysed. Included in the tables (part b) are a few species upon which the rabbits grazed heavily during the population crash of 1969-70. Many of these plants were very fibrous and, as suggested in part 4.133, although they

TABLE 13(a). Fibre content of ephemeral plants on the study area. Values are for whole plants except where specified. Potential foods for the rabbit marked with asterisk.

Species	Fibre content (%)
Atriplex eardleyi	29.3*
Bassia birchyptera	38.8*
Bassia lanicuspis	28.3*
Bassia patenticuspis	31.5*
Chaenopodium cristatum	41.1
Danthonia caespitosa	52.6
Echium plantagineum	44.1
Enneopogon polyphyllus	48.1
Euphorbia drummondi	32.7*
Geranium sp.	33.8*
Helipterum laevae	37.1*
Lotus cruentus	36.4*
Pelargonium sp.	27.9*
Salsola kali	36.6*
Schismus barbatus	42.5
Sida corrugata	41.5
Stipa variabilis	41.7
Tetragonium eremaea	25.1*
Zygophyllum idiocarpum	22.6*

TABLE 13 (b). Components of perennials eaten during the population crash.

Species		Fibre content	Water content
Acacia victoriae	(leaves)	34.0*	54.1
	(bark)	42.1	45.4
Cassia sp.	(leaves)	16.1*	55.8
	(stems)	42.1	52.1
Heterodendrum olefolium	(bark from roots)	55.7	36.6
Loranthus sp.	(leaves)	17.4*	62.2
	(stems)	41.8	48.1
Senecio magnificus	(leaves)	32.5*	82.3
	(stems)	54.4	70.4

provided enough water they contained too little digestible energy to be of use to the rabbit.

The water content of the species eaten during the crash has been included in table 13 b but it is worth noting that the values are likely to be under-estimated. When eating bark for instance, the rabbits may have discarded the dry outer layers and eaten only the sap-filled inner layers. However, there was no way of deciding this from the evidence of rabbit damage to the vegetation so that I could only collect samples equivalent to those which the rabbits had apparently eaten.

4.25 The distribution of food on the study area

To obtain an idea of the distribution of food on the study area at Witchitie I listed the species of plants which occurred within three meters of each of one hundred randomly chosen points. From these data I intended to compile maps showing the general distribution of each plant species in turn but I found that this type of analysis could be substantially reduced by firstly testing for associations between plant species then mapping the distribution of 'communities' rather than individual species.

To test for association between plants I used a 2 x 2 contingency table and applied a χ^2-test with Yates correction which allows for small sample size, i.e.

		Species A		
		+	-	
Species B	+	a	b	a + b
	-	c	d	c + d
		a + c	b + d	n

$$\chi^2 = \frac{n\{(ad - bc) - \frac{1}{2}n\}^2}{(a + c)(b + d)(a + b)(c + d)}$$

The results, shown in table 14, demonstrated that some species of plants occurred together more frequently than expected from chance, i.e. they were closely associated. Other species were strongly dissociated.

The major plant association included *Atriplex eardleyi* and *Bassia patenticuspis* as well as many of the soft, winter-growing annuals. General observations also showed that this association produced by far the greatest amount of vegetation which the rabbit could use. The general distribution of the association is approximated by the distribution of *Atriplex eardleyi* as shown in fig. 14a.

A knowledge of the general distribution of food provided a useful basis for assessing the influence of this resource on the rabbit population; fig. 14 b shows how closely the distribution of rabbits on the study area in late 1969 was related to distribution of the soft annual plants. The comparison indicates that the rabbits were grouped in close proximity to their food supplies.

During 1971 and 1972 the correlation between the distribution of rabbits and vegetation remained. Furthermore, figure 15 shows that there were plenty of empty warrens available on parts of the area which lay beyond the areas dominated by the soft annual vegetation. It seemed therefore that the distribution of plants might be important in determining the distribution of the rabbit.

Nevertheless it was necessary to explain why the rabbits were able to colonize and successfully breed in the outlying warrens in some years, and I proposed that in years

TABLE 14. Association of plant species on study area at Witchitie.

$*$ $P < 0.05$
$**$ $P < 0.01$
$***$ $P < 0.001$
n.s not significant

	Stipa	Danthonia	Bassia pa.	Bassia la.	Bassia sp.	Bassia br.	Echium	Atriplex	Salsola	Sida	Erodium	Pelargonium	Tetragonia	Schismus	Boerhavia	Goodenia	Chaenopodium
Stipa	X																
Danthonia	ns	X															
Bassia pa.	ns	ns	X														
Bassia la.	ns	ns	ns	X													
Bassia sp.	ns	ns	ns	ns	X												
Bassia br.	ns	ns	ns	ns	ns	X											
Echium	$+^{*}$	ns	$+^{**}$	ns	ns	ns	X										
Atriplex	ns	ns	$+^{***}$	$-^{**}$	ns	ns	$+^{***}$	X									
Salsola	$+^{*}$	$+^{*}$	$+^{***}$	ns	ns	ns	$+^{*}$	ns	X								
Sida	ns	ns	$-^{***}$	ns	ns	ns	ns	$+^{*}$	$+^{**}$	X							
Erodium	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	X						
Pelargonium	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	X					
Tetragonium	ns	ns	ns	ns	ns	ns	$+^{**}$	$+^{**}$	ns	ns	$+^{***}$	$+^{*}$	X				
Schismus	ns	ns	$+^{***}$	$-^{*}$	ns	ns	$+^{***}$	$+^{***}$	ns	ns	$+^{*}$	ns	$+^{*}$	X			
Boerhavia	ns	ns	ns	ns	ns	ns	$+^{**}$	$+^{**}$	ns	ns	ns	ns	$+^{**}$	$+^{**}$	X		
Goodenia	ns	$+^{**}$	$+^{*}$	ns	ns	ns	$+^{*}$	$+^{***}$	ns	ns	ns	ns	ns	$+^{*}$	ns	X	
Chaenopodium	ns	ns	$+^{***}$	$-^{**}$	ns	ns	$+^{**}$	$+^{***}$	$+^{*}$	ns	ns	ns	$+^{***}$	$+^{***}$	$+^{**}$	$+^{*}$	X

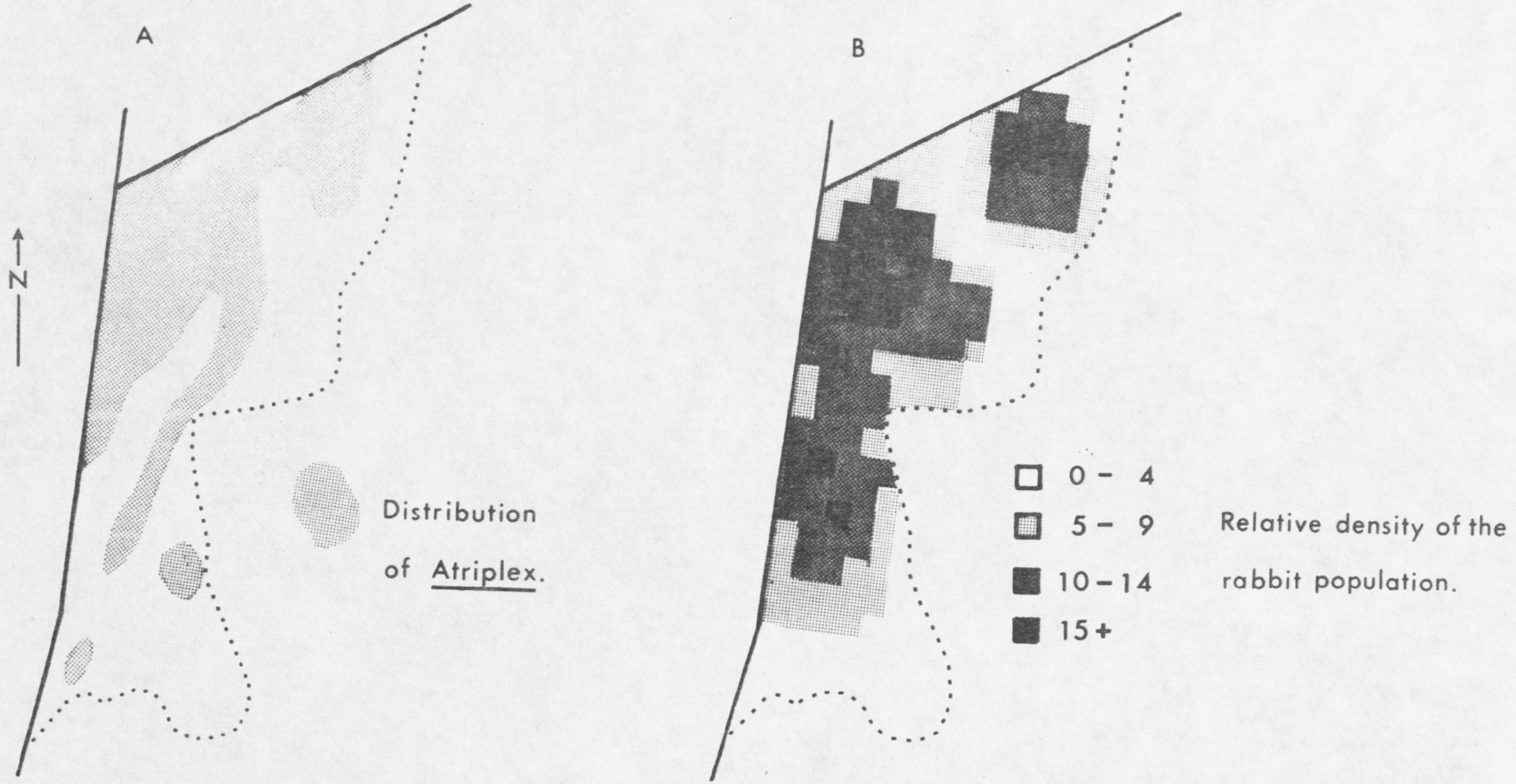

Fig. 14 The distribution of rabbits in relation to their major food source. The rabbits are clearly grouped in those areas where soft plants such as <u>Atriplex</u> grow most widely.

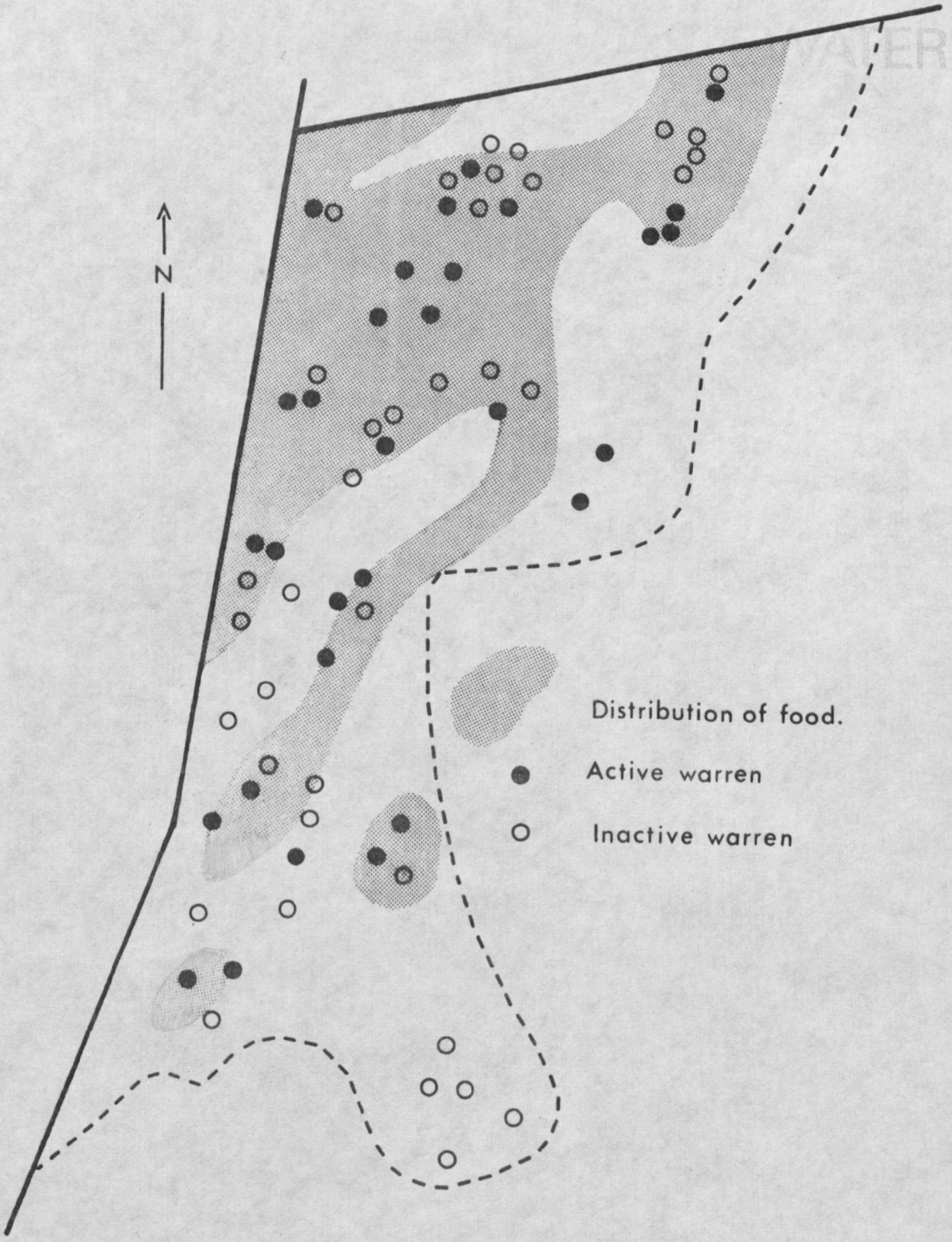

Fig. 15 The distribution of food and active rabbit warrens on the study area in late 1972. All active warrens lie within close range of food supplies.

of very good rainfall sufficient soft vegetation to support rabbits grew all over the study area. This was not to say that soft annuals such as *Atriplex eardleyi* colonized new areas but simply that ubiquitous species such as *Pelargonium* and *Erodium* grew more densely. In drier years the soft annuals grew in sufficient density only along gutters and in the hollows, so that the areas suitable for the rabbit were much reduced. These observations would suggest therefore, that the distributions of specific plant species are of less importance than the actual density of useful vegetation in explaining the distribution of the rabbit.

