# A STUDY OF THE BIOLOGY OF THE WILD RABBIT IN CLIMATICALLY DIFFERENT REGIONS IN EASTERN AUSTRALIA

## I. PATTERNS OF DISTRIBUTION

# By K. MYERS\* and B. S. PARKER\*

### [Manuscript received May 31, 1965]

### Summary

Patterns of distribution of warrens of the wild rabbit *Oryctolagus cuniculus* (L.) in subalpine, subtropical, and semi-arid areas are described.

At Snowy Plains, a subalpine valley in eastern New South Wales, 866 warrens occurred on an area of 9 square miles. There were 175 warrens per square mile on open country grazed by stock, but only 9 warrens per square mile on adjacent forested country.

At Mitchell, in subtropical southern Queensland, 871 warrens were mapped on 165 square miles. There were 44 warrens per square mile on alluvial deposits of sand along the margins of the Maranoa River and less than one warren per square mile in other habitats.

At Tero Creek in semi-arid north-western New South Wales, 4910 warrens were mapped on 250 square miles. Warren density per square mile was 38 on sand dunes, 19 on stony tablelands, eight on flat desert loams, six on stony pediments, and none on Mitchell grass plains. The preferred habitat was sand.

Mean warren size and distribution of warren sizes varied significantly between sites and habitats. The upper limit to warren size lay between 50 and 60 burrow entrances per warren.

The largest mean warren size occurred in the heavier soils. Mean warren size in sandy soils and in areas where rabbit control was practised was lower.

Patterns of use of warrens also showed significant differences from habitat to habitat. At Snowy Plains the smaller warrens were more inactive and at Mitchell and Tero Creek the larger warrens were more inactive. After a harsh, dry summer at Tero Creek a further significant decrease in activity in the larger warrens was measured.

Predation on nestling rabbits by foxes (Vulpes vulpes L.) was confined almost completely to warrens in sandy soils.

Traverse sight-counts of rabbits above ground at night showed good correlation between warren distribution and rabbit numbers.

Distribution of rabbit populations in relation to warren distribution is discussed.

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# I. INTRODUCTION

# (a) General

The wild rabbit, *Oryctolagus cuniculus* (L.), has now inhabited Australia for approximately a century. During that period it has colonized the southern half of the continent (Fig. 1) and invaded a wide variety of habitats, including subalpine plains, sandy and stony deserts, and subtropical grasslands. Eyewitness accounts of the huge plagues which swept inland Australia during the 1890's and the early 1900's present graphic evidence of the success and ease with which the species spread and increased during the 50 yr following its release. From time to time single rabbits,

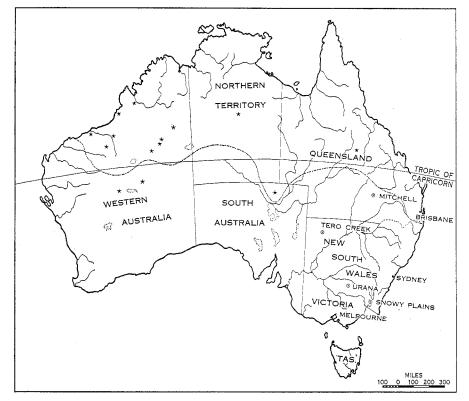


Fig. 1.—Map of Australia showing approximately regions of permanent distribution of rabbits in Australia and areas mentioned in this paper. \* Recent sightings of individual rabbits;  $\bigcirc$  study areas; (-----) approximate northern limit of permanent rabbit distribution.

probably emigrants from settled regions, have been reported in areas of the far north and in high alpine habitats, but the great colonizing movements now appear to be over. No major shift in regional distribution has occurred since approximately 1910 when the subalpine plains and coastal valleys were finally reached.

The problem of controlling the rabbit in a country the size of Australia is enormous, and the great variety of climatic regions and types of habitat in which the species lives are undoubtedly exerting selective pressures to produce changes in

morphology, physiology, and behaviour, making its control yet more complex. Some measure of the ways in which the rabbit in this country has responded to the environmental problems it has had to meet, and especially some evidence on the direction and development of evolutionary changes are clearly necessary from both practical and academic points of view.

This contribution, the first of a series of papers\* describing various aspects of rabbit biology in climatically different regions of eastern Australia, deals with the effects of climate and habitat on patterns of distribution.

# (b) Description of Sites

Most of the observations described in this and in the following related papers were made at four sites in eastern Australia. Three of these were selected as representing areas close to the margins of the zone of permanent rabbit distribution, and the fourth as a favourable area in the centre of its range.

# (i) Snowy Plains, New South Wales

Rabbits are permanently distributed in subalpine areas to an altitude of approximately 5000 ft. Beyond this severe winters and late thaws appear to act as barriers to reproduction and survival, and rabbits move upwards only during the summer months.

The Snowy Plains, in the Snowy Mts. of New South Wales, latitude 36°15'S., longitude 148°35'E., lie at an altitude of 4500 ft, approximately 35 miles west of Cooma. The study area, approximately 9 square miles in extent and falling mostly within the boundaries of the Kosciusko State Park, occupies part of the senile valley of the Gungarlin River, with a grass cover forming a subalpine complex and moderately steep timbered sides forming a wet sclerophyll forest (Costin 1954). The floor of the valley is broken by weathered outcrops of granite. Small terminal moraines block some of the small creeks leading into the valley. Most of the large Kosciusko glaciers reached the Brassy Mts. which lie just to the west of the Gungarlin. Plate 1 shows a panorama looking westwards across the valley.

The soils of the valley floor form an alpine humus association, consisting mainly of alpine humus and small areas of valley bog peats near the meandering river. On the slopes the soil is principally a brown podzol forming a major part of the transitional alpine humus soil association. The soils are friable, easy to dig in, and susceptible to erosion.

The climate of Snowy Plains is fairly rigorous; average temperatures range from 67°F mean maximum in January to 25°F mean minimum in July (Fig. 2).

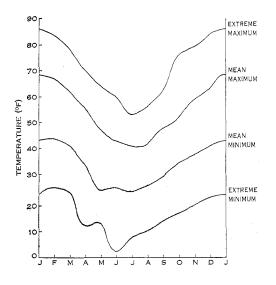
\* The project introduced in this paper was a group activity with workers from several disciplines cooperating under the leadership of the senior author. It is expected that some 20 papers will be submitted to the following journals. Ecological papers: to *CSIRO Wildlife Research* (K. Myers and assistants); papers on skin glands and behaviour: to *Animal Behaviour* and *CSIRO Wildlife Research* (R. Mykytowycz); papers on parasitology: to *Parasitology* (J. D. Dunsmore); papers on reproduction: to *CSIRO Wildlife Research*, *Australian Journal of Zoology*, and *Reproduction & Fertility* (L. Hughes); and a paper on the adrenal glands to *Comparative & General Endocrinology* (K. Myers).

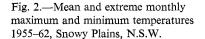
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Extremes of 86°F maximum and 2°F minimum have been recorded. The precipitation averages 33 in. and is fairly evenly distributed (Fig. 3). Costin (1954) estimated the average annual rainfall for Snowy Plains to lie between the 50 and 60 in. isohyets, in a map compiled from data from a few surrounding stations. It thus appears that Snowy Plains lies in an area of rain shadow, caused by the Brassy Mts.

Snow lies in the valley and on the hills during the winter months, the amount depending on the severity of winter. During an average winter there are always patches of vegetation exposed in the lee of drifts and among the timber.

The major native grasses in the valley are Danthonia nudiflora (rigid wallaby grass), Poa caespitosa (snow grass), and Themeda australis (kangaroo grass). Carex





species (sedges) and Sphagnum cymbefolium occur in and around the bogs and several species of Epacris, Oxylobium ellipticum, Podocarpus alpinus, and Kunzea muelleri form heath areas. There is a gradual transitional zone from the open valley flora to that of the timbered slopes; Eucalyptus niphophila (snow gum) makes an appearance and gives way to E. delegatensis and E. dalrympleana, which form the major species of the sclerophyll area. The main grass forming the floor beneath the trees is Poa caespitosa.

