THE DISTRIBUTION OF RED KANGAROOS, *MEGALEIA RUFA* (DESMAREST), ABOUT SOURCES OF PERSISTENT FOOD AND WATER IN CENTRAL AUSTRALIA

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Summary

Data from aerial surveys primarily designed to estimate the numbers of red kangaroos, *Megaleia rufa* (Desmarest), on about 4000 square miles of central Australia have been used to define the animals' distribution about sources of persistent food and water, both during severe drought and 6 months later after good rains had fallen.

During the drought, 67·4% of kangaroos were sheltering in woodlands within ⅛ mile of open plains and water-courses (where food persisted), and only 17·4% were further than 1 mile away. After the rains, only 29·5% were within ⅛ mile of these drought refuges; 51·8% were further than 1 mile away, but only 6% were beyond 6 miles out, i.e. beyond the mulga woodlands.

Kangaroos were densest (seven–eight per square mile) during drought on land 2–4 miles out from bores and dams and within ⅛ mile of open plains because at that distance grasses on the plains respond to the grazing of cattle by sprouting green shoots which kangaroos prefer. Kangaroos drank at the bores and dams only during severe drought and may, therefore, get sufficient water from their food at most times.

It is concluded that the kangaroos' distribution and changes in it are controlled primarily by their search for green herbage and shady trees.

I. INTRODUCTION

Newsome (1965) estimated the number of red kangaroos, *Megaleia rufa* (Desmarest), on an area of 4000 square miles in central Australia once after prolonged drought and again 6 months later, about 3 months after good rains had fallen. During the drought the kangaroos seemed to be concentrated along the margins of water-courses and open plains that dissected the mulga woodland. They rested under the shade of the mulga trees (*Acacia aneura*) during the day, and came out to feed at night at depressions in the plains and water-courses which were almost the only places where any green grass could be found during the drought. These places have been called "drought refuges" (Newsome 1965). When the same area was sampled a second time after good rains had fallen, the kangaroos seemed to be scattered throughout the woodland in which green herbage was temporarily abundant.

Because the investigation was primarily aimed at estimating numbers, the method of sampling did not yield the maximum amount of information about the distribution of kangaroos. Nevertheless, it has been possible to rearrange the results to quantitatively describe the distribution of the kangaroos relative to food and water, two resources that are important because they can be scarce.

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II. Methods

The method used in collecting data has been described elsewhere (Newsome 1965) but, briefly, it was as follows. The aircraft was flown at about 300 ft above the ground and 80 m.p.h. so that in 10 sec it travelled 2/9 of a mile. The area scanned in that time was defined as a quadrat whose width depended on the nature of the terrain, and it was demarcated by sighting through calibrated marks on the wing struts of the aircraft. The areas of quadrats in square miles were 0·119950 over open plains, 0·106061 over lightly wooded country, 0·069024 over mulga woodland, and 0·031986 over densely wooded country. The sizes of the quadrats over variable country differed according to the nature of the terrain on either side of the aircraft.

The study area was divided into a number of blocks, and randomly chosen transects in them were flown approximately at right angles to the edges of open plains and water-courses, the sources of persistent food, so that data in successive quadrats could be used to compare the density of kangaroos at various distances from them. Kangaroos were counted on the first occasion from October 2 to October 6, and from October 9 to October 12, 1961, after 6 months of drought; and on the second occasion from April 24 to April 28, and from April 30 to May 2, 1962, 3 months after good rains, yielding from 2 to 4 inches, fell over the entire study area.

The lanes flown were plotted on the map of the study area, and divided into segments 2/9 in. long to represent four consecutive quadrats. The position of any green herbage seen during drought was also plotted but the positions of bores and dams were already given on the map. The distances from the mid-point of each aggregate of quadrats to sources of persistent food and water were then measured in twelfths of an inch ($\frac{1}{12}$ in. representing $\frac{1}{3}$ mile on the ground). Quadrats were classified according to their distances from food and from water, and arranged on two-way frequency tables (like that in Table 1). The lowest number of quadrats in any category on the tables was 40.

III. Results

In the sample taken during the drought 1017 kangaroos were seen in 7212 quadrats, and in that taken after rains, 1102 kangaroos were seen in 9748 quadrats. These data were used to determine the number of kangaroos at various distances from food and water. The steps required to do this are given below.