4.26 The abundance of vegetation

A rapid method for recording changes in the amount of vegetation present on the study area was developed. A number of quadrats measuring 60 x 90 cm were permanently marked with galvanized nails pushed into the soil at each corner. By using a small step ladder these quadrats could be photographed from directly above and later the colour transparencies (Kodachrome II, 25 ASA, 35 mm) were projected onto a screen so that the vegetation cover at each of 100 points on the image could be recorded. The cover at each point was recorded as follows. Firstly, if the point fell upon plant material, the species of the plant was recorded. Secondly, the plant matter was listed under one of the following classes: green, actively growing material; green, mature or quiescent vegetation; dry vegetation; and litter. When the point did not fall on vegetation a record of bare earth, or occasionally, animal dung resulted.

Classification of the vegetation required a good knowledge of individual plant species. A healthy plant could be regarded as actively growing whereas a plant showing signs of yellowing or wilting was classed as quiescent. Mature vegetation was recognized by the presence of seed-heads or early signs of drying-off. Dry vegetation, even if it was fragmented, could be distinguished from litter which was material which had lost the colour of straw and begun to turn grey as it decomposed.

The results from two of the four quadrats which were photographed on average every six weeks from August 1968 to the end of 1972 are shown in figure 16. This provides a general picture of seasonal changes in the pastures, particularly the new growth which followed adequate rains, the maturation of plants and finally, the weathering of dry straw.

Since 1970, data from three more quadrats have also been collected along with information from a few quadrats from which rabbits and domestic stock have been excluded. These more recent results are considered briefly in part 4.28.

Before progressing to examine the availability of food in more detail it is necessary to establish that changes in the vegetation cover provided a reliable measure of real changes in the amount of vegetation present.

4.261 The relationship between cover and the mass of vegetation

Because the plants at Witchitie were generally low-growing species which seldom formed a continuous ground cover, it seemed likely that there would be a reasonably good correlation between the percentage cover and the mass of vegetation.

The data necessary to test this idea was obtained by photographing, then harvesting, drying and weighing the

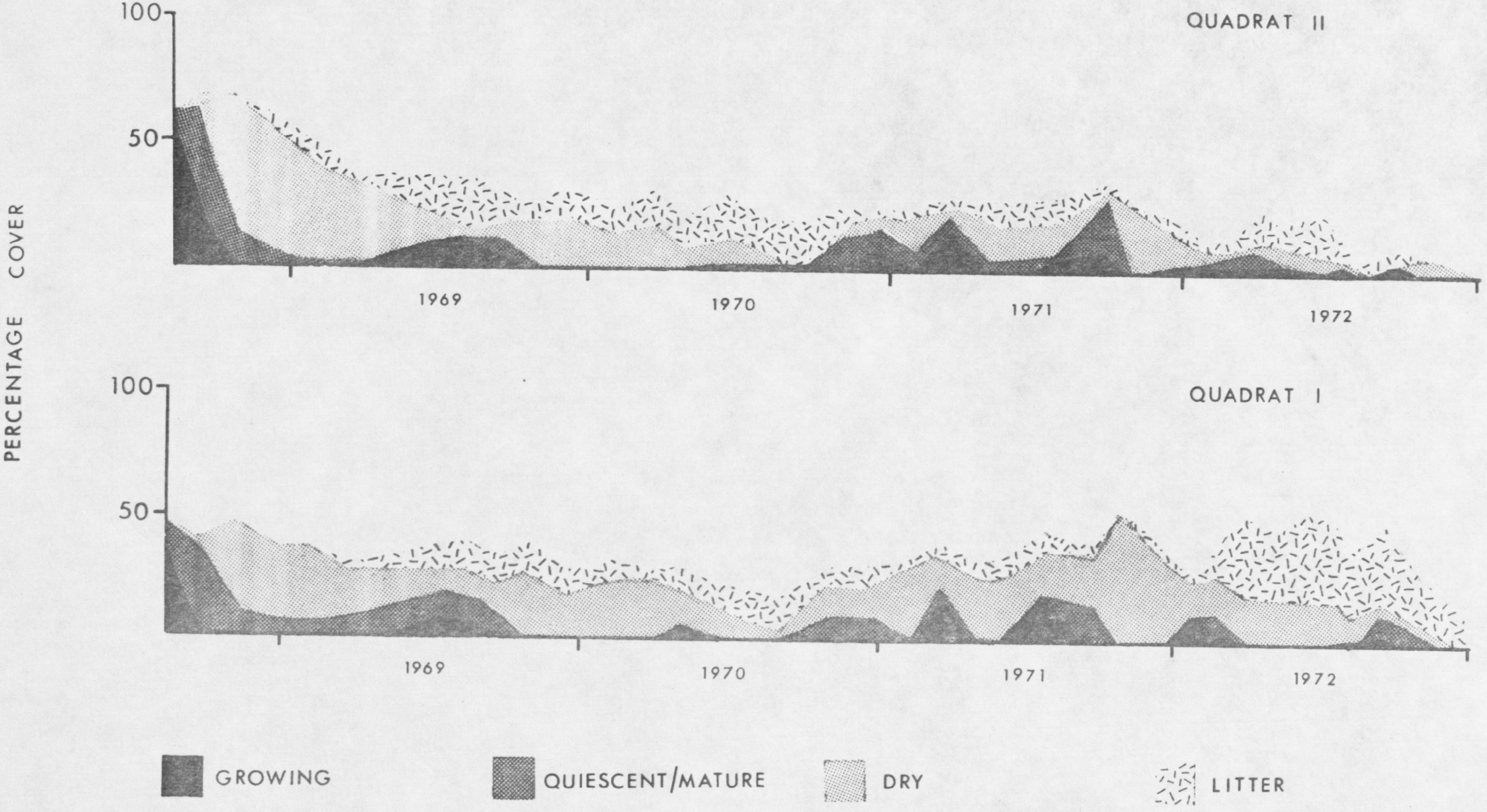

Fig.16 The abundance and composition of vegetation on two of the permanent quadrats at Witchitie, 1968–72.

plants from twenty-three quadrats. In practise, a few quadrats were photographed and harvested on each visit to the study area over a period of a year. This ensured that the data were representative of plants at all stages of growth. The results are given in table 15.

A good correlation was found between the total mass of dry-matter present and the percentage cover which was transformed from percentages to degrees to meet the prerequisites for analysis ($r = 0.9403$, d.f. = 22, $P < 0.001$). Furthermore, at the low densities of plants normally found on the study area, percentage cover was almost directly proportional to the mass of vegetation present. Ground cover could therefore be accepted as a convenient measure of the amount of vegetation on the quadrats and in later considerations of the availability of food I have used the percentages rather than attempting to calculate the weight of food present.

We can now turn to consideration of the availability of food for the rabbit.

4.27 Index of the abundance of food

Because the proportion of each plant species in the total plant cover on the quadrats was known, and the chemical analyses had indicated those species most likely to be useful to the rabbit, an index of the availability of food could be derived.

However, the fibre content of a few uncommon plant species was not known so that it was most convenient in practise to simply disregard the species known to contain too much fibre and class the remaining plant cover as food.

Furthermore, some of the plants on the quadrats were at times quite useful to the rabbits yet at other times,

TABLE 15. Relationship between cover and mass of vegetation.

Quad. No.	% cover	Arc sin (%)	Total dry matter (g)
1	8	16.43	2.47
2	8	16.43	7.10
3	20	26.57	14.88
4	13	21.13	25.12
5	31	33.21	59.72
6	37	37.46	69.12
7	19	25.84	25.69
8	12	20.27	17.58
9	41	39.82	61.91
10	9	17.46	13.90
11	12	20.27	16.71
12	52	46.15	66.38
13	13	21.13	15.91
14	36	36.87	12.00
15	35	36.27	20.70
16	3	9.97	3.47
17	9	17.46	9.52
18	16	23.58	8.15
19	83	65.65	243.3
20	96	78.46	336.4
21	100	90.00	438.8
22	50	45.00	99.9
23	41	39.82	149.0

usually because of grazing, were so defoliated that the fibrous stems were useless as food. The most important of these species were *Bassia patenticuspis* and *Atriplex eardleyi*. Samples of these species, collected from near the photographic quadrats on each visit to the study area, were therefore analysed for fibre and the plants could be rejected or classed as food accordingly. These data may be found in table 16.

The final problem in deriving an index of the food available to the rabbit arose because the use of plant cover to indicate the bulk of food present was occasionally misleading. This occurred despite the generally good correlation between cover and mass of vegetation. Early in the growing season, for instance, a high percentage of cover sometimes resulted from a thick growth of tiny, freshly germinated dicotyledons. These seedlings only weighed a milligram or so, consequently it would be quite unreasonable to consider that they formed a significant part of the rabbits' diet. Small dicotyledons were therefore excluded from estimates of the amount of food present. A second instance of this type came at the end of the growing season when dry vegetation was flattened by trampling or weather and an increase in plant cover resulted without a real increase in the abundance of food. In the one case where vegetation was obviously flattened I obtained an index of the food available by simply averaging the indices from the samples taken immediately before and after the one in question. It is worth stating that because vegetation is only flattened at the end of the growing season when there is usually plenty of food present this problem in no way detracts from the usefulness of the index in defining periods of food shortage.

TABLE 16. Fibre in plants on quadrats (% dry weight)

Date	*Atriplex eardleyi*	*Bassia patenticuspis*
22.11.70	27.6	27.4
18.12.70	25.1	32.6
4. 2.71	26.1	30.0
14. 3.71	33.7	28.7
30. 4.71	46.0*	44.1*
25. 5.71	52.0*	31.5
21. 7.71	n.a.	35.3
22. 9.71	23.7	36.0
22.10.71	29.3	35.2
9.12.71	23.7	50.3*
21. 1.71	34.4	29.4
17. 2.72	34.3	32.5
30. 3.72	29.2	30.5
5. 5.72	41.0*	35.4
22. 6.72	45.8*	28.9
22. 7.72	51.4*	35.8
4. 8.72	45.1*	31.2
14. 9.72	31.5	32.4
26.10.72	31.5	30.4
15.12.72	32.7	30.7

* plants considered not useful to the rabbits

n.a. = no plants available.

In most instances therefore the problems in estimating the changes in the food available to the rabbit could be overcome. By combining the data on the abundance and quality of plants a rough but reliable index of the availability of food was obtained. This index is given in table 17 and shown graphically in figure 17.

It was of great interest to find that the availability of food often bore little relationship to the abundance of vegetation in general. For example, the total amount of vegetation present rose throughout 1971 then fell again in 1972 yet there were two distinct periods when useful vegetation was readily available and two periods when food for the rabbit was judged to be scarce.

I could not help but notice a general correlation between these changes in the availability of food and changes which had occurred in the number of rabbits on the study area. This was the first good evidence that the availability of food had profound effects on the rabbit population.

Before discussing the influence of food upon the rabbit in more detail however, it is worth considering the causes of the food shortages very briefly.

4.28 The causes of food shortage

Apart from the two periods of food shortage just mentioned, the photographic records at the time of the major population crash of 1969-70 showed that although there had been plenty of vegetation present, most was useless to the rabbits. Even though the fibre contents of such important species as *Atriplex eardleyi* and *Bassia patenticuspis* were not known it was assumed from their badly overgrazed appearance that they would not provide food for the rabbits. All

TABLE 17. Index of abundance of food for the rabbits at Witchitie. - Mean percentage cover on four quadrats.