Introduced plants also are present in the valley, the two main species being *Trifolium repens* (white clover) and *Phalaris minor*. Numerous small annual species (*Festuca, Rumex, Hypochaeris, Bromus, Hordeum*), which have been brought in by animal agents, also form a considerable part of the pasture.

The portion of the study area, which is held by private landholders on a freehold tenure, is used to provide summer grazing for both sheep and cattle, usually from December to May. Grazing has completely altered the nature of the sward. The

tussocks of snow grass have in the main disappeared and the *Poa* now grows diffusely scattered among low-growing clovers, grasses, and broad-leafed weeds (Costin 1954).

The snow usually commences to thaw during late July-August and some plant growth commences simultaneously. The main period of growth occurs in October-November, and the grasses set seed from January to March. By April the pastures are mature and with the first frosts shortly afterwards start to lose their nutritive value.

# (ii) Mitchell, Queensland

Rabbit distribution in Queensland is limited to the southern inland (Fig. 1).

The Mitchell study area is centred on the township of Mitchell, latitude 26°30'S., longitude 148°00'E., about 350 miles west of Brisbane and covers approximately 165 square miles of varied habitats. It is divided by the large Maranoa

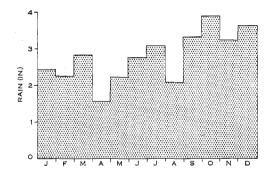


Fig. 3.—Mean monthly precipitation 1955-62, Snowy Plains, N.S.W.

River, which runs roughly north-south, and flows intermittently after heavy rain. The Leichhardt Rabbit Board until 1963 maintained a rabbit-proof fence which runs across the area south of Mitchell and no longer acts as a complete barrier to movement. The Maranoa is bordered by red gum, *Eucalyptus camaldulensis*, and flows through a gently undulating black soil plain, a large proportion of which is subjected to flooding and on which lie a number of low, alluvial sandhills.

The black soil plain (Plate 1) carries an open tussock grass association dominated by several species of Mitchell grass, *Astrebla*. After rains the inter-tuft spaces are occupied by various annual grasses, especially *Iseilema* spp. (Flinders grasses) and *Dactyloctenium radulans* (button grass). Scattered trees occur on the plain, chiefly box (*Eucalyptus populnea*), myall (*Acacia pendula*), brigalow (*Acacia harpophylla*), and whitewood (*Atalaya hemiglauca*), and several other species.

The sandy hills (Plate 1) carry a savannah woodland box-pine association (*E. populnea*, *Callitris glauca*) with iron-bark (*E. melanophloia*) and several minor species of trees also present, and a sparse pasture of *Aristida* spp. (wire grass), *Heteropogon contortus* (black spear grass), *Themeda australis* (kangaroo grass), and numerous annuals which appear after rains.

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On both sides the valley rises to form a tropical woodland (mixed) dominated by *Eucalyptus* spp. (including *E. melanophloia*) on hills with shallow stony soils predominant. Plate 3 shows a vertical aerial photograph of the study area.

The climate is subtropical. The average annual rainfall of approximately 20 in. (Fig. 4) falls principally between November and March as monsoonal storms. Temperatures fluctuate widely both daily and seasonally. In summer (December) the mean

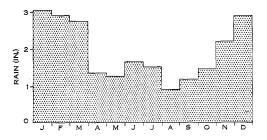
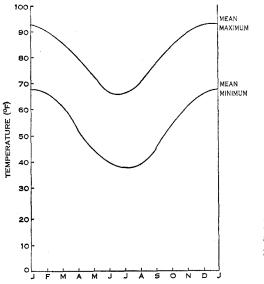
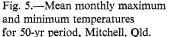


Fig. 4.-Mean monthly precipitation 1884-1951, Mitchell, Qld.

maximum temperature is 92°F and mean minimum 67°F. In winter (July) the mean maximum is 67°F and the mean minimum 38°F (Fig. 5).

The growing season coincides with the period of summer rain. The pastures set seed during February–March and become dry and lose their nutritive value during the winter months.





The study area includes portions of eight properties within its boundaries. One, "Warren Point", is used to run cattle only. The other properties are principally devoted to sheep raising. Small areas on most properties are cultivated for wintergrowing oats and summer sorghum, while one property grows 1000 ac of wheat (1963).

### (iii) Tero Creek, New South Wales

Rabbits are permanently distributed throughout inland Australia south of a line roughly coincident with the Tropic of Capricorn (Fig. 1), irrespective of average annual rainfall (which falls to 4 in. in some regions) and land usage.

The Tero Creek study area is located 90 miles north-west of White Cliffs, in the north-western corner of New South Wales, latitude 30°15'S., longitude 142°45'E. It covers approximately 250 square miles and comprises almost the whole of one sheep station (Tero Creek [210 square miles]) and portions of three others (Yancannia, Gum Poplah, and Quarry View).

There are four major physiographic regions in the area (Plate 4).

- (1) In the east and south lies the Yancannia Range, an old peneplain approximately 400 ft high, of lower Cretaceous shales, sandstones, and conglomerates dissected by numerous dry creeks lined with *Eucalyptus camaldulensis* and surrounded by gently sloping stony pediments. The red stony desert soils and skeletal soils of the hills support stands of *Acacia aneura* (mulga), *Acacia homalophylla, Casuarina cristata* (desert oak), *Hakea leucoptera* (needle bush), and other tree species, a shrub community dominated by *Kochia sedifolia* (bluebush), and *Atriplex vesicarium* (saltbush), and numerous grasses (*Astrebla* spp., *Enneapogon* spp., *Eragrostis* spp.), and herbs (*Bassia spp., Chenopodium* sp.) (Plate 5).
- (2) In the west is an extensive belt of low, consolidated red sand dunes up to 20 ft high and running approximately north-east to south-west. The dunes carry a low-layered woodland dominated completely by A. aneura with scattered specimens of Atalaya hemiglauca, Owenia acidula, Flindersia maculosa, and Heterodendron oleifolium. Some of the run-off has been maintained as channels leading into the sand dunes to form swampy areas of various sizes, supporting Eucalyptus camaldulensis, E. microtheca, Pittosporum phillyraeoides, and other tree species in and about them. A shrub storey is well developed on many dunes and includes mainly Dodonea attenuata, Eremophila sturtii, Cassia spp., and Hakea spp. The grass cover consists mainly of perennials like Eragrostis spp. Aristida arenaria and Enneapogon avenaceus on the dunes, and Themeda australis, Dichanthium sericeum, Astrebla spp., and Panicum spp. in the interdunal depressions. Where the depressions form swampy areas or claypans, nardoo (Marsilea drummondii), annual saltbush (Atriplex spp.), cane-grass (Eragrostis australasica), and lignum (Muehlenbeckia cunninghamii) are also to be found (Plate 6).
- (3) On the north and south-west of the hills lie gently undulating to flat areas of sandy desert loam, supporting a tree, shrub, and grass community similar to that of the sand dune area in general. Some trees, e.g. *Atalaya hemiglauca*, appear mainly in this zone (Plate 7).
- (4) In the centre lies a flat area of heavy alluvial black and grey-brown soils abutting the sand dunes and deposited by run-off from the hills. This area supports no trees or shrubs except along the watercourses (Acacia spp., P.

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*phillyraeoides*, *E. camaldulensis*, *Nicotiana* sp.). A dense pasture of Mitchell grass (*Astrebla* spp.) and other grasses covers the lower parts of the plain, giving way to forbs like *Bassia* sp. at higher and drier elevations (Plate 8).