(*a*) *Estimating the Number of Kangaroos per Square Mile in each Category of Country*

The number of kangaroos in each quadrat was converted into the number per square mile, and these values were treated as normally distributed variates to provide estimates of the mean and variance for each category. Because the sizes of the means and variances were correlated, corrected estimates of the variances were calculated. The estimates of means arranged as two-way histograms are given in Figures 1 and 2; the scales on the axes of these histograms were altered a little from those in Tables 1 and 2.

(*b*) *Estimating the Total Area in each Category*

A rectangular grid with about 6000 intersections was superimposed on a map of the land sampled during drought, and 619 intersections were chosen at random.

TABLE 1

AREAS* OF VARIOUS CATEGORIES OF LAND DURING DROUGHT AND THE PERCENTAGE† OF THE LAND SCANNED

Distance from Water (miles) / Distance from Persistent Food (miles)	0–1	1–2	2–3	3–4	4–5	5–6	6–8	8–10	10–18	Totals
0–⅓	123·9	254·8	136·0	101·6	65·4	17·2	6·9	1·7	—	707·5
	(21·9)	(15·3)	(28·5)	(15·0)	(16·8)	(17·2)	(4·0)	(0)		(19·0)
⅓–1	74·0	160·1	110·2	72·3	39·6	6·9	3·4	—	—	466·5
	(18·4)	(17·8)	(20·7)	(16·7)	(12·7)	(19·0)	(8·0)			(17·9)
1–2	43·0	79·2	120·5	84·3	39·6	10·3	3·4	—	—	380·3
	(18·6)	(20·2)	(13·9)	(14·9)	(10·1)	(16·0)	(0)			(15·5)
2–3	37·9	55·1	93·0	108·4	56·8	17·2	10·1	—	—	378·5
	(12·6)	(16·9)	(12·3)	(7·4)	(8·1)	(4·0)	(0)			(10·2)
3–4	20·7	37·9	63·7	79·2	70·6	24·1	12·2	—	—	308·4
	(16·4)	(14·2)	(8·0)	(10·2)	(5·2)	(3·4)	(2·3)			(8·7)
4–5	13·8	36·1	49·9	62·0	63·7	37·9	15·6	—	—	279·0
	(7·0)	(15·3)	(9·4)	(9·1)	(5·6)	(6·9)	(0)			(8·3)
5–6	9·2	22·3	32·7	48·1	44·8	34·4	20·6	—	—	212·1
	(15·7)	(11·8)	(13·9)	(9·2)	(6·8)	(2·0)	(6·7)			(8·6)
6–7	8·0	19·1	25·8	36·2	37·9	24·1	22·3	—	—	173·4
	(3·5)	(1·4)	(8·0)	(14·1)	(9·8)	(6·3)	(8·7)			(8·6)
7–8	10·3	19·9	25·8	33·0	28·3	17·2	18·9	6·9	—	160·3
	(5·3)	(6·2)	(10·2)	(8·8)	(6·3)	(6·4)	(4·4)	(0)		(6·9)
8–9	10·3	17·9	22·4	29·0	23·3	15·5	20·7	9·5	—	148·6
	(8·0)	(6·9)	(13·0)	(5·7)	(8·9)	(10·7)	(5·3)	(4·4)		(8·5)
9–11	17·2	34·4	39·6	46·5	44·7	29·3	48·2	29·0	5·2	294·1
	(17·8)	(13·2)	(10·5)	(15·0)	(5·3)	(5·2)	(7·7)	(4·3)	(13·3)	(9·3)
11–13	10·3	22·4	27·6	37·9	37·9	27·6	34·4	44·1	13·8	256·0
	(12·1)	(9·2)	(13·0)	(13·8)	(18·2)	(12·0)	(13·2)	(16·7)	(0)	(12·6)
13–16	12·3	24·1	25·8	34·4	41·3	27·6	29·7	39·6	36·1	270·9
	(5·6)	(6·3)	(12·4)	(9·2)	(5·0)	(26·3)	(15·3)	(2·1)	(0)	(7·8)
16–23	15·5	25·8	38·0	37·9	29·3	18·2	21·4	24·1	17·2	227·4
	(10·7)	(18·7)	(11·6)	(9·5)	(6·6)	(9·1)	(27·1)	(9·7)	(31·2)	(13·9)
Totals	406·4	809·1	811·0	810·8	623·2	307·5	267·8	154·9	72·3	4263·0
	(16·6)	(15·1)	(15·7)	(11·5)	(8·3)	(9·2)	(9·2)	(7·9)	(8·4)	(12·5)

* In square miles; † Values in parentheses.