Date	Total vegetation (percent cover)		Vegetation containing less than 40% fibre (% cover)	
	Mean	Range	Mean	Range
22.11.70	18.0	13-24	9.3	5-18
16.12.70	20.0	10-27	9.0	2-17
4. 2.71	23.5	13-31	6.5	1-15
17. 3.71	26.5	13-36	3.0	1-5
28. 4.71	23.0	12-30	0.5	0-1
26. 5.71	24.3	12-42	5.5	0-11
21. 7.71	28.0	19-38	8.5	2-16
22. 9.71	32.8	18-44	12.0	0-28
27.10.71	37.0	26-63	8.5	0-17
8.12.71	30.3	18-42	5.0	0-16
19. 1.72	19.8	10-30	3.3	0-5
16. 2.72	23.5	8-32	5.8	0-10
29. 3.72	19.0	9-28	8.0	0-17
3. 5.72	15.0	10-21	7.0	0-12
20. 6.72	11.0	7-18	2.0	0-4
14. 7.72	6.3	2-23	1.0	0-2
1. 8.72	5.0	0-13	0.5	0-2
12. 9.72	6.0	0-19	1.3	0-4
24.10.72	4.8	1-10	3.5	1-8
12.12.72	3.3	1-5	1.5	0-3

* Although data from more quadrats were collected, only four quadrats occurred on the Atriplex association which the rabbits apparently favoured.

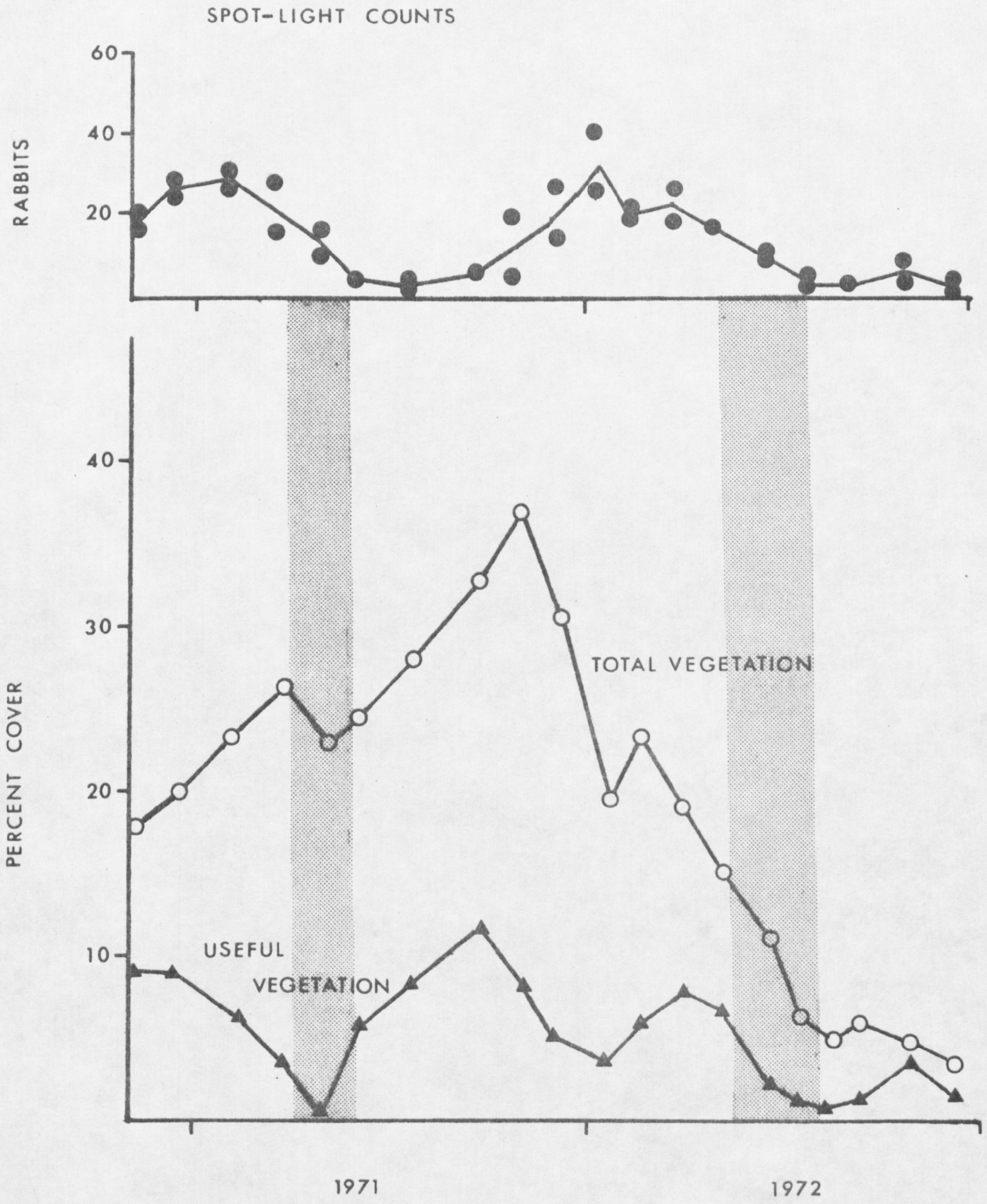

Fig.17 Indices of the abundance of vegetation in relation to the number of rabbits counted on the spotlight transect. The shaded areas define periods when food was short and the rabbit population fell.

quadrats were littered with rabbit dung and the vegetation showed severe damage typical of rabbit grazing with the stems of plants cut through obliquely by chisel-like teeth.

These observations suggested that the rabbits may have eaten much of the available food. Indeed, the rabbits seemed too numerous for the area to support because 600 rabbits were actually caught and tagged there and rough capture-recapture population estimates showed that twice this number of rabbits was present. About 1200 rabbits were therefore living on about 90 ha.

As an approximation to the number of rabbits the area might carry, it could be assumed that 2 or 3 rabbits/ha would be a maximum because the area only supports 1 sheep to 4 ha and a sheep exerts equivalent grazing pressure to about 10 rabbits (see for example Myers and Poole, 1963). It was apparent therefore that with 13 rabbits/ha the supplies of food would not last long once plant growth ceased, especially since the rather mediocre rains of 1969 had only enabled average pasture growth and production.

The second period of food shortage was caused by larvae of the moth *Loxostege affinitalis*. These caterpillars could be found on the area in most years but they did not always occur in such high numbers relative to the amount of food available as in the late summer of 1971 when they completely defoliated the newly germinated winter annuals and even some of the hardier species such as *Atriplex eardleyi* and *Bassia* spp.

It remains unknown why out-breaks of *Loxostege* occur. Plagues of caterpillars are associated with heavy summer rains in the arid and semi-arid parts of South Australia although the moth breeds more or less continuously while growing pastures remain available. Possibly the sudden rains trigger the development of pupae and the adults emerge and lay eggs upon the fresh germination. It can only be guessed how frequently the larvae might be so abundant that they eat most of the available food and profoundly influence the rabbit population.

Sheep appear to have been instrumental in causing the third period of food shortage. From general observations and the appearance of sheep dung on the quadrats it was known that sheep first began to graze the study area in April or May of 1971. However, they ate only moderate amounts of vegetation during the months that followed until the next autumn when about 200 ewes and lambs began to spend most of their time there. The effects of this grazing were assessed by comparing the vegetation cover on quadrats which were grazed with that of quadrats from which the sheep were excluded.

Quadrat IIc, which could be grazed by the sheep, contained far less vegetation than either of the other quadrats (IIa and IIb) from which sheep were excluded. There was, however, no obvious difference between the two protected quadrats even though quadrat IIb was accessible to rabbits.

The differences in the vegetation cover of these quadrats are shown in figs. 18 a-c and plate 3.

Even though obvious differences in the plant cover of the quadrats were observed, if the vegetation which was useful to the rabbits was considered by itself, it can be seen that in 1972 the poor winter rainfall produced very little soft vegetation suitable for the rabbits. The sheep were not solely responsible for the food shortage; but they certainly

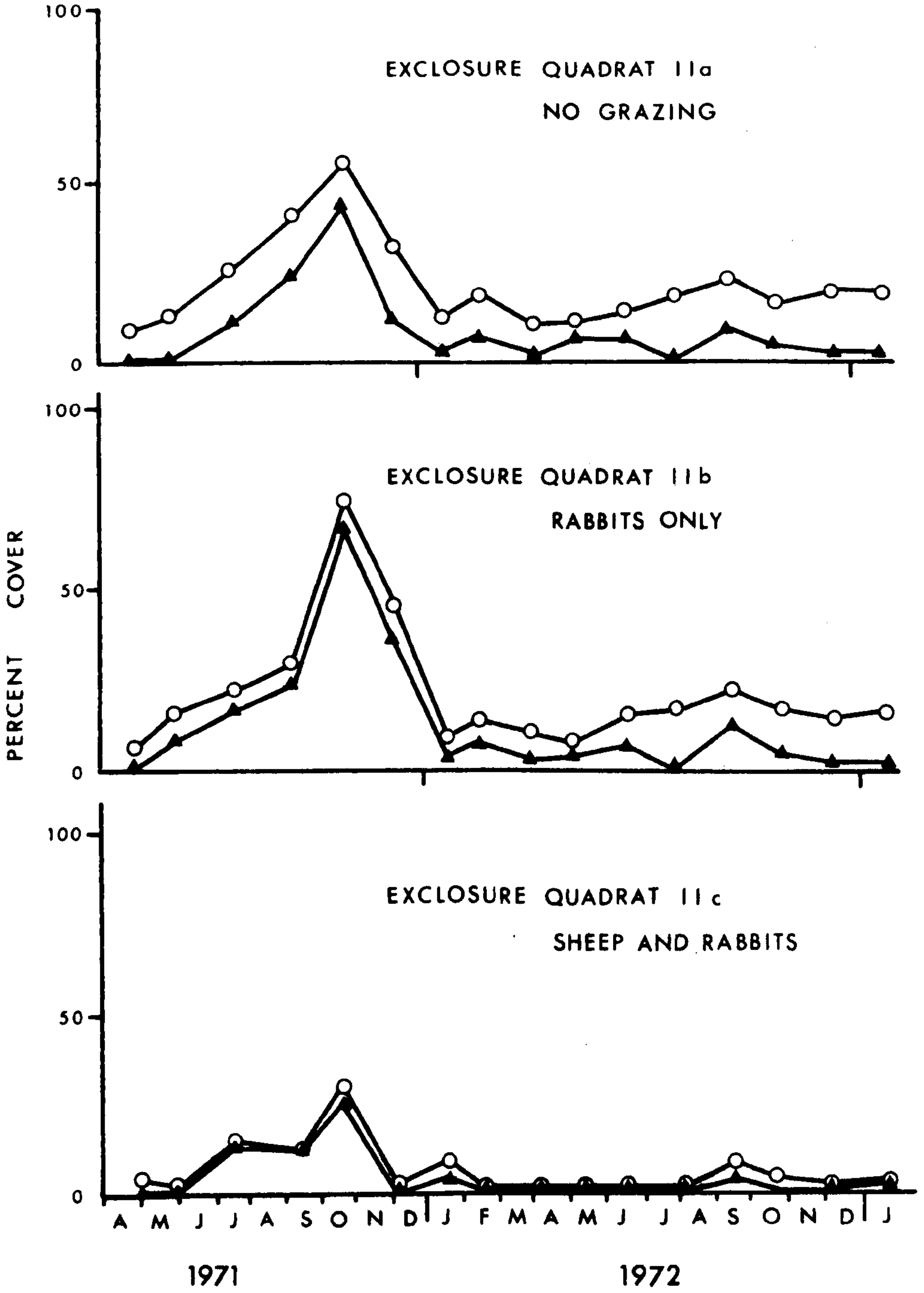

Fig. 18 Plant cover on quadrats subjected to grazing by sheep and rabbits in comparison to a control quadrat. -○- Total vegetation. -▲- Vegetation of use to the rabbits.

PLATE 3 Exclosure quadrat 1 at Witchitie, November 1972. The outer fence only excluded sheep whereas the inner netting fence excluded rabbits as well. Within the exclosure plenty of vegetation remained but sheep had eaten most of the vegetation on the remainder of the study area.

accentuated it.

We can now consider the influence which the changes in the quality and quantity of food had on the rabbits.

4.3 The importance of food and water to the rabbit population

4.31 Introduction

From the information I had collected in the field a great deal was known about the resources available to the rabbit. It was of interest therefore to establish how the rabbit used these resources and ultimately, how the variations in the availability of resources influenced the size of the rabbit population.