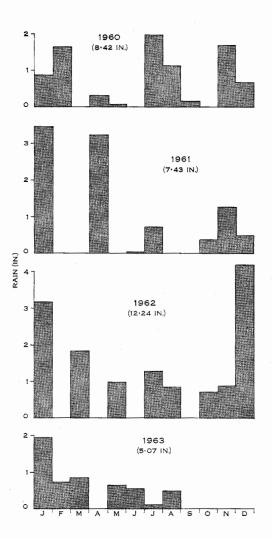
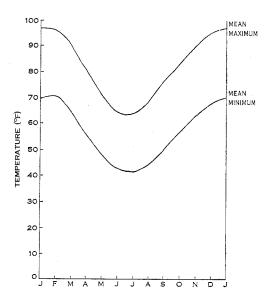
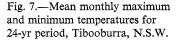


Fig. 6.—Monthly precipitation 1960-63, Tero Creek, N.S.W.

The climate at Tero Creek is classed as semi-arid. Average annual rainfall is approximately 8 in., mostly falling as summer thunderstorms. Falls are erratic and variable (Fig. 6). The average deviation from mean annual rainfall at Tibooburra, 100 miles north-west of Tero Creek, is 40%. Annual amounts of rain reported for Tero Creek vary from 20 in. in 1956 to 3 in. in 1964.

Temperatures cover a wide range. The mean minimum in June at Tibooburra is about 42°F and in summer 72°F. The mean maximum is 65°F in June and 97°F in summer (Fig. 7). Soil surface temperatures reach 132°F in summer, and the annual





rate of evaporation is 93 in. Pasture growth is dependent on rainfall and is thus completely irregular.

The area studied is stocked with sheep and cattle. Large mobs of feral goats inhabitat the stony hills and three species of large macropods (*Megaleia rufa* (Desm.), *Macropus canguru* (Müller), *Macropus robustus* (Gould)) also graze the limited pastures.

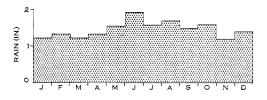
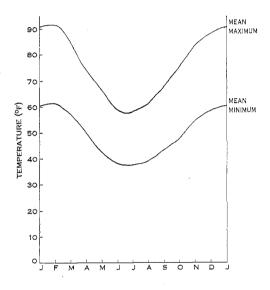


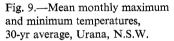
Fig. 8.-Mean monthly precipitation 30-yr average, Urana, N.S.W.

### (iv) Urana, New South Wales

Urana lies on the Riverine Plain of south-eastern Australia (Butler 1950). Climatically, the whole plain falls within a winter rainfall-summer drought zone. It is bounded along its eastern and southern margins by the foothills of the Great Dividing Range with an average elevation of about 500 ft. Rainfall decreases steadily with distance from the hills. The Riverine Plain has always harboured large populations of rabbits, especially around topographical features such as swamps and ox-bow lakes of the river system and large sandhills. The area chosen for study, Lake Urana, is a lake of internal drainage, 18,000 ac in extent. Over the years wind action has formed a great rim of sand around the lake and the area now takes the form of a saucer-shaped depression, elongated north-south, with the lake itself in the centre (Plate 12).

The sandy rim has been colonized by the native pine C. glauca and by the rabbit which finds the sand easy to burrow and obtains food from the lake floor. Dead trees (E. camaldulensis) cover the lake floor, killed by previous heavy floods but the same species is re-establishing itself at the base of the sandy rim. In a region where the





average annual rainfall is 17 in. with 11 dry months (less than 2 in. rain per month) each year (Fig. 8), irrespective of conditions in the surrounding country, the lake has been an oasis for large rabbit populations, which were present in pest proportions for 25 yr or more prior to the epizootics of myxomatosis of 1951 and ensuing years (Myers, Marshall, and Fenner 1952). Mean monthly variations in temperature are graphed in Figure 9.

### II. METHODS

The study areas at Mitchell, Snowy Plains, and Tero Creek were traversed on a grid pattern, by foot and vehicle, and the location of all rabbit warrens plotted on aerial photographs or photo-maps. The Snowy Plains survey was made during January and February 1963, the Mitchell survey during October 1963 and February 1964, and the Tero Creek survey between July and November 1963, and in March 1964. The final period of mapping at Tero Creek occurred after a severe, dry summer. The figures obtained during this period are thus presented separately.

No map of warren distribution was drawn for Urana. Prior to the myxomatosis epizootic in 1951 the sandy rim of the lake carried a very dense rabbit population in large numbers of warrens (Myers, Marshall, and Fenner 1952). The warrens have since been destroyed by mechanical means as an adjunct to rabbit control and small numbers of rabbits now live in logs, scattered burrows, and other debris on the dry lake floor. Patterns of distribution of rabbits on the Riverine Plain are discussed by Myers (1962).

The numbers of burrow entrances, their state of use by rabbits, categorized as active or inactive, and excavation by predators in search of nestling rabbits were recorded for each warren. Soil types and plant associations were also noted.

For the purposes of this part of the work no serious attempt was made to estimate the total numbers of rabbits present but a number of traverse sight counts were made over several evenings in each area to indicate correlation between warren distribution and adult activities. The counts represent the maximum numbers of rabbits seen for each area on any evening during the period of counting.

# III. RESULTS

### (a) Distribution of Warrens in relation to Habitat

## (i) Snowy Plains

Of the 866 warrens plotted on the Snowy Plains site 37 (78 burrow entrances) were situated in or about the roots of the snow gums in the forested sides of the valley. The rest (6076 burrow entrances) were situated on the open valley floor and along the edges of and in small clearings in the forest (Plate 2 and Table 1). All of the warrens in the forest were small, ranging from a single hole to four holes in size. Most of the warrens in the open country were situated on slopes or on prominences on the valley floor, usually around outcrops of granite. There were no warrens in the low-lying and swampy areas.

When the numbers of holes per 10-ac grid square are plotted, the resulting map of density distribution shows the large concentration of burrows in the central and completely open portion of the valley, with the highest concentrations on the small rises around rocky outcrops (less than 80 holes per 10 ac). The small clearings leading out of the main valley into the forest supported lighter concentrations of burrows, (1–10 holes per 10 ac).

Evening sight counts were made between December 16 and 19, 1963 along five traverses. Four of these, A-D, approximately 1 mile each, were made on foot, using binoculars to count every rabbit sighted. One traverse, E, of about 6 miles, was made by spotlight from a vehicle immediately after sunset along tracks and roads within the study area (Plate 2).

The majority of the 435 rabbits that were seen were on the floor of the valley, along the edges of the forest, and in clearings within the forest. Few rabbits (35) were sighted within the forest, and then principally along the road which was cleared

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DATA ON RABBIT WARRENS AT THREE DIFFERENT SITES IN EASTERN AUSTRALIA

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Site and Habitat	Area (square	Total Number	Total Number	Number of Warrens per Square Mile	Number of Burrow Entrances	Ē	Wa: umber of 1	Warren Size (number of burrow entrances)	ances)
	miles)	oi Warrens	on burrow Entrances	(nearest whole number)	per oquare Mile (nearest whole number)	Mean	Mode	Median	Range
Snowy Plains, N.S.W., open grassland	4.75	829	6076	175	1279	7.3	-	4	1-53 and 89*
Snowy Plains, N.S.W., forested areas	4.25	37	78	6	18	2.1	Ŧ	1	1-7
Mitchell, Qld., north of rabbit fence-town area	1.50	0	0	0	0	0	0	0	0
Mitchell, Qld., north of rabbit fence-sandy soil	35	22	88	9.0	2.5	4.0	-	ŝ	1-9
Mitchell, Qld., north of rabbit fence—black soil	46	0	0	0	0	0	0	0	0
Mitchell, Qld., north of rabbit fence-forested area	22	10	22	0-5	1	2.2	-	1	1-10
Mitchell, Qld., south of rabbit fence—sandy soil	18	797	4324	44	240	5.4	4	4	1-35