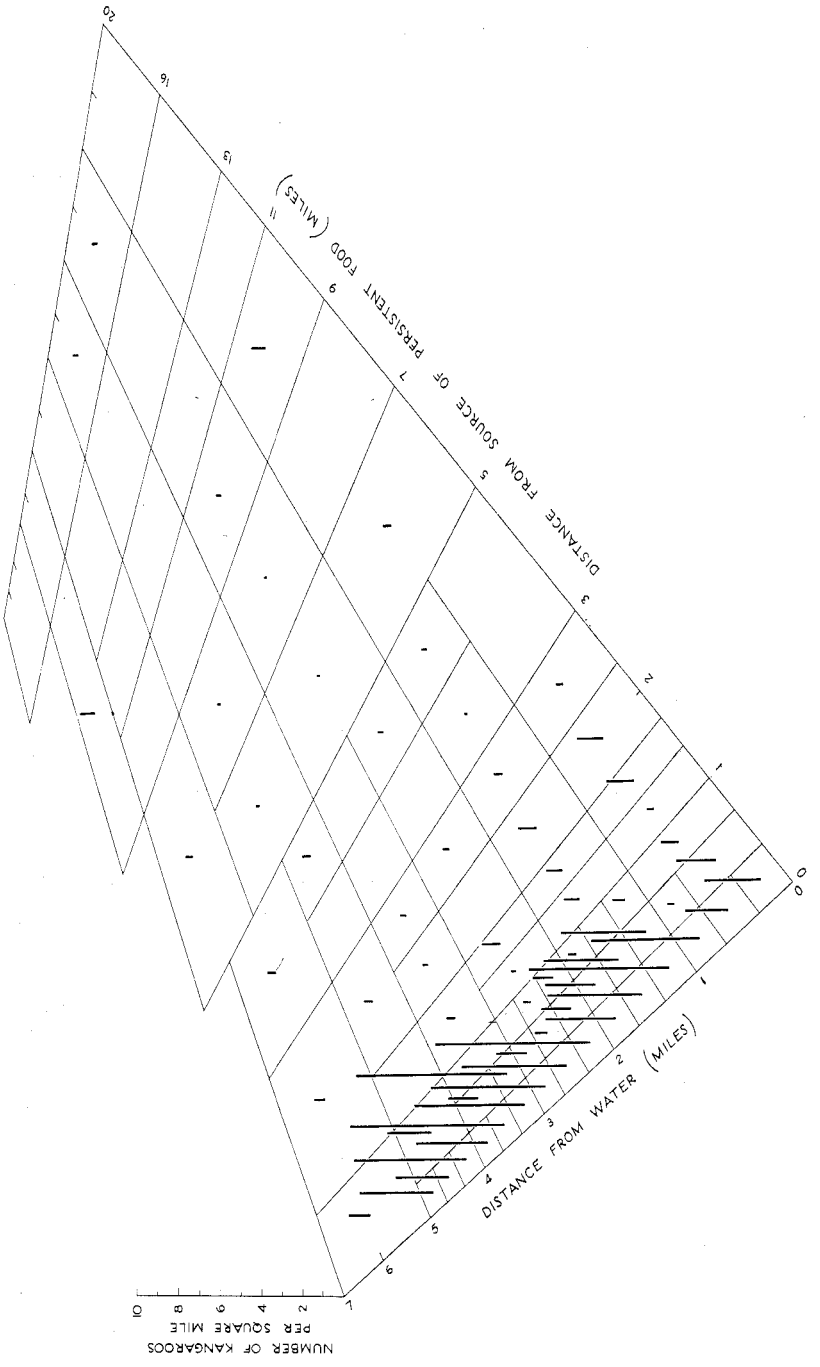

Fig. 1.—Numbers of kangaroos per square mile on various categories of land during drought.