Even though some general correlations between the abundance of resources and the size of the rabbit population were apparent (see for instance fig. 17) it was nevertheless rather pointless to seek such simple correlations because some resources were clearly interrelated and their effects on the rabbits far from simple. As an example of this we saw in parts 4.13 and 4.24 that a shortage of food for the rabbit during the summer of 1969-70 was accentuated because some food was apparently too dry for the rabbits to eat. Thus, the availability of food could not be considered alone, but only in conjunction with other resources such as water.

It was clear therefore that I would need to consider all resources together when attempting to assess their influence upon the rabbits, and the best way to do this seemed to be by using a method such as multiple regression analysis in which the changes in the size or productivity of the rabbit population might be related to a number of variable resources. In using this approach the only major problems lay in selecting the appropriate measures of changes in the rabbit population and the availability of resources.

Obviously the population changes suitable for analysis were those associated with the productivity of the population because there was very little information on mortality available except for the rather general data from spotlight counts. Consequently, I thought that indices of productivity such as weights of the gonads or the growth rates of young rabbits might be most useful for analysis.

The appropriate indices for the availability of resources were, however, more difficult to choose. Not only were there several interrelated resources to consider but an added problem arose because very little was known about the efficiency with which the rabbits obtained their food. This was of particular importance because rabbits have the ability to select good food from the pastures available, yet when food is sparsely distributed they may be limited in their range of movements or the time they can spend searching for it. This meant that the estimates of the availability of food and water derived in parts 4.14 and 4.27 would need to be used with care.

In field studies therefore, it seemed worth investigating not only the interactions between resources but also the use the rabbits could make of them. An understanding of these problems might be useful in selecting the appropriate indices of the availability of resources for the multiple regression analyses which were to follow.

4.32 The quality of food eaten by the rabbits

By recording the quality of food eaten by the rabbits at Witchitie then comparing the results with data on the quality of certain pasture species collected at the same time

I hoped to gain some insight into the efficiency with which the rabbit used its resources.

4.321 Methods

At approximately six-weekly intervals small samples of rabbits were shot in the paddocks adjacent to the main study area at Witchitie and data on reproduction, general physical condition and the incidence of myxomatosis were recorded as described by Cooke, 1970.

In addition a sample of digesta from the cardiac region of the stomach of each rabbit was collected and air dried. In the laboratory these samples were ground finely and analysed for fibre content after the method of Van Soest (1963) and for nitrogen according to the method of Conway (1962). Mostly the pasture conditions on the study area were quite similar to those on the surrounding areas, but in late 1972 sheep grazed the study area more heavily than the areas where the samples of rabbits were obtained. Consequently the response of rabbits to the availability of food and water could not be ascertained during the final few months of the study.

4.322 Results

The percentages of fibre and nitrogen in the digesta are presented in table 18. Analysis of variance showed that there were significant changes in the quality of food eaten at different times during the course of the study (table 19) and it was of great interest to see if these changes were likely to affect the rabbit. We shall consider the results on each dietary component separately.

a) Nitrogen.

Only in eight rabbits out of seventy-four was the level of nitrogen in the food below 2% and the average for

TABLE 18. Fibre and nitrogen content of foods eaten by rabbits.

Date	N	Nitrogen (%)	Fibre (%)
15.12.70	5	2.01 ± 0.34	36.9 ± 5.0
4. 2.71	5	2.18 ± 0.25	35.8 ± 2.6
19. 3.71	5	2.46 ± 0.48	37.8 ± 1.5
30. 4.71	5	2.50 ± 0.28	40.9 ± 2.2
26. 5.71	7	3.52 ± 0.62	31.5 ± 3.2
21. 7.71	5	3.04 ± 0.47	32.3 ± 4.6
18. 9.71	5	2.40 ± 0.18	30.8 ± 2.9
27.10.71	7	2.90 ± 0.39	36.3 ± 1.2
19.12.71	5	2.24 ± 0.24	40.4 ± 5.1
19. 1.72	5	2.77 ± 0.41	35.3 ± 6.1
16. 2.72	5	2.42 ± 0.23	38.3 ± 6.8
29. 5.72	5	2.20 ± 0.37	34.9 ± 2.7
5. 5.72	6	2.23 ± 0.32	35.6 ± 1.4
22. 6.72	6	2.18 ± 0.99	40.2 ± 3.5

TABLE 19. Analysis of variance of nitrogen and fibre in food eaten by rabbits at different times throughout the study.

Nitrogen

Source of variation	S.S.	d.f.	M.S.	F	P
Between samples	14.05	13	1.081	6.75	<0.001
Residual	9.59	60	0.160		
Total	23.64	73			

Fibre

Source of variation	S.S.	d.f.	M.S.	F	P
Between samples	723.27	13	55.63	4.23	<0.001
Residual	750.33	57*	13.16		
Total	1473.60	70			

* a few samples were too small to give reliable estimates of fibre.

rabbits obtained on any given date was always above 2% which is equivalent to about 12.5% crude protein. These results meant that the rabbits on the study area usually had ample quantities of protein in their diet despite the periods when digestible foods were apparently in short supply. There remained however the possibility that protein was sometimes of low quality and so may have been important, especially for lactating does or growing youngsters.

b) Fibre.

From the results it was apparent that the amount of fibre in the rabbits' diet often approached the limit of 40%, set in part 4.22 to define the maximum level of fibre rabbits could be expected to tolerate. There was a strong possibility therefore that the rabbits sometimes ran short of energy. Furthermore it was clear that the rabbits ate the more fibrous foods at times when the photographic records showed that food was scarce. This was not to say however that there were simply no better quality foods available because from tables 16 and 18 it can be seen that the rabbits were not always eating the least fibrous species of plants on the study area.

Instead, it seems more likely that the advantages in selecting the best quality foods might be offset by the energy spent or the risk of exposure to dehydrating conditions or predation in obtaining them.

To take this idea further I considered the relationship between the quality of food eaten by the rabbits and the availability of food (see tables 20 and 21). A highly significant correlation was obtained ($r = 0.4862$, d.f. = 64, $P < 0.001$) and the equation fitted to the data had the formula

$$Y = 40.39 - 0.7319X$$

Table 20. Data collected from female rabbits shot near the study area at Witchitie, 1971 - 72.

No.	Body wt. (kg)	Ovary wt. (g)	Spleen wt. (g)	Adrenal wt. (g)	Stomach wt. (g)	Liver wt. (g)	Kidney wt. (g)	Food in stomach (%Fibre)	Food in stomach (%Nitrogen)	Age (Days)	Food (% Cover)	Soil moisture (mm)	Daylength (Hours)
1	1.600	.122	.550	.129	105.0	35.0	13.325	33.2	2.19	197	6.5	- 127.7	13.7
2	1.725	.104	.284	.137	75.0	35.0	12.636	39.8	1.78	221	6.5	- 127.7	13.7
3	1.600	.300	.443	.135	90.0	35.0	12.168	36.7	2.19	185	6.5	- 127.7	13.7
4	1.600	.242	.470	.136	70.0	35.0	11.048	38.7	2.22	234	3.0	40.8	12.3
5	1.575	.277	.517	.178	75.0	40.0	13.091	37.8	2.62	670	3.0	40.8	12.3
6	1.600	.159	.549	.175	65.0	40.0	11.097	36.1	2.99	250	3.0	40.8	12.3
7	1.950	.253	.436	.172	105.0	60.0	16.087	43.3	2.81	702	.5	23.1	10.9
8	1.300	.062	.305	.125	50.0	30.0	8.502	39.2	2.67	180	.5	23.1	10.9
9	1.350	.070	.272	.147	55.0	30.0	10.350	42.9	2.13	173	.5	23.1	10.9
10	1.500	.158	.335	.141	55.0	45.0	11.253	38.4	3.22	264	5.5	11.1	10.2
11	1.550	.127	.406	.163	60.0	45.0	10.982	35.2	3.67	260	5.5	11.1	10.2
12	1.700	.128	.550	.177	75.0	50.0	14.487	29.5	4.54	366	5.5	11.1	10.2
13	1.850	.352	.432	.244	95.0	55.0	16.554	32.5	3.00	309	5.5	11.1	10.2
14	1.675	.217	.461	.224	65.0	55.0	15.179	25.4	4.09	736	5.5	11.1	10.2
15	1.700	.473	.643	.167	85.0	45.0	11.823	26.9	2.83	272	5.5	11.1	10.2
16	2.025	.418	.694	.164	80.0	60.0	17.461	33.9	2.32	1135	8.5	22.0	10.1
17	1.700	.598	.694	.242	75.0	75.0	14.704	31.2	3.30	685	8.5	22.0	10.1
18	2.025	.508	.792	.165	60.0	75.0	18.859	32.4	2.30	194	12.0	24.6	11.9
19	2.000	.701	.489	.207	95.0	75.0	15.862	29.8	2.52	530	12.0	24.6	11.9
20	2.200	.877	.374	.260	70.0	75.0	19.388	34.7	3.30	1062	12.0	24.6	11.9
21	1.800	.411	.590	.194	85.0	45.0	12.675	35.8	2.60	433	8.5	- 22.3	13.0
22	1.400	.050	.448	.146	65.0	45.0	10.132	32.3	2.39	147	5.0	49.2	14.3
23	1.700	.287	.590	.091	65.0	40.0	12.755	46.2	2.45	264	5.0	49.2	14.3
24	1.650	.475	.489	.197	80.0	55.0	16.107	43.8	2.33	397	3.5	100.0	14.3
25	1.500	.338	.612	.153	120.0	45.0	11.452	27.8	3.12	169	3.5	100.0	14.3
26	1.550	.232	.739	.122	90.0	45.0	12.073	39.7	2.35	151	5.8	45.9	13.2
27	1.675	.244	.425	.110	90.0	55.0	14.120	37.5	2.44	145	5.8	45.9	13.2
28	1.675	.134	.356	.145	70.0	55.0	17.331	30.3	2.69	276	8.0	- 18.0	12.0
29	1.775	.209	.417	.153	115.0	60.0	12.360	36.4	2.24	272	8.0	- 18.0	12.0
30	1.700	.196	.439	.149	100.0	55.0	16.840	37.1	2.18	794	8.0	- 18.0	12.0
31	1.700	.133	.325	.162	100.0	40.0	10.854	35.6	2.21	309	8.0	- 18.0	12.0
32	1.650	.161	.835	.221	70.0	45.0	14.670	37.1	2.77	319	7.0	- 45.7	10.9
33	1.900	.247	.416	.166	95.0	40.0	16.785	34.7	2.21	938	7.0	- 45.7	10.9
34	1.325	.057	.538	.149	95.0	35.0	13.501	36.0	2.13	145	2.0	- 66.0	9.8

Table 21. Data collected from male rabbits shot near the study area at Witchitie, 1971 - 1972.