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Site and Habitat	Area (square	Total Number	Total Number	Number of Warrens per Square Mile	Number of Burrow Entrances	ц)	War umber of t	Warren Size (number of burrow entrances)	ances)
	miles)	or Warrens	on buildow Entrances	whole number)	Mile (nearest whole number)	Mean	Mode	Median	Range
Mitchell, Qld., south of rabbit fence-black soil	36	0	0	0	0	0	0	0	0
Mitchell, Qld., south of rabbit fence-forested area	17	42	293	6	17	7-0	П	L	1–23
Tero Creek, N.S.W., stony hills	43	806	7268	61	169	0.6	7	9	1–52 and 120*
Tero Crcek, N.S.W., stony pediments	58	371	3386	Q	58	9.1	e	9	1-57
Tero Creek, N.S.W., desert loam (pre-summer)	34	228	2144	7	63	9.4	3, 7, 10	×	1-45
Tero Creek, N.S.W., sand dunes (pre-summer)	49	2886	17,160	59	350	5.9	7	4	1-31
Tero Creek, N.S.W., black soil	25	0	0	0	0	0	0	0	0
Tero Creek, N.S.W., desert loam (post-summer)	8	96	643	12	80	6.7	5	S	1–22
Tero Creek, N.S.W., sand dunes (post-summer)	41	523	4624	13	113	8.8	2	٢	1-34
* Complex warren system formed by amalgamation of separate warrens.	rmed by an	algamation c	f separate wai	rtens.					

TABLE 1 (Continued)

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in places to permit entry to power lines. The observations are in accord with the distribution of warrens described above.

#### (ii) Mitchell

The Mitchell study area covers 165 square miles, 61 of which lie to the south of the old rabbit fence. North of the rabbit fence control operations were practised for many years by the Leichhardt Rabbit Board. In the latter area of 104 square miles only 32 warrens (110 burrow entrances) were found. To the south of the fence 839 warrens (4617 burrow entrances) were plotted (Plate 3 and Table 1).

Almost all the warrens were confined to the alluvial deposits of sand which exist as small hills scattered along the margins of the river. In the gravelly soils of the forested hills and the heavy black and grey alluvial soils on the valley floor very few warrens were found.

When the numbers of burrow entrances per 50-ac grid square are plotted, the resulting density distribution shows the large concentration of burrows on the sand hills along the river (600 ac with more than 80 holes per 50 ac).

Traverse sight counts were made by spotlight in the early evening of five nights in February 1964 from a vehicle progressing at 10–15 m.p.h., along a route utilizing roads and tracks both above ( $45 \cdot 5$  miles) and below the rabbit fence ( $25 \cdot 5$  miles) and sampling the main habitat types. The maximum numbers of rabbits seen on any night and the routes traversed are shown in Plate 3. To the north of the fence 15 rabbits, and to the south 108 rabbits were counted.

The majority of the rabbits observed were in areas near the concentrations of warrens in the sand hills. Small pockets of rabbits were also observed along tracks in the forest in the south-west, and in the black soil plain near a wheat crop in the north-east of the study area. The map of warren distribution thus does not completely explain the pattern of population distribution, although it appears to account for it in great part.

### (iii) Tero Creek

The Tero Creek study area covers approximately 250 square miles and includes five main types of habitat.

(1) Stony Tableland.—The mapping disclosed 806 warrens (7268 burrow entrances) on 43 square miles of stony tableland habitat, in which are included both the old peneplain surface and the steep talus erosion slopes (Table 1). A sample map of warren distribution in this habitat is shown in Plate 9.

The warrens in this area clearly showed two different patterns of distribution. On the steeper erosion slopes they were distributed in close relationship to the drainage pattern, occurring in outcrops of soft white shales, both on the sides and at the bottom of talus slopes and in deposits of sand along the banks of the watercourses. On the peneplain surface warrens occurred in small discrete clumps in surface layers of soft shales principally along the margins of the plain, and especially at the heads of erosion gullies. Almost all of the warrens in the stony country occurred in stands of bluebush (K. sedifolia) and saltbush (A. pyrimidata).

(2) Stony Pediments.—Along the northern and western sides of the hills were 58 square miles of gently sloping and undulating stony pediments cut by watercourses carrying water from the hills to the Mitchell grass plains. In this region 371 warrens (3386 burrow entrances) were mapped (Table 1), scattered and in low density and mostly associated with outcrops of light shales in slightly raised areas. Many of the warrens mapped were strung out in lines following the exposed rock strata. This type of distribution is shown in the western portion of Plate 9.

(3) Sand Dunes.—The area of low sand dunes, 90 square miles, contained 3409 warrens (21,784 burrow entrances). The major pattern of distribution of warrens was markedly determined by the direction of the dunes, the warrens being strung out

Habitat	Numbers of Miles Driven	Numbers of Rabbits Seen	Numbers of Rabbits Seen per Mile
Sand dunes	40	166	4 · 1
Stony hills	7.2	8	1.1
Desert loam	7	5	0.7
Stony pediments	12	1	0.1
Black soil	6.8	0	0

 TABLE 2

 NUMBERS OF RABBITS SIGHTED ON TERO CREEK TRAVERSES

in lines along the dunes in a north-easterly to south-westerly direction. The larger dunes carried higher concentrations of warrens. As in the stony habitats, the warrens on each dune were divided into small discrete clumps or colonies. This pattern of distribution is well portrayed in Plate 10.

(4) Desert Loam.—The area of desert loam, 42 square miles, contained 324 warrens (2787 burrow entrances) (Table 1). The scattered colonies of warrens were built on small prominences of slightly more sandy soil near depressions which generally took the form of small claypans. This type of distribution is shown in the north-eastern quarter of the area covered in Plate 10.

(5) *Mitchell Grass Plains.*—No warrens were found on 25 square miles of Mitchell grass plains.

When the 35,225 mapped burrow entrances are plotted on a 250-ac square grid the resulting density distribution shows clearly the relative importance of the five habitats (Plate 11). Most of the burrows were situated on the sand dunes and the

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rocky hills (Table 1). The density of burrow entrances per square mile in the sand dunes was double that on the hills. Since this was during a period of low rabbit numbers it is likely that this difference could increase many times during good years.

A traverse of  $72 \cdot 75$  miles was made by vehicle on several evenings in March 1964 using tracks which crossed all habitats, and 180 rabbits were counted by spotlight. Of these eight were seen in a distance of  $7 \cdot 25$  miles in the rocky hills, one in 12 miles

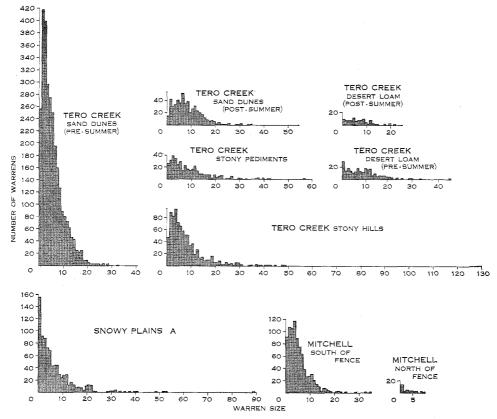


Fig. 10.—Distributions of warren sizes in main habitats at three sites in eastern Australia.

on the stony pediments, five in 7 miles in the sandy loam, none in 6.8 miles of Mitchell grass plains, and 166 on 40 miles of sand dunes (Plate 11 and Table 2). The highest density of rabbits was seen in the sand dunes (4.1 per mile) and rocky hills (1.1 per mile).

### (b) Relationships between Warren Size and Habitat

The distributions of warren sizes at the different sites and in different habitats are presented in Figure 10 and Tables 1 and 3.

Tests of significance between the main distributions are presented in Table 7 (see p. 22). The low numbers of warrens in the forested areas of Snowy Plains and Mitchell precluded satisfactory statistical treatments.

FREQUENCY DISTRIBUTION OF RABBIT WARREN SIZES IN VARIOUS HABITATS AT THREE SITES IN EASTERN AUSTRALIA TABLE 3

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\* Totals of all habitats.