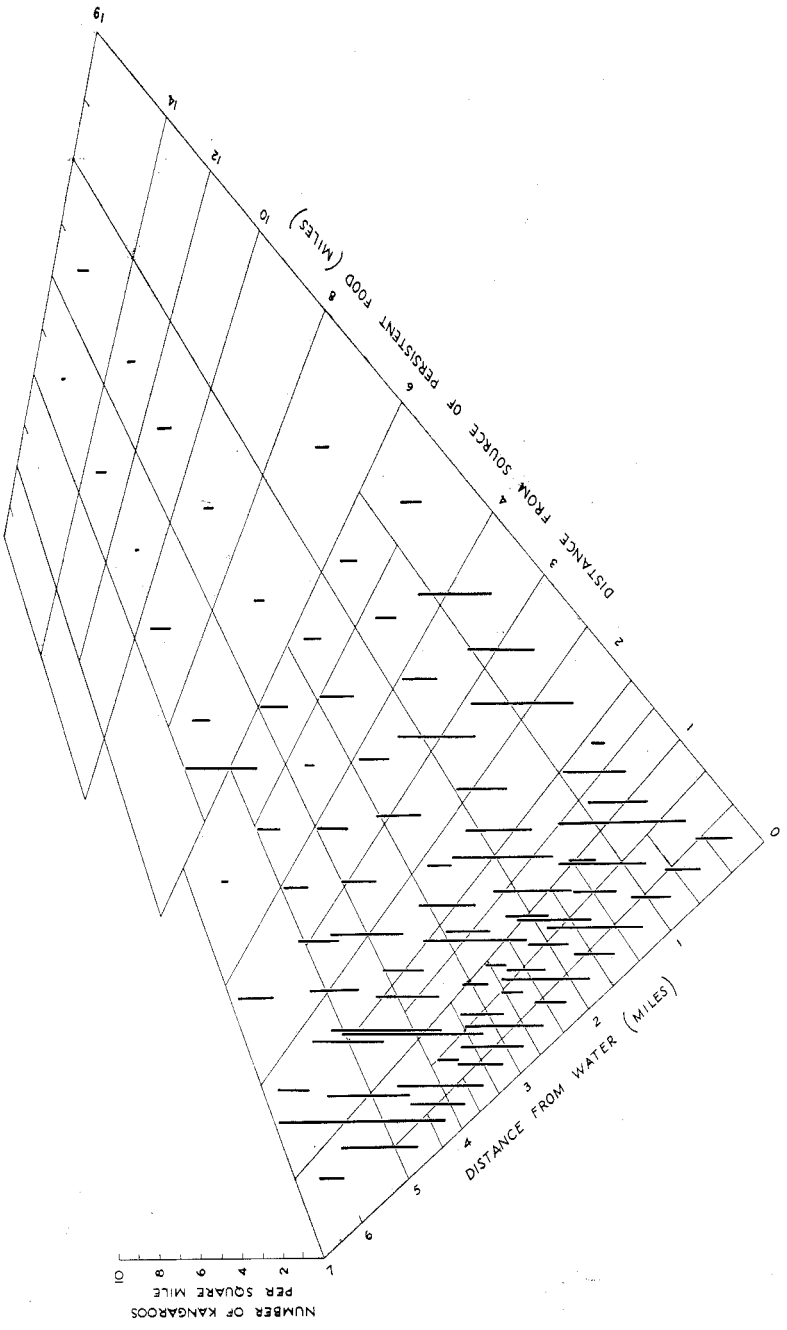

Fig. 2.—Numbers of kangaroos per square mile on various categories of land after rain.