No.	Body wt. (kg)	Testes wt. (g)	Spleen wt. (g)	Adrenal wt. (g)	Stomach wt. (g)	Liver wt. (g)	Kidney wt. (g)	Food in stomach		Age (Days)	Food (% Cover)	Soil moisture (mm)	Daylength (Hours)
								Fibre(%)	Nitrogen(%)				
1	1.550	2.663	.237	.122	75.0	45.0	14.723	35.1	1.58	149	9.0	- 20.0	14.7
2	1.525	2.010	.282	.185	45.0	40.0	12.739	32.2	2.43	670	9.0	- 19.3	14.7
3	1.525	1.155	.417	.271	85.0	45.0	12.313	32.7	2.33	530	9.0	- 19.3	14.7
4	1.775	1.727	.240	.270	90.0	30.0	12.353	38.7	2.49	736	6.5	- 127.7	13.7
5	1.375	1.309	.518	.134	50.0	30.0	11.441	38.7	2.21	185	3.0	40.8	12.3
6	1.500	2.283	.199	.239	55.0	50.0	12.191	37.8	2.24	456	3.0	40.8	12.3
7	1.500	2.805	.300	.208	85.0	40.0	11.352	38.3	2.58	187	.5	23.1	10.9
8	1.750	3.564	.300	.223	70.0	50.0	12.469	40.8	2.31	314	.5	23.1	10.9
9	1.550	4.002	.432	.209	65.0	45.0	11.776	32.3	3.28	234	5.5	11.1	10.2
10	1.600	4.722	.485	.232	50.0	40.0	13.037	31.9	3.14	360	8.5	22.0	10.1
11	1.625	5.014	.203	.269	40.0	45.0	12.684	36.6	2.88	885	8.5	22.0	10.1
12	1.825	4.644	.295	.377	45.0	50.0	13.604	27.3	2.41	670	12.0	24.6	11.9
13	1.400	2.525	.404	.119	50.0	30.0	10.787	37.1	2.32	147	8.5	- 22.3	13.0
14	1.450	3.168	.433	.245	85.0	45.0	10.247	37.3	2.97	182	8.5	- 22.3	13.0
15	1.700	1.506	.300	.262	65.0	40.0	12.156	39.3	1.74	2237	5.0	49.2	14.3
16	1.525	1.375	.300	.113	85.0	40.0	9.385	42.0	2.07	199	5.0	49.2	14.3
17	1.575	2.476	.448	.160	65.0	45.0	14.597	42.1	2.04	175	5.0	49.2	14.3
18	1.400	1.694	.295	.124	80.0	40.0	11.429	31.6	2.74	205	3.5	100.0	14.3
19	1.375	1.357	.359	.164	85.0	45.0	11.548	37.7	3.14	131	3.5	100.0	14.3
20	1.300	2.646	.608	.158	60.0	35.0	10.491	35.1	2.38	163	5.8	45.9	13.3
21	1.400	2.963	.548	.143	65.0	40.0	12.513	42.4	2.66	189	5.8	45.9	13.3
22	1.550	1.601	.507	.145	70.0	40.0	10.957	37.5	2.27	224	5.8	45.9	13.3
23	1.475	3.396	.439	.142	70.0	35.0	10.629	35.0	1.65	221	8.0	- 18.0	12.0
24	1.400	2.735	.322	.165	60.0	35.0	10.965	36.0	2.18	213	7.0	- 45.7	10.9
25	1.500	3.821	.330	.252	80.0	35.0	13.062	35.6	2.23	292	7.0	- 45.7	10.9
26	1.725	2.303	.317	.238	75.0	40.0	13.734	36.8	2.04	541	7.0	- 45.7	10.9
27	1.625	3.762	.378	.277	60.0	45.0	13.337	33.7	1.96	237	7.0	- 45.7	10.9
28	1.725	3.114	.359	.171	75.0	40.0	13.581	40.3	2.46	300	2.0	- 66.0	9.8
29	1.700	2.966	.579	.296	65.0	45.0	12.840	47.0	1.20	300	2.0	- 66.0	9.8
30	1.375	1.059	.375	.140	60.0	35.0	10.214	37.0	2.07	149	2.0	- 66.0	9.8
31	1.550	2.806	.432	.163	55.0	40.0	10.378	36.0	2.13	288	2.0	- 66.0	9.8

where Y = fibre content of food (% dry weight) and X = index of available food (% cover). Data for males and females could be pooled because slopes derived from data for each sex did not differ significantly.

The intercept on the y axis, 40.39% fibre, was consistent with the hypothesis that rabbits could not cope with foods which contained more than about 40% fibre. If this level of fibre, selected initially from the literature, had been unrealistic, the rabbits should have eaten the more fibrous foods available or survived during periods when food was judged to be scarce.

My results had much in common with the results of Hamilton, Hutchinson, Annis and Donnelly (1973) who described some aspects of the feeding behaviour of grazing sheep. These authors found that the digestibility of the food eaten by the sheep depended largely upon the amount of food available although when the availability of food increased beyond a certain level the quality of food eaten approached an asymptote.

In a similar experiment to that of Hamilton et al. (1973) Arnold and Dudzinski (1967) had shown that as the availability of food increased, the dry-matter intake of grazing sheep also increased but approached asymptotic values if food was abundant.

The data from the two experiments suggested therefore that the amount of food eaten by sheep and the quality of food they ate would be strongly correlated. Subsequently, a search through the relevant literature showed that such a correlation had frequently been observed in hand fed sheep (e.g. Rossiter, 1966). Sheep which were given poor quality foods ate relatively little compared with the amount of good quality food they would eat. Their behaviour was therefore similar to that described for rabbits by Voris et al. (1940) as detailed in part 4.22.

The similarity in the results obtained for two species of grazing mammals was encouraging, and enabled a general conclusion to be reached. When food becomes scarce it becomes uneconomical for grazing mammals to seek the most digestible components in the pastures but instead smaller amounts of poorer quality food are eaten.

Because there was no indication that the quality of food selected by the rabbits at Witchitie began to approach an asymptote as the availability of food increased, it could be argued that the abundance of food probably influenced the quality of food eaten at all times during the study.

Of several conclusions which could be drawn from the results the most important was the fact that the availability of food always had a strong influence on the quality of food eaten. This meant that the multiple regression analysis could be greatly simplified because instead of using measures of the fibre or energy content of food, the index of the availability of food would be sufficient. The nitrogen content of the food could also be deleted, not only because the nitrogen content of the foods the rabbit ate was influenced by the availability of food but also because the rabbits were apparently never short of nitrogen.

In short, there was no need to use measurements of the quality of food eaten to allow for variable use of the resources by the rabbit because the availability of food proved to be of over-riding importance.

On theoretical grounds too, it seems wise to avoid using measurements of the quality of food eaten by the rabbits as variables in multiple regression analyses. These measurements were not strictly independent of the data on reproduction collected at the same time and although significant regressions between the protein content of food and, say, fecundity might be obtained, there would be no way of determining whether the rabbits were breeding because they were eating good quality food or whether the demands of breeding made it necessary to seek good food. On the other hand, the index of the abundance of food provided a completely independent variable.

4.33 Productivity of the rabbit in relation to the abundance of food and water

Organs such as the gonads, stomach, liver, adrenals and kidneys were collected from the small samples of rabbits shot during each visit to the study area. They were preserved in 10% buffered formalin and later weighed in the laboratory. These organs varied considerably in weight from one sample to the next and the differences were thought to result from environmental changes because Casperson (1968) in a similar study found that the weights of organs and other physiological parameters were far more variable at a site in arid N.S.W. than at sites of mediterranean, sub-tropical and sub-alpine climate where environmental changes were less severe.

As far as the data collected from the rabbits at Witchitie were concerned the weights of gonads were of greatest importance because they could be readily interpreted in functional terms to provide a measure of the productivity of the population. It had been found, for example, that male rabbits with testes exceeding 2.0 g in weight were usually fertile (Cooke, 1970). Similarly, for female rabbits, ovaries weighing more than 150 mg usually contained well developed follicles or corpora lutea. Furthermore, does were found to have ovaries weighing at least 300 mg whenever kittens were emerging from the nests and so it could be concluded that this was the minimum weight of ovaries with properly developed, active corpora lutea of lactation.

Regression analysis of the weights of gonads upon a number of environmental variables could therefore be used to show whether these variables influenced productivity. The weights of other organs including the stomach, liver, adrenals, kidneys and spleen could also be used in this way although the results obtained would be more difficult to interpret in functional terms.

The environmental variables most likely to influence the ability of the rabbits to reproduce were considered to be

X_1 availability of food (% cover)
X_2 availability of water (soil moisture, mm)
X_3 age of rabbit (days)
X_4 day length (hours)

Whereas the first two variables need no explanation, age and daylength were included because they were known to have some influence upon breeding in rabbits. Myers and Poole (1961) found, for instance, that older does bred more readily and were more fecund that young adults in the same enclosures. It had also been shown experimentally by Walter, Martinet, Moret and Thibault (1968) that daylength could influence reproduction in both male and female rabbits. Decreasing daylength caused the testes of rabbits to increase in size so that the males would be fertile when the females became reproductively active partly as a result of the stimulus provided by increasing daylength in spring.

The multiple regression analyses were done on the CDC 6400 computer of the University of Adelaide using the multiple regression analysis sub-routine (M.R.A.). The input data is given in tables 20 and 21.

4.331 Results

a) Weights of gonads.

The availability of food, availability of water and age were found to have a significant influence on the weights of ovaries (Y_o); the best estimate is given by the formula

$$Y_o = -0.024659 + 0.037103X_1 + 0.001344X_2 + 0.000188X_3$$

with a standard error, S.E. $Y_o = \pm 0.052910$

The analysis of variance and significance tests for the regression coefficients are given in table 22.

Likewise, testes weights (Y_t) were best explained by the availability of food and water but daylength replaced age as a significant variable i.e.

$$Y_t = 8.055235 + 0.232454X_1 + 0.006863X_2 - 0.547538X_4$$

$$\text{S.E. } Y_t = \pm 0.920259$$

Tables 22a and b also give the regression coefficients in standard measure (β) so that the variables can be ranked according to their importance in determining the weights of the gonads. In male rabbits for instance we see that daylength is of greatest importance in determining the weights of the testes. Food appears next in order of importance and the availability of moisture has a very small role. Likewise, food is the most important variable which affects the weights of ovaries, whereas age and then the availability of water follow in order of importance.

TABLE 22.

a) Ovary weights.

Variate	Regression coefficient b	β	S.E.	*t*	*P*
X_1 Food available	0.037103	0.5150	0.008191	4.53	<0.001
X_2 Water available	0.001344	0.3401	0.000422	3.18	<0.001
X_3 Age	0.000188	0.3716	0.000087	2.16	<0.05

Analysis of variance

Source of variation	S.S.	d.f.	M.S.	F	P
Regression	0.718907	3	0.239636	14.57	<0.001
Residual	0.493405	30	0.016447		
Total	1.212312	33			

b) Testes weights.

Variate	Regression coefficient b	β	S.E.	*t*	*P*
X_1 Food available	0.232454	0.6100	0.044373	5.23	<0.001
X_2 Water available	0.006863	0.3347	0.002559	2.68	<0.02
X_4 Day length	-0.547538	-0.8950	0.079909	6.85	<0.001

Analysis of variance

Source of variation	S.S.	d.f.	M.S.	F	P
Regression	23.744444	3	7.91480	18.75	<0.001
Residual	11.392124	27	0.421931		
Total	35.136568	30			

Although the relationship between gonad weight and the availability of food seems straightforward, the results dealing with the availability of water must be interpreted with caution. Water shortage could either affect the rabbits directly by limiting their food intake (see part 4.13), or alternatively the rabbits might respond to changes in the quality of pastures as the soil dried. Actually, this alternative seems most likely because from figure 19 in which the weights of ovaries (mg) are plotted against the availability of soil moisture (mm), it can be seen that female rabbits were unable to reproduce successfully if the soil dried out. The end of breeding could only have been associated with cessation of plant growth because many pasture species still contained plenty of water at such times and remained succulent well into the periods of drought (part 4.143).

These observations from Witchitie generally support those of Myers and Poole (1961) and Stodart and Myers (1966) who showed that growing vegetation was necessary for reproduction in rabbits of both sexes.

Even though the analyses presented in this section were confined to sexually mature rabbits with a gutted body weight of 1 kg or more, age was nevertheless found to bear a significant influence on the fecundity of the does. This was in agreement with conclusions drawn from the enclosure studies of Myers and Poole (1961).

Finally, the importance of daylength is worth considering. By responding to a proximate factor such as daylength the male rabbits can clearly become fertile in advance of the female rabbits which normally come into oestrous when the autumn rains cause new plant growth. Even so, daylength is a

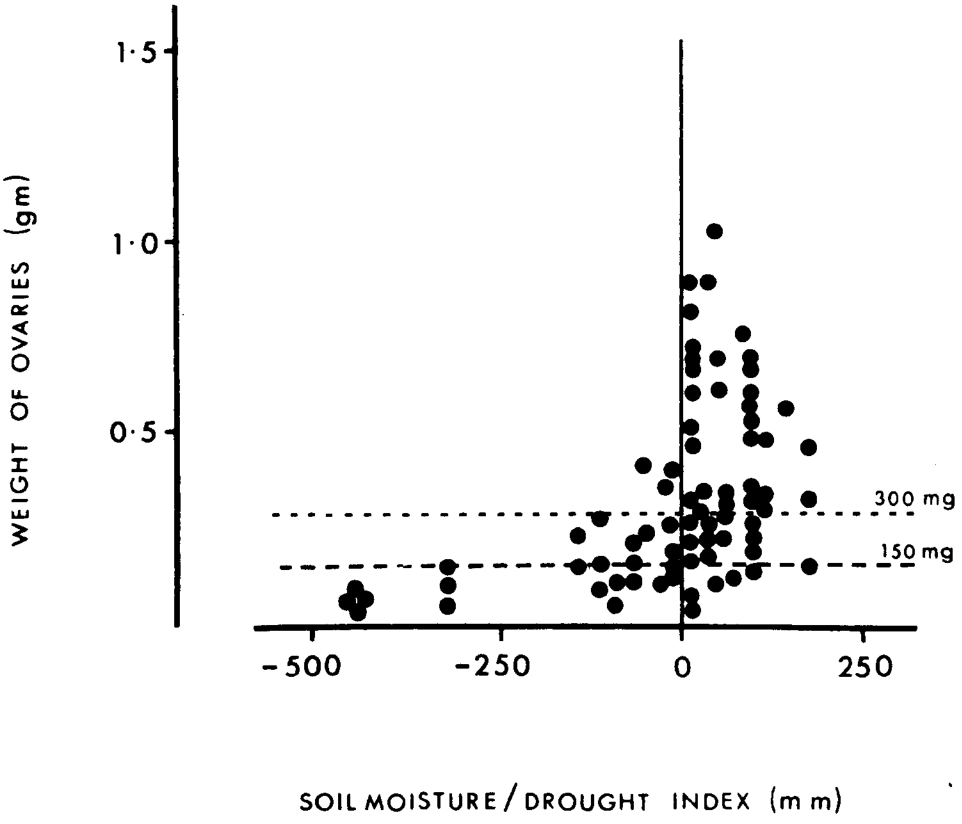

Fig. 19 The weights of ovaries in relation to the availability of soil moisture and the severity of drought. The limit of 150 mg is the minimum weight of ovaries at ovulation. Ovaries with fully-developed corpora-lutea of lactation weigh at least 300 mg.

stimulus which acts with equal intensity at a given time each year and if we wish to know why male rabbits are fertile for a longer period in some years than in others, we must turn to the availability of food or water to explain these seasonal differences.