TABLE 4

Frequency distribution of rabbit warrens with 0-50% burrow entrances active at three sites in eastern australia

								M	Warren Size (number of burrow entrances)	Size	unu)	lber c	if bur	row e	ntrar	Ices)			:			
She and Habitat	-	2	ю	4	5	9	7	8	6	10	11	12	13	14	15	16	17	18	19	20	21	Over 21
Snowy Plains, N.S.W.*	12	10	5	8	0	9	5	Э	-	0	7	5	0	7		i					0	2
Mitchell, Qld., north of rabbit fence*	1					-	·														0	0
Mitchell, Qld., south of rabbit fence*	s.	6	12	28	15	23	22	15	14	6	13	10	6	5	-	7	7				0	7
Tero Creek, N.S.W., stony hills	11	21	Π	22	12	16	10	6	13	7	5	4	ŝ		-		Т	7	-	<u> </u>	0	5
Tero Creek, N.S.W., stony pediments	4	14	7	∞	4	6	9	15	7	9	e	S	S	ŝ	-	7	ŝ	17	7	4	0	×
Tero Creek, N.S.W., desert loam (pre-summer)	-		ŝ			Ś		4	ŝ	8	4	ŝ	6	<b>***</b>	Annel	3		7	-		-	1
Tero Creek, N.S.W., sand dunes (pre-summer)	ş	41	26	26	9	6	6	13	12	10	5	12	14	7	10	8	~	ŝ	ŝ	7		e
Tero Creek, N.S.W., desert loam (post-summer)	-	6	ŝ	9	5	7	4	7	9	7	Ţ	4	1	-						7	0	-
Tero Creek, N.S.W., sand dunes (post-summer)	4	24	13	19	21	21	29	13	16	1	16	18	12	12	∞	5	S	5	7	9		11
* Totals of all habitats.																						

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Mean warren sizes and distributions of warren sizes varied greatly and displayed significant differences between both sites and habitats.

The distribution of warren sizes on the Snowy Plains differed significantly from both the Queensland site and the main arid zone habitats. In Queensland most of the warrens were smaller than those on the Snowy Plains and in the arid zone there were more larger warrens in the stony habitat and more smaller warrens in the sand dunes (Tables 1 and 3). The reduced size of warrens in sandy soils was common throughout.

At Snowy Plains mean warren size in the open grazed areas was 7.3 burrow entrances, more than three times the size of warrens in the forest (P < 0.001). At Queensland the warrens south of the rabbit fence were almost twice as large as those north of the fence (Table 1).

The upper limits of numbers of burrow entrances per warren appeared to lie in the middle 50's. Only two warrens in the many thousands measured were larger, and probably resulted from the amalgamation of two separate growing warrens (Table 1). The great majority of warrens possessed less than 10 entrances.

The distributions of warren sizes in the sand dunes and on the sandy loams at Tero Creek differed significantly before and after the hot summer period which intervened between periods of mapping (Tables 3 and 7). During the hot summer high winds caused sand drift which filled in many of the inactive warrens and the density of burrow entrances on the dunes dropped from 350 to 113 per square mile.

## (c) Relationships between Warren Size, Activity Patterns, and Habitat

Not only were there differences in warren size in different habitats, but patterns of use of the warrens also showed significant differences (Tables 4–7). Distributions of activity patterns for the four most important habitats and for the sand dunes after the dry summer are graphed in Figure 11.

The most significant difference in the less active warrens (0-50% active) is a marked inactivity in the small warrens at Snowy Plains, and large warrens at Mitchell and Tero Creek (Table 4). There are also significant differences between patterns of distribution in the 0-50% activity group in different habitats at Tero Creek. Thus more large warrens are inactive on the stony pediments and sand dunes than on the hills. There is also a very significant difference in activity in the large warrens in the sand dunes before and after summer. There are more large warrens inactive after the summer than earlier.

Differences of this nature suggest basic differences of ecology in the different habitats. Higher mortalities may be imposed on the inhabitants of the small warrens at Snowy Plains and the larger warrens in the arid area, since those warrens tended to be underpopulated when others were active. The difference in activity patterns between warrens on the stony tablelands and elsewhere in the semi-arid environment also suggests differences in ecology affecting rabbit numbers.

TABLE 5	

Frequency distribution of rabbit warrens with 51-75% burrow entrances active at three sites in eastern australia

Site and Wahitet								War	Warren Size (number of burrow entrances)	ize (n	umbe	r of	purro	w en	rance	(s						-
	-	7	e.	4	S	9	~	~	6	10	II II	12 1	13 1	14 1	15 1	16 17		18 19		20 2	21 (	Over 21
Snowy Plains, N.S.W.*	•	0	4	∞	5	<i>m</i>	5	4	4	0	5	4	0	5	4		0		0			7
Mitchell, Qld., north of rabbit fence*	0	0	7	7	-	Η	0	0		<b>***</b>	0	0									0	0
Mitchell, Qld., south of rabbit fence*	0	0	9	12	15	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	14	14	4	6	12		s.	4	0			2		0	1	4
Tero Creek, N.S.W., stony hills	0	0	30	25	14	16	19	24	Ξ	10	19	6	·2	4	5		4	5		5	1	19
Tero Creek, N.S.W., stony pediments	0	0	∞	8	ñ	Ś	5	4	5	Ś	11	10	4	5		4					0	12
Tero Creek, N.S.W., desert loam (pre-summer)	0	0	7	7	7	7	7	S	9	4	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	7	4	4	<i></i>			5		3		5
Tero Creek, N.S.W., sand dunes (pre-summer)	0	0	27	14	12	17	30	17	13	52	17 2	21	12	14	10					2	7	6
Tero Creek, N.S.W., desert loam (post-summer)	0	0	ŝ	0	9	3	7	4	7	-	0	e.	0	0		0					•	0
Tero Creek, N.S.W., sand dunes (post-summer)	0	0	9	10	10	10	19	16	17	6		13 1	11	5	6		17	5				1
* Totals of all habitats.																						

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frequency distribution of rabbit warrens with 76-100% burrow entrances active at three sites in eastern australia TABLE 6

								3	arren	Size	una)	per	of bu	Warren Size (number of burrow entrances)	entra	nces)						
Sue and fladuat	-	3	3	4	5	9	7	8	6	10	Ξ	12	13	14	15	16	17	18	19	20	21	Over 21
Snowy Plains, N.S.W.*	142	83	80	57	99	39	38	37	26	18	27	52	12	15	6	5	~	6	2	∞	6	33
Mitchell, Qld., north of rabbit fence*	11	7	5		5	0	7	0	-	0												
Mitchell, Qld., south of rabbit fence*	87	66	88	62	58	43	27	6	∞	8	ŝ	9	3	-	-	e		0	0	0	0	1
Tero Creck, N.S.W., stony hills	36	68	41	40	45	33	28	18	27	17	15	5	19	6	×	5	S	9	7	Ś	S	29
Tero Creek, N.S.W., stony pediments	52	17	24	18	17	14	5	ŝ	٢	3	7	9	4	ŝ	0		ŝ	13	0	0	Η	7
Tero Creek, N.S.W., desert loam (pre-summer)	10	14	13	12	∞	8	10	4	7	9	4	5	4	4	0	0	en.	7	-	-	-	4
Tero Creek, N.S.W., sand dunes (pre-summer)	256	377	346	257	257	224	159	130	102	57	58	40	36	26	33	13	6	13	1	Ś	7	6
Tero Creek, N.S.W., desert loam (post-summer)	6	6	7	7	-	-	Ţ	-	7	-	0	0	-	0	0							
Tero Creek, N.S.W., sand dunes (post-summer)	11	19	6	s.	10	5	S	9	5	•	7	0		3	0		13	0	0	0	0	1

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TABLE 7	TESTS OF SIGNIFICANCE BETWEEN DISTRIBUTIONS OF SIZE AND PATTERNS OF ACTIVITY IN RABBIT WARRENS IN DIFFERENT HABITATS AT THREE SITES (SNOWY	PLAINS, N.S.W, MITCHELL, QLD., AND TERO CREEK, N.S.W.) IN EASTERN AUSTRALIA
	TES	