TABLE 2

AREAS* OF VARIOUS CATEGORIES OF LAND AFTER RAIN AND THE PERCENTAGE† OF THE LAND SCANNED

Distance from Water (miles) / Distance from Persistent Food (miles)	0–1	1–2	2–3	3–4	4–5	5–6	6–8	8–11	Totals
0–⅓	83·2	251·1	126·1	92·0	57·7	11·9	7·8	—	629·8
	(38·4)	(18·6)	(27·8)	(27·3)	(13·3)	(15·1)	(7·1)		(23·5)
⅓–1	62·4	158·2	78·7	44·8	25·1	3·3	0·9	—	373·4
	(23·6)	(20·0)	(36·6)	(33·7)	(17·3)	(12·6)	(71·8)		(25·6)
1–2	45·5	84·7	101·9	96·4	49·1	12·3	1·4	—	391·3
	(16·7)	(34·8)	(22·5)	(15·8)	(10·2)	(20·5)	(30·3)		(21·1)
2–3	27·3	50·9	102·8	80·5	42·8	11·0	3·2	—	318·5
	(15·4)	(20·0)	(19·1)	(17·4)	(17·3)	(35·1)	(19·5)		(18·7)
3–4	16·4	35·5	61·0	67·3	44·6	17·3	5·0	—	247·1
	(22·3)	(17·4)	(21·7)	(25·1)	(18·2)	(11·6)	(11·0)		(20·4)
4–5	13·6	33·7	46·4	45·6	28·2	10·0	5·7	—	183·2
	(18·5)	(22·7)	(21·2)	(14·0)	(18·4)	(14·5)	(18·8)		(18·4)
5–6	6·5	14·6	31·8	40·9	23·7	6·4	3·4	—	127·3
	(28·1)	(21·3)	(22·0)	(13·3)	(11·8)	(42·3)	(49·7)		(19·2)
6–7	5·5	12·7	22·7	21·9	19·1	12·7	8·2	—	102·8
	(21·5)	(49·0)	(31·7)	(32·1)	(19·5)	(12·5)	(16·4)		(27·6)
7–8	5·5	15·5	29·1	20·0	12·8	7·3	5·5	—	95·7
	(29·1)	(19·2)	(28·9)	(22·9)	(25·9)	(3·8)	(5·0)		(22·3)
8–10	13·7	34·5	43·7	29·2	33·6	14·6	13·6	—	182·9
	(16·8)	(11·9)	(20·4)	(18·2)	(15·2)	(34·2)	(25·0)		(18·6)
10–12	9·1	21·8	31·9	43·7	65·5	19·5	22·7	10·9	225·1
	(7·7)	(26·5)	(35·4)	(13·5)	(13·1)	(24·1)	(17·6)	(19·3)	(19·2)
12–14	7·2	19·9	29·1	40·0	29·2	20·9	18·2	7·3	171·8
	(8·6)	(13·1)	(21·0)	(13·0)	(23·9)	(15·3)	(23·1)	(46·6)	(18·9)
14–19	10·5	27·3	35·0	39·6	36·4	38·7	40·5	26·4	254·4
	(43·8)	(26·4)	(10·8)	(1·8)	(19·0)	(13·7)	(14·3)	(3·0)	(13·8)
Totals	306·4	760·4	740·2	661·9	467·8	185·9	136·1	44·6	3303·3
	(23·2)	(20·1)	(24·5)	(18·3)	(15·9)	(18·5)	(18·0)	(14·0)	(20·2)

* In square miles; † Values in parentheses.

Each intersection chosen was classified according to its distance from persistent food and water, and entered on to a two-way frequency table. The values on this table were then smoothed by fitting free-hand curves first through the rows and then through the columns. The curves were then used to construct a second two-way frequency table of smoothed values. These smoothed frequencies were converted into proportions, and multiplied by the total number of square miles in the area sampled. For the blocks sampled after rain, 454 points chosen at random from a possible 4300 were treated similarly. The results for the two areas sampled are shown in Tables 1 and 2; the values in parentheses show the total area of quadrats in each category as a percentage of the area of land in that category.

(c) Estimating the Number of Kangaroos in each Category

The number of kangaroos per square mile were then multiplied by the number of square miles to give the number of kangaroos on each category of country. For example, it was calculated that there were 0·22 kangaroos per square mile on land lying 2–3 miles from food and from water during drought, and Table 1 shows that there were 93 square miles of country in that category. Multiplying these two values together gives an estimate of 20 kangaroos there (Table 3). Similar calculations were made for all categories of country and the results are presented in Tables 3 and 4. Confidence limits ($P=0·05$) are attached to totals shown in the margins of the tables, and to the grand totals. Marginal totals are also expressed as percentages of the grand totals.

IV. Discussion

(a) The Nomadism of Red Kangaroos

The difference between the distributions of the kangaroos during the drought and after rain was striking. During the drought, 67·4% of kangaroos were estimated to be within $\frac{1}{3}$ mile of drought refuges, and only 17·4% were further than 1 mile away. After the rains, however, only 29·5% were within $\frac{1}{3}$ mile of drought refuges, whilst 51·8% were beyond 1 mile of them. However, only 19·3% were further than 3 miles away.