In general, the most important factors which affected the reproductive capacity of the rabbit population were those which affected the female rabbits, i.e. the abundance of food, the age structure of the population and, indirectly, the availability of water.

b) Weights of organs other than the gonads.

Although data on body-weight and the weights of the spleen, adrenals, stomach, liver and kidneys were analysed using multiple regression methods and the weights of some organs were found to be correlated with the availability of food or water, age and daylength, I could find no way of demonstrating that these weight changes were associated with the productivity of the population. Although there are some interesting possibilities, such as relating changes in liver weight to changes in metabolism (see Chevillard and Mayer, 1939) there is little point in speculating about the observed correlations between organ weights and environmental variables in the absence of detailed experimental work.

One final aspect of successful reproduction remained for investigation. It was necessary to consider the requirements of young weaned rabbits and the factors which might prevent them from growing to maturity. Data from young rabbits which had been live-trapped on the study area at Witchitie were used for this purpose.

4.34 Growth rates of young rabbits

Southern (1940) showed that irrespective of their age, immature rabbits grew at a fairly constant rate (g/day). Similar observations at Witchitie suggested that rabbits up to 1.2 kg in weight grew rapidly but there were no obvious differences in the absolute growth rates between rabbits of different sizes. Consequently, by confining analysis to rabbits which had not reached 1.2 kg at the time of recapture, growth rates could be considered independently of body-size. To obtain regressions of these growth rates upon the environmental variables I had to use mean values of the availability of food and water for the periods during which the growth rates were recorded.

4.341 Results

Data on growth rates, body size and the availability of food and water are given in table 23.

The index of the availability of food proved to be the only important variable which influenced growth rates. The regression obtained was

$$Y = 0.257 + 0.952X$$

where Y = growth rate (g/day) and X = availability of food (% cover) ($r = 0.7236$, d.f. = 25, $P < 0.001$).

Even by using multiple regression analysis none of the other variables such as the availability of water were found to have any significant effects on growth. This was a little surprising because Stodart and Myers (1966) suggested that young rabbits benefitted greatly from the availability of growing food, and earlier Dudzinski and Mykytowycz (1960) had shown that the growth rates of young rabbits increased shortly after effective rains fell and the pastures responded. One

TABLE 23. Data on growth rates of young rabbits compared with environmental variables.

Animal No.	Growth Rate (g/day)	Mean Weight (gm)	Water Available (mm)	Food Available (% cover)
1	10.16	675.0	-.7	9.6
2	7.76	450.0	-.7	9.6
3	10.00	450.0	-8.6	10.8
4	7.50	312.5	42.9	1.0
5	13.04	725.0	3.8	11.4
6	9.38	450.0	42.9	14.3
7	13.24	487.5	42.9	14.3
8	3.13	837.5	44.2	8.5
9	7.41	650.0	-38.1	9.6
10	14.28	775.0	40.9	14.3
11	19.44	687.5	40.9	14.3
12	10.94	912.5	42.9	14.3
13	21.43	650.0	42.9	14.3
14	1.09	1050.0	-134.6	5.8
15	4.94	925.0	-28.7	7.6
16	2.38	1050.0	0.0	.1
17	8.04	987.5	-38.1	8.1
18	5.00	962.5	-28.7	7.6
19	6.38	887.5	-28.7	7.6
20	8.87	725.0	-7.9	9.3
21	16.47	762.5	36.8	13.5
22	8.84	712.5	-84.1	7.1
23	7.07	850.0	-84.1	7.1
24	7.14	1075.0	31.2	13.1
25	20.83	1062.5	40.9	14.3
26	11.25	962.5	42.9	14.3

possible explanation for the lack of correlation in my data lies in the fact that very few young rabbits were recaptured after periods of moderate drought and most growth rates were therefore recorded during times when soil-moisture was adequate for plant growth.

The initial assumption that growth rates would be independent of body size was tested by means of a regression of the observed growth rates against the mean weight of the rabbits during the periods when growth was measured. No inverse relationship was found as might have been expected if the rabbits grew more slowly as they became older. Consequently, the assumption was valid.

5. DISCUSSION

From the foregoing results some general conclusions have been drawn about the influence of the availability of water and food on a rabbit population. However, a number of issues are raised by the results; some, though incidental, are nevertheless promising lines for further research. The other problems raised show gaps in our knowledge of factors which might act to limit the size of animal populations.

5.1 The availability of water

The results of a field experiment which was begun to try to discover the causes underlying a population crash suggested that lack of water may have been partly responsible. Rabbits which did not drink supplementary water lost more weight and probably had reduced chances of survival compared to the rabbits which drank.

The shortage of water was caused by a combination of drought and overgrazing of the succulent, drought-resistant pasture species by unusually large numbers of rabbits. Consequently, with the normal source of water depleted the rabbits turned to the woody perennials and, although they obtained adequate water, they were forced to eat such fibrous, indigestible vegetation that they probably had great difficulty in obtaining enough energy. Presumably, by drinking supplementary water the rabbits could eat enough dry food which was sufficiently digestible to enable them to maintain their bodyweight.

In most years, rabbits do not require supplementary water because succulent, drought resistant plants persist well into the hottest months (part 4.144).

The rabbit is able to conserve water by using a burrow

(Hayward, 1961); nevertheless its water requirements are high and, as shown in part 4.13, the rabbit generally requires food containing 60% water or more. The rabbit's kidney does not concentrate urine strongly, for the maximum concentrations were in the order of 2,000 mosm/l.

In contrast to some other small mammals the rabbit seems at first ill-adapted for exploiting the arid zone. Consider for instance, some of the desert rodents which produce highly concentrated urine reaching 6,000 mosm/l and eat air-dry foods which contain only 10% free water. However, the niche of the rabbit as a small grazing herbivore must be taken into account and comparisons with seed-eating desert rodents are tenuous to say the least.

The rabbit which grazes fairly fibrous vegetation must apparently select plants which contain less than 40% fibre if it is to meet its energy requirements (see parts 4.22 and 4.322). Consequently, rabbits at Witchitie almost certainly had a relatively high water intake because the properties of the common, drought-resistant plants in this area are such that plants which contain less than 40% fibre almost invariably contain more than 60% water. The relationship between the water and fibre contents of the four most common species of plants at Witchitie appears in figure 20.

Because the rabbits' food normally contains a high proportion of water, it follows that kidneys of relatively poor concentrating ability are of no disadvantage: further, there could be little selection for a more powerful kidney under these circumstances. The niche of the rabbit therefore contrasts strongly to those of the desert rodents which exploit dry, highly digestible foods. It would be far more

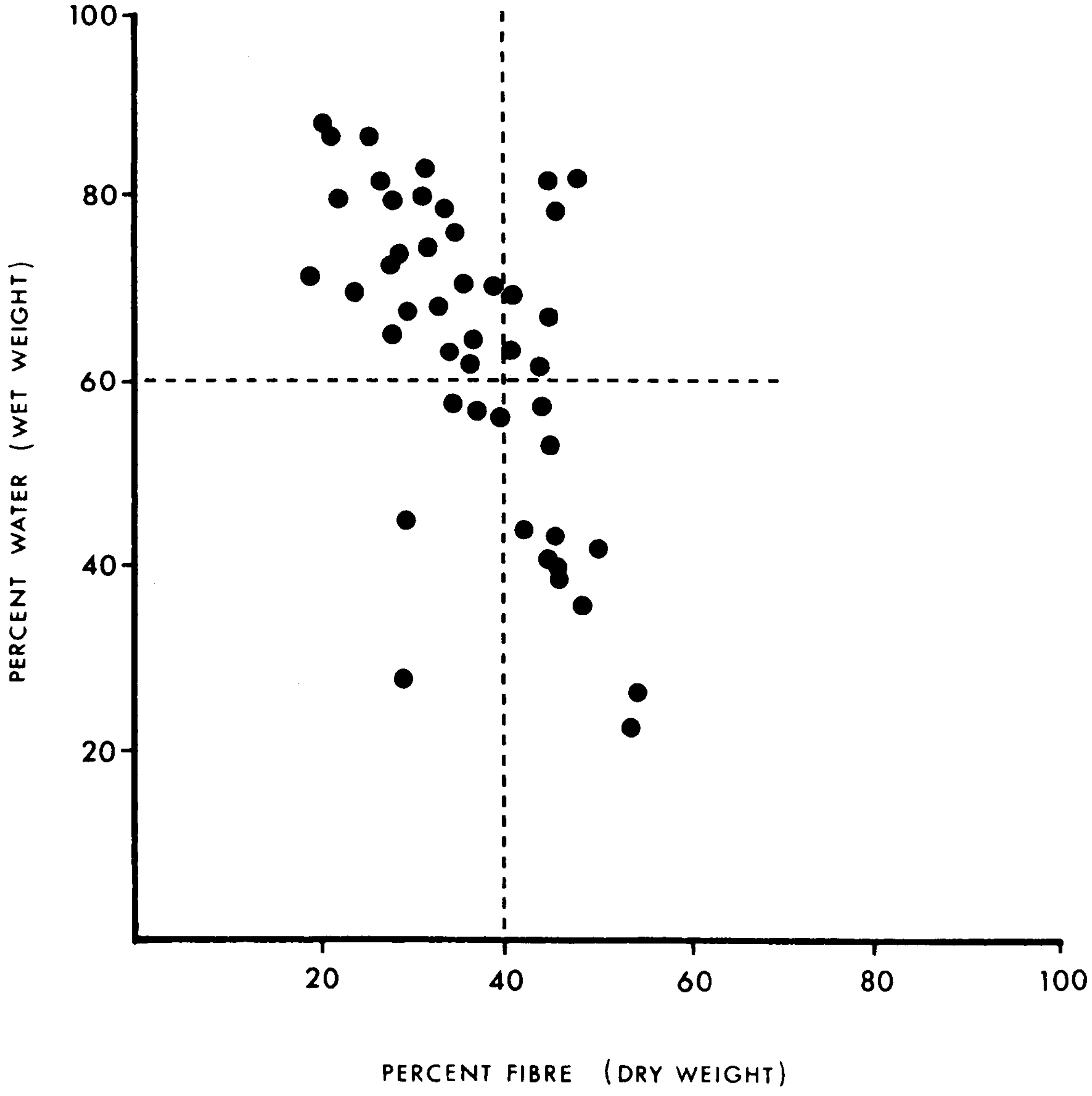

Fig. 20 The relationship between the fibre and water contained in the common pasture species at Witchitie.

useful to compare the rabbit with rodents like the desert-dwelling pack-rat (*Neotoma* sp.) which rely on green, succulent foods such as cactus (Schmidt-Neilsen, 1964).

One interesting observation which arose from the experiments in which rabbits were deprived of water (part 4.13) was the discovery that the osmoconcentration of the urine did not differ between the three groups of rabbits given different amounts of water daily. This was all the more surprising because in the group which was most severely restricted the nitrogen concentration of the urine was considerably higher than in the other groups. Although I made no attempt to explore this problem because it was peripheral to my main arguments, it seems that the osmoconcentration of the urine differs from what was expected from the known concentrations of nitrogen and electrolytes. The osmoconcentration was higher than expected for the rabbits given ad lib water but lower than expected for the rabbits deprived of adequate water. Possibly these irregularities might be explained by the large quantities of precipitate, which appears to include calcium carbonate, found in the urine of the rabbits deprived of water. Further work should be done on this problem, especially since other small, grazing herbivores such as the guinea pig, *Cavia* sp., and the pack-rat, *Neotoma* sp., also produce large quantities of urinary precipitate. Schmidt-Neilsen (1964) has suggested that excretion of calcium ions in the urine might facilitate the excretion of oxalic acid and in this respect the rabbit is known to absorb calcium from the gut quite well in comparison to other animals such as the sheep (Yoshida et al., 1968; Braithwaite, 1972). Furthermore, many of the plants eaten by the wild rabbit, the chaenopods for instance, are likely to contain considerable amounts of oxalic acid.