				Proportion	s of Bu	Proportions of Burrow Entrances Active in Warrens (%)	nces Ac	tive in Wa	rrens (%	े ि			Totz	Total Size
Sites and Habitats		0		1–25	5	26-50		0-50	5]	51-75	-9L	76–100	Distr	Distribution
	×3	Signifi- cance	χ3	Signifi- cance	χ²	Signifi- cance	x <sup>a</sup>	Signifi- cance	χ	Signifi- cance	χ²	Signifi- cance	x	Signifi- cance
Snowy Plains: Mitchell, south of fence	23.92	0.001	*		16-31	0.001	42.12	0.001	1.39	n.s.	130-66	0.001	103 · 39	0.001
Snowy Plains: Tero Creek, stony hills	5.61	n.s.	*		0-98	n.s.	11.03	n.s.	1.75	n.s.	60-35		0.001 107.39	0.001
Snowy Plains: Tero Creek, desert loam	*		*		*		*	-	5.66	n.s.	17.79	n.s.	91 - 55	0.001
Snowy Plains: Tero Creek, sand dunes (pre-summer)	*		*		1.77	n.s.			1.67	n.s.	189-76	0.001	188-75	0-001
Snowy Plains : Tero Creek, sand dunes (post-summer)	*		*		9.13	between 0.01 and 0.001			3.74	n.s.	16-81	n.s.	154-61	0.001
Mitchell, south of fence : Tero Creek, stony hills	7.83	between 0.01 and 0.001	*		21 · 56	21.56 between 0.01 and 0.001	19.38	n.s.	15.73	n.s.	156-36	0.001	112-64	0.001

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														-
			ł	Proportions of Burrow Entrances Active in Warrens (%)	s of Bur	row Entra	nnces Ac	tive in Wa	rrens ( <sup>o</sup>	¢			Tota	Total Size
Citon and Unhitate		0	-	1–25	26	26-50	0	050	S.	51-75	76–100	100	Distri	Distribution
DICS and Lauran	ײ	Signifi- cance	x <sup>2</sup>	Signifi- cance	$\chi^2$	Signifi- cance	$\chi^{2}$	Signifi- cance	×2	Signifi- cance	x²	Signifi- cance	X <sup>2</sup>	Signifi- cance
Mitchell, south of fence : Tero Creck, desert loam (pre-summer)	*		*		*		*		1.75	n.s.	58.65	100-0	128-41	0.001
Mitchell, south of fence : Tero Creek, sand dunes (pre-summer)	*		5.29	n.s.	40.94	0.001			23.17	n.s.	71 - 39	0.001	29.89	n.s.
Mitchell, south of fence : Tero Creek, sand dunes (post-summer)			0 · 565	n.s.									172-46	0.001
Tero Creek, stony hills: Tero Creek, stony pediments	3.76	n.s.	*		12.87	n.s.	27 · 27	between 0.01 and 0.001	27-77	between 0.01 and 0.001	19-64	D.S.	40 • 92	n.s.
Tero Creek, stony hills: Tero Creek, sand dunes (pre-summer)	21.18	0.001	16.94	0.001	29 · 50	0.001	45.59	0.001	21 - 11	n.s.	199.69	0.001	172.82	0.001
Tero Creek, pediments: Tero Creek, sand dunes (pre-summer)	*		*						21.35	n.s.			144.76	0.001

TABLE 7 (Continued)

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	_				IAB	I ABLE / (Continued)	ntinued)							
				Proportions of Burrow Entrances Active in Warrens (%)	ns of Bu	rrow Entra	ances Ac	tive in W	arrens (;	୍ଦ			Tot	Total Size
Sites and Habitats		0		1–25	Ñ	26–50		0-50	5	51-75	76-	76-100	Distr	Distribution
	X²	Signifi- cance	$\chi^{2}$	Signifi- cance	$\chi^2$	Signifi- cance	X2ª	Signifi- cance	X <sup>2</sup>	Signifi- cance	×°	Signifi- cance	x²	Signifi- cance
Tero Creek, desert loam (pre-summer) : Tero Creek, sand dunes (pre-summer)	*		*		*		*		*				131-77	0.001
Tero Creek, sand dunes (pre-summer): Tero Creek, sand dunes (post-summer)	18.10	0.001	9.35	between 0.01 and 0.001	35.45	100 - 0	53 · 62	0.001	21 20	n.s.	7.30	n.s.	175-97	0-001
Tero Creek, desert loam (pre-summer) : Tero Creek, desert loam (post-summer)	*		*		*		*		*				25.42	between 0.01 and 0.001
Tero Creek, desert loam (post-summer): Tero Creek, sand dunes (post-summer)	* -		*		*		*		*		*		28.00	n.s.

TABLE 7 (Continued)

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\* Insufficient warrens to carry out  $\chi^2$  test.

# (d) Evidence of Predation on Nestling Rabbits

During the breeding season nestling rabbits form a large part of the diet of the fox in some areas. The fox is able, probably by sound, to detect the presence of nestlings beneath the surface of the ground and burrows down almost vertically to the nest, leaving behind the signs of its activities.

In Queensland, the sand goanna, *Varanus varius* (Shaw), also feeds on nestling rabbits, but burrows into the nest more horizontally and leaves a gaping hole 2–3 ft wide.

The signs of predation by foxes in all the warrens observed are tabulated in Table 8.

Site and Habitat	Total Numbers of Warrens	Numbers of Warrens attacked by Foxes	Numbers of Nests destroyed by Foxes
Snowy Plains, N.S.W.	829	0	0
Mitchell, Qld.	871	66	78
Tero Creek, N.S.W. stony hills	806	11	12
Tero Creek, N.S.W., stony pediments	371	46	58
Tero Creek, N.S.W., desert loam (pre-summer)	228	136	230
Tero Creek, N.S.W., desert loam (post-summer)	96	12	25
Tero Creek, N.S.W., sand dunes (pre-summer)	2886	1242	2376
Tero Creek, N.S.W., sand dunes (post-summer)	523	97	144

TABLE 8

EVIDENCE OF PREDATION BY FOXES (VULPES VULPES (L.)) ON NESTLING RABBITS AT THREE SITES IN EASTERN AUSTRALIA

Predation of nestlings by foxes was heaviest in the warrens built in sandy soils. Over half the warrens constructed in sandy loam and sand dunes in the semi-arid area showed evidence of predation by foxes. Approximately two nests per warren were destroyed, and thus about 10,000 young.

In the higher rainfall at Mitchell, predation by foxes was much lighter, only 66 out of 871 warrens having been attacked. Predation was also light on the stony habitats. At Snowy Plains no nestlings were taken. Light predation of nestlings by sand goannas occurred only at Mitchell, where 35 warrens showed signs of attack.

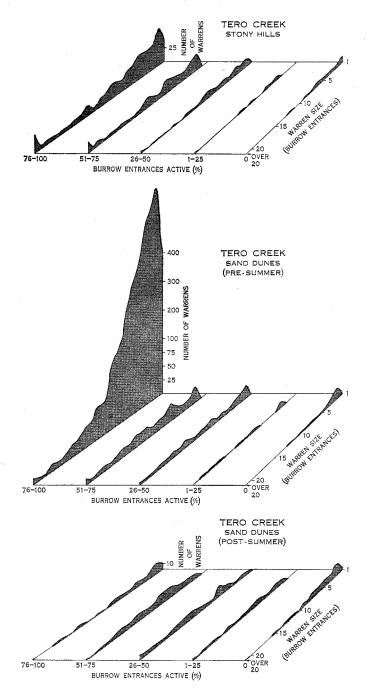


Fig. 11.—Distributions of patterns of activity in warrens of different sizes in some major habitats at Snowy Plains, Mitchell, and Tero Creek. Note the dramatic increase in inactivity in warrens in sand dunes, Tero Creek (post-summer) and the relatively greater inactivity in warrens on the stony tablelands when compared with the other habitats.