The marginal totals in Tables 3 and 4, expressed as percentages, form frequency distributions from which the average distance of kangaroos from the drought refuges can be calculated. During the drought, kangaroos were on the average 1·351 miles away, and after the rain, 2·020 miles away. Thus, kangaroos had moved an estimated net distance of only 0·669 miles away from their drought refuges in the time between samples. The average distance of kangaroos within 6 miles of the drought refuges was 0·517 miles during drought, and 1·448 miles after rain. This represents a net shift of 0·831 miles away from the open plains and water-courses.

Estimates of densities, summarized in Figures 1 and 2, show the same trends. During the drought, kangaroos reached their highest densities within $\frac{1}{3}$ mile of drought refuges, but after rain there was no obvious pattern to the densities on land within 6 miles of them. Moreover, Table 4 shows that 93·6% of kangaroos were on land within 6 miles of open plains and water-courses after the rains. At about this

TABLE 3

NUMBERS OF KANGAROOS ON VARIOUS CATEGORIES OF LAND DURING DROUGHT

Distance from Water (miles) / Distance from Persistent Food (miles)	0–1	1–2	2–3	3–4	4–5	5–6	6–8	8–10	10–18	Totals	Percentage
0–⅓	481	973	759	520	246	16	7	2	—	3004 ±389	67·384
⅓–1	67	330	96	151	24	7	3	—	—	678 ±193	15·209
1–2	46	71	39	29	12	5	2	—	—	204 ±79	4·576
2–3	13	19	20	26	10	8	5	—	—	101 ±136	2·266
3–4	0	9	0	0	0	10	5	—	—	24 ±19	0·538
4–5	0	7	11	0	25	15	6	—	—	64 ±58	1·436
5–6	3	8	5	7	9	7	6	—	—	45 ±27	1·009
6–7	3	7	4	5	8	5	7	—	—	39 ±23	0·875
7–8	0	0	3	3	4	3	6	2	—	21 ±29	0·471
8–9	0	0	2	3	3	2	7	3	—	20 ±21	0·449
9–11	10	21	9	10	0	0	0	32	6	88 ±46	1·974
11–13	0	0	0	0	0	0	0	48	15	63 ±46	1·413
13–16	0	0	0	0	0	0	0	43	39	82 ±53	1·839
16–23	0	0	7	7	7	4	0	0	0	25 ±29	0·561
Totals	623 ±52	1445 ±280	955 ±188	761 ±213	348 ±135	82 ±44	54 ±29	130 ±66	60 ±39	4458 ±487	100·0
Percentage	13·975	32·414	21·422	17·071	7·806	1·839	1·211	2·916	1·346	100·0	

TABLE 4

NUMBERS OF KANGAROOS ON VARIOUS CATEGORIES OF LAND AFTER RAIN

Distance from Water (miles) / Distance from Persistent Food (miles)	0–1	1–2	2–3	3–4	4–5	5–6	6–8	8–11	Totals	Percentage
0–$\frac{1}{3}$	125	737	296	221	271	13	9	—	1672 ±339	29·525
$\frac{1}{3}$–1	241	393	157	161	99	4	1	—	1056 ±237	18·647
1–2	149	292	204	262	142	19	2	—	1070 ±260	18·895
2–3	80	201	184	184	95	23	7	—	774 ±221	13·668
3–4	59	59	83	95	53	16	4	—	369 ±140	6·516
4–5	14	34	75	21	28	2	1	—	175 ±90	3·090
5–6	6	12	26	56	83	1	1	—	185 ±129	3·267
6–7	4	8	9	8	15	10	0	—	54 ±25	0·954
7–8	4	10	11	8	10	6	0	—	49 ±22	0·865
8–10	0	0	20	13	33	15	0	—	81 ±46	1·430
10–12	3	6	22	30	8	2	0	0	71 ±39	1·254
12–14	0	0	11	15	14	10	0	0	50 ±34	0·883
14–19	0	0	19	22	8	8	0	0	58 ±60	1·006
Totals	685 ±214	1752 ±343	1117 ±222	1096 ±246	859 ±254	129 ±57	25 ±16	0	5664 ±585	100·0
Percentage	12·095	30·938	19·725	19·354	15·169	2·278	0·441	0	100·0	

distance out, the mulga woodland gives way to extensive spinifex tracts. Thus, most of the kangaroos restricted their movements after the rains to the mulga woodlands, and avoided the spinifex tracts even though food was temporarily abundant there at the time. It is likely that they did this for the same reason that they deserted the open plains soon after the rains: they prefer to remain in the shelter of woodlands by day and night if possible (Newsome 1965).