Apart from the affects of water shortage during the occasional severe summer, another more important way in which water influences the rabbits is through its affect on the availability of growing vegetation. Rabbits must have a good supply of growing vegetation if they are to breed successfully (Poole, 1961; Stodart and Myers, 1966), and so rainfall and evaporation clearly determine the periods when reproduction can occur.

It would be interesting to determine precisely the components in growing vegetation which are essential for the rabbits to breed. Vitamin A or its precursor, carotene, has been suggested (R.L. Hughes, pers. comm.) but a survey of the literature suggests that even dry hay would contain enough carotene to enable ovulation and to meet the requirements of a lactating doe despite the fact that carotenes are not converted to vitamin A very efficiently (Moon, 1939a; Lamming, Salisbury, Hays and Kendall, 1957a,b; Millen and Dickson, 1957; Crampton and Lloyd, 1959; Coates, Gregory and Thompson, 1964). Because the rabbits at Witchitie eat green foods rather than hay or dead plant matter it might be anticipated that their diet would never be deficient in carotene.

Many substances likely to be of importance in the diet of the rabbit are known to increase in plant cells whenever growth occurs (see for example Moon, 1939a). Soluble carbohydrates, nucleic acids, organic phosphates and amino-acids all become more readily available to herbivores. As mentioned in part 6.1 of the Appendix, there is some evidence that the diet of rabbits may at times be deficient in certain essential amino-acids and so it would be interesting to see whether the amino-acid requirements of pregnant or lactating rabbits can be met only when actively growing pasture is plentiful. This possibility warrants further investigation.

5.2 The abundance of food

From the results of feeding trials carried out on laboratory rabbits by Voris et al., (1940) I broadly defined the food of the rabbit as 'plants which contain less than 40% fibre'. Although this definition was very approximate it was not refuted by field observations. Rabbits rarely ate food which contained on average more than 40% fibre, furthermore the rabbit population fell whenever plant species which contained less than 40% fibre became scarce.

Because the fibre content of food is inversely related to the amount of energy a rabbit can obtain from it, the level of 40% fibre indicates those foods which contain barely enough digestible energy to maintain a rabbit.

The inability of rabbits to digest fibre readily is of great interest firstly from a general physiological point of view and secondly because it leads to some general ideas which might provide a basis for the study of the importance of food to small mammals in natural populations.

Fibre presents a problem for grazing mammals because fibrous cell walls increase the bulk of the diet and protect the cell contents from digestion. However, enzymes from symbiotic bacteria can break down cellulose and many mammals have specialized digestive systems so that full advantage is taken of bacterial fermentation of fibre.

The ruminants are sometimes regarded as being the most specialized herbivores in this sense and they are also regarded as being the most efficient at digesting fibre. Yet specialized physiology is not the only important factor which determines how efficiently fibre will be digested. Hungate, Phillips, McGregor, Hungate and Buechner (1950) argued that body size was also important. They found that small ruminants had relatively high metabolic rates per unit weight but their rumen occupied about 10-11% of their total body size; the same relative proportion as found for larger ruminants. It was obvious that to meet their high energy requirements the small ruminants would need to maintain a relatively high rate of fermentation. They could achieve this by selecting highly digestible foods or by passing foods through the digestive system quickly so that only the most rapidly fermented components of the diet were used.

Actually, the proportion of the body occupied by the gut is remarkably constant for a number of species of mammals. It amounts to 15% by weight in the rabbit and is therefore similar to that found for kangaroos (Tribe and Peel, 1962) and for sheep (Dr B. Howard, Waite Institute, pers. comm.). The ideas of Hungate et al. (1959) gain further support from the general correlation between body size, the rate of passage of food, and the ability to digest fibre found for several species of grazing mammals including rabbits, quokkas and kangaroos, and ruminants such as goats, sheep and cattle (Voris et al., 1940; Calaby, 1958; McIntosh, 1966; Crampton, Campbell and Lange, 1940; Castle, 1956). Possibly, ruminants may not be greatly superior to other herbivores in their ability to digest fibre if body size is taken into account.

On a standard diet such as oaten chaff, small herbivores pass food through the digestive tract much more rapidly than larger species. About half the residue from food eaten by a rabbit can be recovered from the faeces within 24 hr (Yoshida et al., 1968) whereas in large herbivores such as sheep or kangaroos foods are retained in the gut for 2-3 days on average (McIntosh, 1966).

These comparative studies would therefore indicate that for the physiological reasons outlined above, small mammals cannot use fibrous foods as efficiently as larger mammals. Possibly the limit to the size of the digestive tract of small mammals is set by physical factors such as their need for mobility or agility. In any case it might be anticipated that small grazing mammals in general would select foods low in fibre. Indeed, Voris et al. (1940) found that rabbits often refused to eat fibrous foods and Calaby (1958) found that quokkas would not eat an experimental diet of fibrous oaten hay. When small mammals can be induced to eat relatively fibrous foods the ingesta is likely to be passed through the gut so rapidly that fibre would be poorly digested.

It follows that in studies of the availability of food for small grazing herbivores such as rabbits, rats or voles the fibre content and preferably the digestible energy content of the foods must be considered. Very small rodents are likely to digest fibre so poorly that in normal mixed pastures only a few plant species would provide suitable food. Soft dicotyledons, i.e. forbs, which are generally much less fibrous than the grasses are likely to be the most important foods for small mammals. This might explain why rodents often reach high numbers in newly established plantations or overgrazed rangelands where weedy dicotyledons colonize the disturbed soil and persist for a number of years until the trees grow or the grasses again become dominant (Smith, 1940; Vohries and Taylor, 1933; Osborn, 1942; Chitty, 1952).

A small mammal may, if good quality food is scarce, need to eat some of the less digestible components in a pasture. This was suggested by the observation that the quality of food eaten by the rabbits was strongly influenced by the amount of food available. It was obvious that the rabbits did not always eat only the least fibrous plant species. In tables 16 and 19 it can be seen for instance that during November 1970 both *Atriplex eardleyi* and *Bassia lanicuspis* were much less fibrous than the plants the rabbits actually ate. A relationship of this type might arise if the advantages of eating the highest quality foods were offset by the energy expended in obtaining them or the risk of exposure to dehydrating conditions or predators.

Even among sheep, it is found that poorer quality food is eaten as herbage in general becomes scarce (Hamilton et al., 1973). Again the benefits of eating the most digestible plants appear to be offset by the energy or time spent in seeking them out.

This relationship between the availability of food and the quality of food eaten can probably be regarded as general among grazing mammals. It must certainly be carefully considered when assessing the availability of food for populations of small mammals because it indicates how efficiently they can use that resource.

At Witchitie food shortages occurred with sufficient frequency to be the most important factor affecting the size of the rabbit population. Weather and grazing herbivores such as insects or sheep usually determined the availability of food although on one occasion the rabbits themselves ate most of the food available. Supporting evidence from Koonamore vegetation reserve showed that prior to the introduction of myxomatosis in 1952 rabbits may have become sufficiently numerous to eat most of the available food one year in every five (Hall et al., 1963; Cooke, 1970). However, in areas where rabbits compete with sheep, and since myxomatosis has become established, the rabbits probably reach high levels far less frequently than the data from Koonamore would suggest.

In general it seems that the rabbit population at Witchitie was ultimately limited in size by the availability of food but the ceiling imposed on the population varied greatly from year to year. Although the rabbits always used some of the food the amount they ate was normally an insignificant factor in the food shortages which occurred.

In terms of the general theory proposed by Andrewartha and Birch (1954) to explain the numbers of animals in natural populations, the availability of food can be seen to influence all four of the parameters considered to be important.

Firstly it determined to some degree the timing and extent of mortality and consequently the numbers of rabbits which survived a period of food shortage to form a nucleus for the next population increase. Secondly it determined the rate at which the population could increase because it affected fertility, fecundity and weaning and through its effect on growth rates it determined how rapidly the young could grow to enter the breeding population. Thirdly, in conjunction with the availability of soil-moisture it determined the duration of periods suitable for breeding. Fourthly it set the ceiling to which the population might rise before being limited by food shortage.

However, before suggesting that food could entirely account for the size of the rabbit population it is necessary to emphasise that a major deficiency of this study is a complete lack of knowledge of the actual causes of death of the rabbits. Most importantly it is not known whether some factor such as predation might act in conjunction with food shortage to hold rabbits below the levels they might reach if checked by food shortage alone. It is worth considering this possibility briefly.

5.3 The possible effects of predation or disease on population size

To appreciate the potential effects of predators and pathogens it is convenient to again refer to the model proposed by Andrewartha and Birch (1954). There are two points in the model where predators or pathogens could readily exert an effect on the size of a rabbit population. Firstly, if predators or disease removed most of the young produced during a favourable period they could prevent a population increase. Secondly, they could determine the numbers of rabbits left at the end of a population decline and consequently the nucleus left for the next population increase.

Because the rabbit population at Witchitie increased quite rapidly whenever growing vegetation was plentiful it seems that predators were unable to substantially reduce population increases. In fact the age structure of the population suggested that large numbers of young were normally recruited into the breeding population each year. It follows therefore that the most likely influence of predation or disease would be in determining the size of the residual population at the end of a population decline. Since food shortage is obviously important in the timing of such declines, it is worth exploring the possibility that disease and predation could act in conjunction with food shortage. This appears likely in the case of predators because rabbits apparently become more vulnerable to predators when they are short of food (J.Gibb, pers. comm.). Despite the low numbers of predators seen on the study area at Witchitie they may nevertheless have been numerous relative to the rabbits whenever the rabbit population fell. At times there were probably less than twenty rabbits on the study area so that even if the predators took only one or two occasionally they might substantially reduce the number of rabbits which survived until conditions again became favourable for increase.

There is clearly a need to know more about the predators at Witchitie. This includes avian predators such as Ravens (*Corvus* spp.) and Wedgetailed Eagles (*Aquila audax*) as well as the feral cat and the fox.

Myxomatosis, like predation, also seems likely to act in conjunction with food shortage and there are several good reasons for investigating this further. Firstly, it is the general concensus of landholders in the area about Witchitie that rabbits are not as ubiquitous as they were before myxomatosis became established. The regeneration of native plants at Koonamore vegetation reserve provides even better evidence of this because rabbits have not destroyed seedlings so consistently in recent years as in the past (M. Crisp, Department of Botany, University of Adelaide, pers. comm.). Yet, as seen in part 1 the peak of rabbit numbers at Witchitie in 1969 was probably as great as any previous peak, and this suggests that even though myxomatosis might hold rabbits well below their former numbers in most years its importance and effect on the population could vary from year to year.

Secondly, Williams, Parer and Dunsmore (1972) have recently proposed that rabbits can carry latent myxoma virus which can be activated if the rabbit is stressed, and then spread to susceptible rabbits to initiate an epizootic. Although the stresses mentioned by these authors were hormonal, thermal and social, and no specific mention was made of food shortage, we have seen in part 4.331 that the hormonal changes that occur as breeding ceases are in fact associated with changes in pasture quality. Furthermore food shortage itself is likely to provide acute stress which might impair resistance to a pathogen. It would be of value to test this possibility by experimenting with caged wild rabbits known to have recovered from myxomatosis.

The third reason for investigating the possibility of a synergistic relationship between changes in food quality and the occurrence of myxomatosis is largely theoretical. Rendel (1971) showed that at current rates of morbidity, 80% or so, it was necessary to postulate a mortality of infected rabbits of the order of 25% to explain the current resistance of rabbits to field strain virus. However, in mediterranean-type regions mortality caused by myxomatosis is considered to be less than this; possibly only 10% or so, and my own observations at Belton and Witchitie also suggest that mortality must have been very low during an epizootic which occurred when food was abundant (Parer and Williams, 1972; Cooke, 1970). Nevertheless Rendel's theoretical considerations might not necessarily be wrong if myxomatosis was more lethal when food was scarce. If about 40% of the infected rabbits died when food was short an average annual mortality of about 25% might be attained despite the low death rate from myxomatosis in seasons when food was abundant.

Unfortunately, the blood samples and other data on the incidence of myxomatosis collected at Witchitie are not good enough to determine whether myxomatosis is associated with food shortages.

Referring again to Andrewartha and Birch's model it can be seen that if myxomatosis reduced the rabbit population by, say, another 40% on top of the mortality imposed by food shortage the size of the population at the end of the next favourable period would be correspondingly reduced. In short, myxomatosis could greatly affect the total numbers of rabbits on the study area without necessarily killing a large proportion of the rabbits produced each year.

5.4 General conclusion

To summarize, it was apparent that the availability of water was not normally of direct importance to the rabbits but it had a marked influence in determining the periods of plant growth and the availability of suitable food which the rabbits needed for breeding. The abundance of food probably had the greatest influence of any resource upon the rabbits because it directly affected reproduction, growth and apparently survival. However, before any generalizations can be made about these results it must be remembered that the importance of food to rabbit populations remains largely unknown. In other arid areas or in areas of higher rainfall other factors may be more important and limit rabbit populations at levels where they could not eat much of the available food. Nevertheless the results of the study at Witchitie provide a basis for assessing whether food should be considered as a significant environmental variable elsewhere in the rabbit's range.