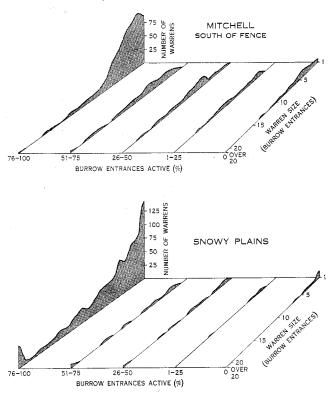


Fig. 11 (Continued)

### IV. DISCUSSION

The measurement of patterns of distribution of a species of mammal as small as the rabbit in a country the size of Australia is complicated by all sorts of methodological problems. The greatest of these are posed by vast areas and varied habitat. Under such circumstances some compromise is clearly necessary. The work described in this paper is an initial attempt to find out what kind of information can be obtained by studying warrens, the places in which rabbits live.

The rabbit is a burrowing mammal. Earlier work (Myers 1958) has shown that the rabbit must burrow to breed, and that very little burrowing occurs outside the breeding season (Myers and Poole 1961). It seems likely on the available evidence that this form of behaviour is intimately tied up with the endocrine state of the female, since bursts of digging occur rhythmically in relation to pregnancy or pseudopregnancy (Myers and Poole 1962; Hughes and Myers, unpublished data) and after fresh germinations of pasture when rain falls following dry periods. Additionally to this, rabbits are attracted to warrens at the beginning of the breeding season by social factors, and each warren becomes the centre of interest of breeding groups (Mykytowycz 1960; Myers and Poole 1961). During the breeding season all rabbits undoubtedly attach to a warren if there is one available (Myers and Schneider 1964; Mykytowycz and Gambale 1965).

Outside the breeding season the warren reverts essentially to a place for shelter. In arid and subtropical climates, such as Tero Creek and Mitchell, without shelter of this kind in summer the rabbit could not exist. In more temperate climates, when the social bonds attracting rabbits to warrens become weak the numbers of rabbits living on the surface away from warrens probably increase. Such rabbits represent major problems in assessments of population distributions. There is little doubt, nevertheless, that warren distribution is synonymous with rabbit distribution throughout all of the hotter parts of Australia and in almost all of Australia during the breeding season.

Within the region of higher rainfall where warren destruction is practised assiduously as a method of rabbit control, e.g. Lake Urana, warrens are small, sparse and scattered. The area in Queensland north of the fence also provides a good example of such a situation. In the other areas described warren destruction occurs only by natural agencies, and the patterns of distribution and size and usage of warrens are those determined by the biological requirements of the rabbit itself. There is much to be learnt about the biology of a species by studying such phenomena.

In the subalpine environment the warrens are almost completely limited to areas with either present or past histories of grazing by stock. In this habitat the rabbit probably depended heavily upon grazing stock for transforming the dense tussocks of snow grass into a low sward of mixed annual and perennial grasses suitable to feed on. The high density of burrows per square mile indicates that very large populations of rabbits have been present in some past period. The warrens are well underpopulated at present. Work is needed to show whether rabbits still need to accompany stock in order to maintain populations of any size, or whether in fact stock-grazing has any effect on rabbit numbers at all. Pasture degradation may have advanced to such an extent that rabbit grazing alone may suffice to hold pastures in check.

The distribution patterns in Queensland and at Tero Creek emphasize the complete favourability of sandhills as rabbit habitat. Elsewhere in Australia the predilection of rabbits for sand is well known. In the Riverine Plain of southern New South Wales every sandhill surrounded by flat grasslands once carried large populations of rabbits (Myers 1962) and remain as perpetual refuges for those rabbits still evading control activities.

The value of sand to the rabbit probably derives from two sources—its suitability as a medium in which to burrow and place young, and the quickness with which its flora responds to rains. Given sufficient food there is little doubt that population increase takes place on sand more quickly than in any other habitat, where difficulty in digging, wet nests, and poor pasture response to rains, all place heavy restrictions on successful breeding. The almost complete restriction of rabbits to sand in the Queensland study area is probably due to bad drainage during the heavy monsoonal rains in other habitats.

The sandy habitat has its disadvantages in that predators, principally the fox, find no difficulty in burrowing down to capture nestlings at considerable distances

below the surface. In dry periods sandy warrens collapse or are blown over. The easy digging, however, ensures no lack of shelter when breeding commences.

Warrens in stony habitats, as at Tero Creek, pose a different ecological problem. They remain as memorials to a once-thriving rabbit population, probably in the 1890's. The rocky and stony habitat in which the warrens exist appears to be alien to the rabbit and it is altogether likely that the diggings represent old and completely destroyed warrens of the burrowing marsupial *Bettongia lesueuri* Quoy and Gaimard. Usually constructed in soft shales and situated in stands of saltbush (*Atriplex* spp.) or bluebush (*Kochia* spp.), these warrens sometimes form hills of ejected material 3 ft above the surface of the ground, and are clearly very ancient. Such warrens may have, indeed, helped the rabbit in its first amazing spread across arid Australia. The lower density of burrows in stony habitats suggests that rabbit populations do not build up to numbers there comparable with those on sand. Work is needed to compare the productivity of these major arid zone habitats.

The work strongly suggests that there are great differences in productivity between major habitats and there are also gradients of favourability within each. Thus, in subalpine and semitropical areas, with their wet soils, raised and well-drained sites are at a premium. In arid zone habitats need for water is the main factor influencing rabbit distribution. Arid zone rabbits obtain their water from plants, and warren distribution thus follows watercourses in the hills and the edges of swamps and creeks and large inter-dune depressions in the sand, where plant growth is concentrated, especially during the hot summer months.

The importance of different soil types is probably limited to whether they afford easy digging or not during the breeding season.

The value of warren density distribution and patterns of warren usage as indices of population numbers is not yet known.

In areas of firm soils or of rocky and gravelly terrain the warrens present are representative in some way of the highest population of rabbits that have existed in the area for many years past—probably upwards of 50 yr in arid zone habitats—and are thus indices of the total population the habitat can support.

In sand dunes and very light soils, on the other hand, warren density distribution is probably a fairly accurate index of the population present during recent times, since the existence of warrens in such habitats is dependent upon continual burrowing activities by rabbits.

The relationships which numbers of holes in a warren and the proportion of them which are actively used bear to total numbers of rabbits can only be determined by accurate observations on warren populations. For the present it can only be assumed that a large number of holes not used in a warren signifies a depression in population numbers. On this assumption all of the populations surveyed in this work were well below their possible peaks, since large numbers of inactive burrows occurred in most habitats.

One of the fascinating aspects of the observations relates to warren size and groupings. The upper limit to warren size appears to lie between 50 and 60 burrow

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entrances. It is possible that this represents the upper limits to the numbers of rabbits which can live together in one colony and that social factors determine this size. Social factors also may be operative in the grouping together of several warrens to give a clumped distribution of warrens in large areas of similar habitat. During the mapping no evidence was obtained to suggest habitat differences as a cause for warren grouping along sand dunes.

The work described in this paper is essentially exploratory. Further surveys of other habitats are planned, when more emphasis will be placed upon spatial relationships, situation of warrens in relation to minor features of environment, and relationships between activity patterns and total population.

# V. ACKNOWLEDGMENTS

The authors wish to thank Mr. R. Lethbridge, Mitchell, Queensland, for permission to use "Warren Point" as a base for operations, Mr. Graham Green for permission to work on "Tero Creek", and Kosciusko State Park Trust for permission to work within the boundaries of the Kosciusko State Park. The interest shown and assistance given by the above are gratefully acknowledged.