Thus, although kangaroos may move 10–20 miles after rain (Newsome 1965), they keep to the mulga woodlands and do not move far from the open plains and water-courses. This may explain the sudden appearance of animals in numbers on the open plains after a month or two of drought.

The densities estimated during the drought (Fig. 1) showed a second trend; those within $\frac{8}{8}$ mile of drought refuges rose to a maximum of seven–eight per square mile 2–4 miles out from water. The cause of this seems clear. Cattle graze on the grassy plains mostly within 3 miles of water (Perry 1962). Catchment dams and bores have been placed about 5 miles apart to cater for them. Land close to waters has been badly trampled so that little grass grows there, whilst land beyond 5 miles (what little there is) has barely been grazed at all. In between, cattle crop the climax vegetation of long dry grass (mostly woolly-butt, *Eragrostis setifolia*) causing it to sprout from the crown, so providing kangaroos with food, for they prefer green grass to eat (Chippendale 1962), especially during drought (Newsome 1962). When green herbage was abundant after the rains, no trend in the densities with respect to water was obvious (Fig. 2).

This implies that, even during drought, food was more important to kangaroos than water. Indeed, as Table 3 indicates, during drought no more than 10% of kangaroos were further than 3 miles from a drought refuge but over 33% were further than that from water. Moreover, those animals which do not find their way back to the open plains and water-courses probably die (Newsome 1965). Green shoots of *Eragrostis* contain from 16% to 25% water by weight during dry weather, but ungrazed mature stands contain only about 8% (Siebert, personal communication). It may be possible, therefore, for kangaroos to obtain sufficient water from their food, especially when it is abundant. When it is scarce, however, they may need to drink. It was only in severe drought that kangaroos were seen at bores and dams regularly, and on one occasion those grazing on an open plain almost devoid of green herbage were watched throughout the night. They moved gradually towards the water grazing the while, and after drinking, retreated to the depressions harbouring the scant green shoots of *Eragrostis*.

(*b*) *Statistical Methods*

Estimates of means calculated are unbiassed because no bias entered into the choice of quadrats. But the estimates of variances are biassed because the sample of quadrats in each category of country were not chosen randomly. Quadrats in different lanes were randomly related because lanes were chosen randomly, but those in the same lane were systematically related. This bias was overcome to some extent by having no fewer than 40 quadrats in each category. In fact, many categories had many more, the average number of quadrats per category being 129 during drought

and 165 after rain. Moreover, Milne (1959) found that a number of systematic samples, treated as if they were random, yielded estimates of parameters no less reliable or precise than those obtained from random samples. But he found a tendency for systematic samples to provide smaller estimates of standard errors than random samples, but the difference was not quite significant at the 5% level. Hence, any bias involved in calculating statistics in this paper may not be serious. This conclusion is supported by the close agreement between the estimates of total numbers of kangaroos on the study area obtained by the present analysis, 4458 ± 487 during drought, and 5663 ± 585 after rain, and those obtained when the data were analysed strictly according to the requirements for random sampling, 4563 ± 712, and 5654 ± 799 (Newsome 1965).

Because an estimate of a variance has a variance proportional to the size of the true variance, estimates of large variances are likely to depart considerably from the true values. This tendency in the present study was corrected because the sizes of the estimated means and variances were related curvilinearly. The equations to these relationships were obtained by transforming the statistics from each sampling to natural logarithms and by calculating the linear regression of log. variance on log. mean, weighting each point according to its degrees of freedom. The equations obtained were then re-transformed, providing the relationships:

$$s^2 = 22 \cdot 916 \bar{x}^{1.40273} \text{ during drought, and } s^2 = 33 \cdot 586 \bar{x}^{1.34634} \text{ after rain.}$$

The marginal and overall means and their variances used for calculating confidence limits in Tables 3 and 4 were weighted values.

V. Acknowledgments

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