The availability of food is determined by two major factors, namely, weather and grazing by herbivores. But although the effects of weather seem reasonably predictable, it is at present clear only that other herbivores may strongly influence the rabbit by competing for limited supplies of food. The actions and the influence of competitors remain quite unpredictable. Likewise the probable influence of predators and pathogens in determining the size of rabbit populations remains unknown. The direct and indirect effects of other animal species upon the rabbit population therefore remain among the most difficult problems in understanding the fluctuations in the numbers of rabbits in natural populations.

6. APPENDIX

6.1 Review of the digestive physiology of the rabbit

Before beginning a study on the food of the rabbit, a review of the literature on the digestive physiology of the rabbit was essential. Although much of the rather formidable literature on digestion in the domestic rabbit had little relevance to the ecology of wild rabbits I attempted nevertheless to review the more important research so that the nutritional requirements of the rabbit might be defined more carefully. This enabled me to decide those dietary components most likely to be in short supply for wild rabbits and consequently the most useful lines of research to follow in field studies.

The major problem in interpreting the availability of energy and nitrogen in pastures arose from the rabbits' reliance on coprophagy as a normal part of digestion. There were two reasons for this. Firstly, it was stated that coprophagy in conjunction with bacterial fermentation in the caecum was important in determining the amount of energy and protein obtained from foods (e.g. Thacker and Brandt, 1955). Secondly, Myers (1955) had shown that the rabbit apparently recycled a greater proportion of its food when eating poor quality pasture than when growing pasture was available. Thus it seemed that coprophagy might obviate or at least reduce the impact of apparent shortages of nitrogen and energy in the pastures.

To understand the importance of coprophagy it was necessary to know certain details, especially the proportion of digesta which was recycled, and the extent of bacterial fermentation. However, early research on digestion in the rabbit left these problems unresolved mainly because soft and hard faeces were thought to originate by quite different processes and the role of fermentation in each process was unclear. For example, Thacker and Brandt (1955) found that soft faeces were similar to caecal contents in composition and concluded that these must originate in the caecum. On the other hand these authors thought that hard faeces were formed from digesta which passed through the proximal caecum so quickly as to avoid fermentation. Huang et al. (1954) had shown however that absorption of nutrients from the colon could account for the two types of faeces and proposed that soft faeces were formed when the caecum contracted and forced digesta through the colon quickly enough to avoid absorption. Like Thacker and Brandt (1955), Huang et al. considered that a proportion of digesta effectively by-passed the caecum - although their data did not really support this view.

The mechanism proposed by Huang et al. was never really accepted because Herndon and Hove (1955) showed that caecectomized rabbits still produced a type of soft pellet. Nevertheless Herndon and Hove concluded from their results that hard and soft pellets still had separate origins so the basic problem still remained - there was no means of assessing the proportion of food which was recycled.

Quite recently however, Henning and Hird (1972) proposed a novel mechanism. They argued that since digesta in the proximal colon was similar in composition to the caecal contents but remained unchanged irrespective of the type of faeces being formed then hard and soft faeces must have a common origin. Bonnafaus and Raynaud (1963, 1967) had shown that the colon had a powerful bacteriolytic action which liberated bacterial cell contents for absorption. Thus, Henning and Hird were able to argue that soft faeces were able to avoid absorption in the colon not because they passed along too quickly but because they were protected by a tough mucoid coating as described by Griffiths and Davies (1964). Henning and Hird's hypothesis was further strengthened because it agreed with evidence of earlier workers. For example, a caecectomized rabbit would be expected to form 'soft' faeces as Herndon and Hove (1955) had shown because Griffiths and Davies (1964) had demonstrated that the mucoid coat was formed on soft faeces posterior to the sacculated part of the colon.

The proposals by Henning and Hird (1972) of an acceptable mechanism for the formation of soft faeces in the colon and the demonstration that hard and soft faeces probably have a common origin, and are subjected to a similar degree of fermentation, meant that the proportion of the food intake which was recycled could be estimated. Data from earlier work e.g. Thacker and Brandt (1955), Huang et al. (1955) could be re-examined to estimate the importance of coprophagy.

Since coprophagy seemed to be a mechanism which enabled the rabbit to get certain products of bacterial fermentation the significance of coprophagy was considered with reference to each of these products namely: energy, protein and vitamins.

Energy.

Fermentation of fibre by bacterial enzymes in the caecum and proximal colon liberates fatty-acids such as acetic and lactic acid which the rabbit can metabolize (Alexander and Chowdhury, 1958; Henning and Hird, 1972). The relative importance of this energy source is shown by the fact that mammary tissue from a rabbit can synthesize milk-fats from acetates and is superior to equivalent rat tissues but inferior to those of sheep in this respect (Folley and French, 1956).

Yoshida et al. (1968) compared digestion in germ-free rabbits and normal rabbits fed the same diet. In germ-free rabbits only 3.6 ± 1.2% of the fibre was digested compared with 8.5 ± 1.2% in normal rabbits. Huang et al. (1954) and Thacker and Brandt (1955) found that rabbits which were prevented from reingesting soft faeces had a lowered ability to digest food and thus a lowered energy gain. Huang et al. found that the ability to digest food was lowered from 74 ± 2% to 69 ± 3% and Thacker and Brandt found a similar reduction from 72.4 to 65.5%. However, this reduction in efficiency was largely attributable to the loss of soft faeces which were highly digestible, whereas to understand the importance of coprophagy one must consider what would happen if the rabbit formed no soft faeces at all. Actually this consideration becomes possible in the light of Henning and Hird's (1972) contention that hard and soft faeces have a common origin. For example, Huang et al. (1954) provided data on the quantity and composition of hard and soft faeces produced each day. Furthermore, since the proportion of an indigestible marker substance, chromic oxide, was known for both types of faeces, the proportion of the initially marked food which gave rise to each type of faecal pellet could be calculated. The experimental data showed that 66% of the dry-matter was digested when the rabbits formed hard faeces, but because the normal digestibility of dry-matter in the labelled diet was only 69%, coprophagy must have had only a marginal effect on the total digestibility of food.

Similarly, Thacker and Brandt (1955) provided data on the proportion of lignin in hard and soft faeces. Because lignin is indigestible (Crampton, Campbell and Lange, 1940) it acted as a natural marker so that the data suggest that coprophagy increased the digestibility of dry-matter from 70.1 to 72.4%.

It can be concluded therefore that coprophagy only increases the energy gains of the rabbit by 2 or 3% even if a fairly large amount of digesta, roughly one-fifth of the daily food intake, is recycled.

Nitrogen.

Yoshida et al. (1968) found that the caecal contents of germ-free rabbits contained less total nitrogen but more non-protein nitrogen than those of normal rabbits. This was not unexpected because Griffiths and Davies (1964) had shown that about 80% of the protein in the caecal contents of normal rabbits was contained in bacterial cells. However, the data did suggest strongly that the bacteria could synthesize protein from non-protein nitrogen.

This suggestion was strengthened considerably when Houpt (1963) presented some evidence that the rabbit (*Oryctolagus*) could use urea to synthesize protein during periods of protein deficiency. Nolan and Heisinger (1971) have since shown that urea can also be used by cotton-tails (*Sylvilagus*) to improve their nitrogen balance when they are fed on a diet low in protein.

Presumably, if urea was directed to the caecum instead of being excreted, new proteins might be synthesized. The importance of coprophagy might therefore be to enable the rabbit to get bacterial proteins which would otherwise be lost. There are two observations which support this idea.

Firstly, amino-acids and small peptides can be absorbed from the hind-gut but proteins are not normally absorbed. Secondly, it would be surprising if the colon possessed a general means of breaking down protein because a mucoid coat apparently protects soft faeces from proteolysis. Nevertheless, pepsin has been detected in the tissues of the colon (Altmann and Dittmer, 1964) and mucoitin-sulphate, the common intestinal mucous, is resistant to pepsin. However, the pH of the colon (pH 7.6-7.8) seems to rule out significant activity by enzymes such as pepsin which reach maximum activity at pH 2.

A further aspect of the availability of nitrogen concerns the quality of protein. Rabbits may at times have diets quite deficient in specific amino-acids. For example, Cassady, Damon and Suitor (1961) showed that supplementation of the diet given to female rabbits with lysine caused significant increases in the weaning weights of the young. Similarly Crampton (1934) found that if a very small supplement of casein was added to the grass fed to young rabbits they grew more rapidly. His observations suggest that the quality of the protein in the supplement, rather than any additional energy it contained, was responsible for the increased growth rates. In this context Yoshida et al. (1965) pointed out that many of the foods eaten by rabbits contain only small amounts of lysine whereas gut micro-organisms are rich in lysine. Although coprophagy might function to increase both the amount and quality of protein available to the rabbit there must be some limit to these gains because deficiencies are not always obviated.

In view of the likelihood that urea can be recycled, and the importance of protein quality, it was clear that the levels of nitrogen in natural pastures would need to be interpreted cautiously. Periods of nitrogen shortage would be very difficult to define, especially because there are not sufficient data available to evaluate the role of coprophagy in ameliorating protein deficiencies.

<u>Vitamins</u>.

Water soluble vitamins such as cobalamine, riboflavin, nicotinic acid and pantothenic acid are synthesized by bacteria in the caecum. They are apparently produced in sufficient quantities to meet most requirements because Simnet and Spray (1961) showed that rabbits needed only small amounts of B-vitamins in their diet compared to other animal species such as rats and mice.

Henning and Hird (1972) showed that in hard faeces B-vitamins are present at only about 30% of the concentrations (μg vitamins/g wet weight of faeces) at which they are found in soft faeces. Presumably the concentration of B-vitamins in soft faeces approximates that found in the caecum and proximal colon. Furthermore, it could be calculated from my data on the moisture content of digesta and hard faeces and from the data of Huang et al. (1954) that the wet weight of digesta undergoes a reduction of about 60% during formation of hard faeces. Together these facts mean that only about 12% of the B-vitamins remain - that is, 88% are either absorbed or destroyed in the colon. If such extensive absorption occurs, coprophagy would be relatively unimportant for the rabbit to gain B-vitamins. On the other hand, however, it is possible that certain vitamins are not readily absorbed. Cobalamine, for instance, requires the presence of an 'intrinsic' factor, usually found in the stomach, before it can be absorbed by the gut wall. Coprophagy may thus be important because it enables the rabbit to get certain vitamins; but at present this problem remains unresolved.

Conclusions.

It seems unlikely that the seasonal changes in the digestible energy content of the pastures could be completely offset if the rabbit made full use of coprophagy. As we have seen, coprophagy involving digesta from about one-fifth of the daily food intake increases the digestibility of dry-matter by only 2-3%, yet we know that even for sheep, which can digest far more dietary fibre than the rabbit, the digestibility of pastures can change markedly. In one example given by Rossiter (1966) the pastures were 65% digestible in spring but only 40% digestible in autumn.

Furthermore, it seems unlikely that all the food eaten by the rabbit could be recycled. Coprophagy normally occurs during the day when the rabbit is below ground and would therefore involve only the digesta held in the rabbit's gut at that time. This would amount to some 30 g dry-matter, resulting from perhaps 50 g of dry food - roughly half of the rabbit's daily intake of 100 g.

Coprophagy seems to be quite important in enabling rabbits to get proteins synthesized by bacteria in the caecum yet its role in obviating a general lack of protein or a deficiency of a specific amino-acid remains unknown. It is therefore difficult to assess the significance of the levels of nitrogen found in pastures and ingesta.

The role of coprophagy in enabling the rabbit to get B-vitamins also remains largely unknown - at least in any quantitative way. We know only that bacterial synthesis of these vitamins cannot offset a complete lack of vitamins in the diet. As we found in dealing with protein, the lack of quantitative data makes the significance of levels of vitamins in pastures difficult to assess.

6.2 CRUDE PROTEIN AND ACID DETERGENT FIBRE CONTENT IN FOOD, AND STOMACH OF CAGED WILD RABBITS

- Unpublished data of K. Myers and H. Bults, CSIRO Division of Wildlife Research.

Food	Crude Protein (%) Food	Crude Protein (%) Stomach	Fibre (%) Food	Fibre (%) Stomach
oaten chaff	4.43	4.80	37.60	38.40
oaten hay	6.87	5.43	35.30	38.66
lucerne hay	9.90	7.62	34.50	41.37
green pasture grasses	15.00	10.97	38.90	42.40
green lucerne	17.80	14.50	38.60	41.43
animal house pellets	19.13	16.10	38.00	39.13
clover seed	27.72	18.10	Not measured.	

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