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The Snowy Mountains Authority, Cooma, kindly made available meteorological records and aerial photographs of the Snowy Plains. The Division of National Mapping, Canberra, provided aerial photographs of Mitchell, Qld., and photographed the originals of all maps for publication. The Department of Lands, Sydney, N.S.W., provided aerial photographs and photo-maps of Tero Creek and Urana, N.S.W.

Information on rabbit distribution in Western Australia was supplied by Mr. A. R. Tomlinson, Agricultural Protection Board, Dr. A. R. Main, University of Western Australia, and Dr. W. L. Ride, Western Australian Museum, in the Northern Territory by Mr. A. Newsome, University of Adelaide, and in Queensland by Mr. W. Amory, Leichhardt Rabbit Board. The map is a composite one and represents the best of available data.

Plant names and habitat information were taken from "The Australian Environment", 3rd Ed. 1960 (CSIRO, Melbourne University Press.), Beadle (1948), Blake (1938), and Costin (1954).

Mr. E. Slater, of this Division took all photographs except those of Mitchell, Qld. which were taken by Mr. E. C. Schneider, also of this Division.

#### VI. REFERENCES

BLAKE, S. T. (1938).—The plant communities of western Queensland and their relationships with special reference to the grazing industry. *Proc. R. Soc. Qd.* 69: 156–204.

**BEADLE**, N. C. W. (1948).—"The Vegetation and Pastures of Western New South Wales." (Govt. Printer: Sydney.)

BUTLER, B. E. (1950).—A theory of prior streams as a causal factor of soil occurrence in the Riverine Plain of south-eastern Australia. Aust. J. Agric. Res. 1: 231–52.

- COSTIN, A. B. (1954).—"A Study of the Ecosystems of the Monaro Region of New South Wales." (Govt. Printer: Sydney.)
- MYERS, K. (1958).—Further observations on the use of field enclosures for the study of the wild rabbit, Oryctolagus cuniculus (L.). CSIRO Wildl, Res. 3: 40-9.
- MYERS, K. (1962).—A survey of myxomatosis and rabbit infestation trends in the eastern Riverina, New South Wales, 1951–60. CSIRO Wildl. Res. 7: 1–12.
- MYERS, K., MARSHALL, I. D., and FENNER, F. (1954).—Studies in the epidemiology of infectious myxomatosis of rabbits. III. Observations on two succeeding epizootics in Australian wild rabbits on the Riverine Plain of south-eastern Australia 1951–53. J. Hyg. 52: 337–60.
- MYERS, K., and POOLE, W. E. (1961).—A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. II. The effects of season and population increase on behaviour. *CSIRO Wildl. Res.* 6: 1–41.
- MYERS, K., and POOLE, W. E. (1962).—A study of the biology of the wild rabbit, Oryctolagus cuniculus (L). in confined populations. III. Reproduction. Aust. J. Zool. 10: 225-67.
- MYERS, K., and SCHNEIDER, E. C. (1964).—Observations on reproduction, mortality and behaviour in a small, free-living population of wild rabbits. *CSIRO Wildl. Res.* 9: 138–43.
- MYKYTOWYCZ, R. (1960).--Social behaviour of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.) III. Second breeding season. *CSIRO Wildl. Res.* 5: 1-20.
- MYKYTOWYCZ, R., and GAMBALE, S. (1965).—A study of the inter-warren activities and dispersal of wild rabbits, *Oryctolagus cuniculus* (L.), living in a 45-ac paddock. *CSIRO Wildl. Res.* **10**: 111–23.

#### EXPLANATIONS OF PLATES 1, 4, 5, 6, 7, 8, and $12^*$

#### Plate 1

- Fig. 1.—Panorama across valley of the Gungarlin River, Snowy Plains, N.S.W., showing the open valley floor, the meandering river, and forested hills. Rabbit warrens are built in and about the outcrops of granite on the valley floor and along the margins of the forested slopes.
- Fig. 2.—Photograph from top of small sand hill at Mitchell, Qld., looking down on Mitchell grass plains, cut by river bordered with red gums (*Eucalyptus camaldulensis*). The sand hill carries a concentration of rabbit warrens, in a scattered savannah woodland. The trees in the foreground from left are sandalwood (*Santalum lanceolatum*), boonery (*Heterodendron olaefolium*), and two dead ironwood wattles (*Acacia excelsa*).
- Fig. 3.—Photograph of Mitchell grass plain rising to *Eucalyptus* forest, Mitchell, Qld. No rabbit warrens occur on the plain.

#### Plate 4

Aerial photograph of Tero Creek, N.S.W., showing the main physiographic regions: (1) stony tablelands; (2) stony pediments; (3) Mitchell grass plains; (4) flat red sandy loams; (5) low sand dunes. Area A was mapped prior to the summer of 1963-64, and area B after the summer.

\* Plates 2, 3, 9, 10, and 11, together with the explanations of these plates, will be found in the wallet attached to the inside back cover.

#### PLATE 5

- Fig. 1.—Panorama from the air of stony pediments showing rabbit warrens in light shales bordering dry watercourse lined with red gum (*E. camaldulensis*). Tree cover principally mulga (*A. aneura*).
- Fig. 2.—Photograph of warren in stony pediments surrounded by saltbush (*Atriplex* sp.) and bluebush (*Kochia* sp.). Residual hill with flat peneplain surface (top left). Principal tree species, mulga (*A. aneura*) and desert-oak (*C. cristata*).

#### Plate 6

Fig. 1.—Photograph from air of junction of sand dunes, desert loams (upper right), and Mitchell grass plains (middle right) at Tero Creek, showing continuation of drainage patterns into the dune area and the presence of swamps of various sizes. Rabbit warrens are concentrated on the dunes near the large lignum swamp in centre and along the dunes to the north.

Fig. 2.—Close-up of sand dune surface from air showing rabbit warren in stand of mulga, Tero Creek.

### Plate 7

Fig. 1.—Aerial photograph of sandy desert loam with scattered mulga, Tero Creek.

Fig. 2.—Photograph of desert loam, Tero Creek, carrying a savannah woodland dominated by mulga. Rabbit warrens occur in low density throughout this habitat.

#### Plate 8

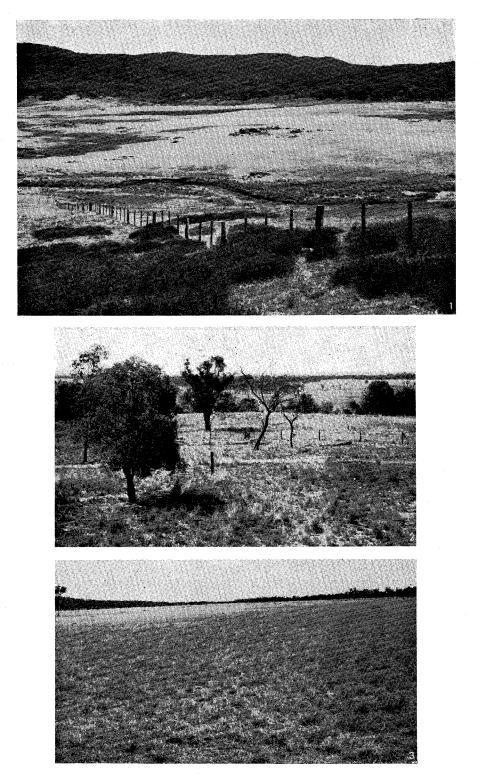
- Fig. 1.—Photograph of Mitchell grass plain, Tero Creek, with stony tablelands and pediments in distance. No rabbit warrens occur in this habitat.
- Fig. 2.—Photograph of large rabbit warren at junction of stony pediments and Mitchell grass plains, excavated in soft, white shales, Tero Creek.

### PLATE 12

Aerial photograph of Lake Urana, N.S.W., a lake of internal drainage in the eastern Riverine Plain. The lake is shallow, fills only after heavy rains, and remains dry for many years at a time. It is surrounded by a rim of sand which has been a refuge for rabbits for the past 80 yr. Scale: 1 in. = approx. 1.4 miles.

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Plate 4

