POPULATION DYNAMICS OF THE QUOKKA, *SETONIX BRACHYURUS*, ON THE WEST END OF ROTTNEST I., WESTERN AUSTRALIA

I. HABITAT AND DISTRIBUTION OF THE QUOKKA

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Summary

Data collected over a period of 10 yr is presented on the distribution of a small wallaby, the quokka, on the isolated West End portion of Rottnest I., Western Australia. The density of quokkas in each locality varied with the density of grasses that composed the major portion of their diet. Generally, the animals are non-gregarious and each quokka has a home range of about 10 ac. The home ranges of groups of 25–150 individuals overlap to form group territories. The boundaries of the group territories are stable and in places coincide with topographical features. Young quokkas usually remain in their natal group territory and rarely do permanent changes in group affiliation by animals of any age occur even after the population of adjacent territories has been greatly reduced.

I. INTRODUCTION

Considerable information has been collected on the population dynamics of small, short-lived, fast-breeding rodents and rabbits. However, very little is known about the population dynamics of large, long-lived, slow-breeding mammals because they are usually difficult to catch and mark in large numbers, and their long life span necessitates a study lasting many years. A macropod marsupial, the quokka, *Setonix brachyurus* (Quoy & Gaimard), has a life span of over 10 yr, breeds slowly, but fortunately it is very easy to catch and handle and has been studied for several years.

Population studies of the quokka on Rottnest I., 12 miles offshore from Fremantle, W.A., were initiated by Sharman and Barker in 1954 (Waring 1956). Later the same year Dunnet took over the study and selected for intensive investigation a population coming to freshwater seepages along the shores of the salt lakes at the eastern end of the island (Dunnet 1956, 1962, 1963). Although he was able to collect abundant data on weight changes, growth rates, and reproduction, his choice of a study area was unfortunate for he was unable to satisfactorily relate these data to changes in density because he knew neither what proportion of the population in the vicinity his data represented nor the size of the area the population occupied.

Fortunately, Dunnet and several others also investigated the quokka population of the West End of Rottnest I. (Hodgkin and Sheard 1959). Shield (1958) compared the haematology of the West End quokkas with those on other parts of the island and on the mainland; Barker (1961) investigated the quokka's trace element requirements, and Storr (1961*a*, 1961*b*, 1964) studied the food habits of the West End quokka.

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Between 1954 and 1961 nearly all animals caught on the West End received an ear tag. They were also weighed, measured, and their reproductive status and age were determined. Consequently, when I began an intensive study of the West End population in April 1961 about 20% of the animals carried ear tags and data were available on over 600 animals.

II. Methods

Quokkas cannot be caught easily during the day because they remain hidden under the vegetation and will not flush unless almost stepped on, but they come into the open soon after sundown and can then be easily caught (Packer 1965). Between 1961 and 1964 most of the animals were caught in the 2 or 3 hours just after sundown.

A floodlight mounted on a bar above the rear deck of a Land Rover was used to spot the quokkas, which were then pursued on foot and caught in a long-handled landing net. When caught, the quokka was carried by its tail and placed in a bag so that it could be transported back to the Research Station for examination. Since the total time to catch and bag one animal could be as short as 30 sec, and over 25 animals have been caught by one person in less than an hour, the total catch for an evening was limited more by the number available for capture than the time taken to effect the captures. After examination they were returned to their place of capture. About one-quarter of the quokkas spotted escaped either because they got into dense vegetation where they could not be followed, hid in their tunnels under the shrubbery, or simply outran the catcher.

As shown in the following tabulation, between 1954 and April 1964 approximately 3585 quokkas were handled and altogether 1491 different animals were tagged.

Year	Number Caught	Number Tagged
1954–5	121	101
1956	229	183
1957	178	97
1958	336	141
1959	109	64
1960	38	36
1961	623	293
1962	699	191
1963	813	251
1964	439	134
Totals	3585	1491

Because the quokkas were caught by different researchers for different purposes, the number caught and tagged each year between 1954 and 1964 varied considerably as did the amount of information collected from each animal. Some tagged animals were never recaptured but some were handled more than 20 times. The overall recapture frequency of males and females and different age groups indicated that the method of capturing the animals did not introduce any serious bias into the data.

I made trips to Rottnest I. approximately every month between May 1961 and May 1963. To avoid causing excessive disturbance and changes in the behaviour of

the animals no more quokkas than the minimum necessary to establish various population parameters were caught in any monthly period. To further minimize the effects of being caught and handled, animals caught a second time during the same monthly trip were not taken back to the Research Station but were released immediately after their number and location were recorded.

Prior to 1962 the first time each quokka was caught it received a tag* in its right ear. Although tag loss was thought to be small, some measure of the loss was considered desirable. Starting in 1962 each tagged animal received a second tag in its left ear and each animal caught for the first time received two tags.

All animals taken back to the Research Station were weighed to the nearest 0·1 kg. Their right hind feet were measured to the nearest millimetre and their tail lengths were measured to the nearest 5 mm. After examination of the pouch, each female was identified as virgin or parous (Sharman and Calaby 1964). If parous they were classified in one of the following categories: (1) with joey (pouch young), (2) without joey but lactating, (3) not lactating but with elongated teat (indicating that they had a joey recently), or (4) with no elongate teats.

The hind foot and tail of each joey was measured to the nearest 0·1 mm, and, if possible, the sex of the joey was determined. In addition, the teat to which the joey was attached was noted.

Using the criterion established by Shield (1958), the age of each animal was determined by examining its teeth. Since quokkas breed seasonally the age of all animals under 30 months could be determined quite accurately; at 30 months they achieve adult dentition. Because tooth wear is slight no reliable measurement of the age of quokkas with adult dentition was possible.

Four age categories were established:

(1) *Joey.*—Age 0–7 months, all young animals until they leave the pouch permanently.

(2) *Yearling.*—Age 7–18 months.

(3) *Juvenile.*—Age 19–30 months, without adult dentition (i.e. with deciduous premolars).

(4) *Adult.*—Age 30 months or over, with adult dentition (i.e. with permanent premolar in place).

All the data were recorded in a field note book and later were transferred to "McBee"-type Keysort Cards measuring 5 by 8 in. and having 105 holes.

III. Habitat

The West End of Rottnest I. consists of an area of 350 ac connected to the remainder of Rottnest I. by a narrow isthmus over ½ mile long and 200–400 yd wide (Fig. 1). The network of trails constructed between 1939 and 1960 was increased in 1961 to bring over 80% of the West End within 100 yd of a roadway.

* Tags used were No. 3 fingerling tags obtained from the Salt Lake Stamp Co., Salt Lake City, Utah, U.S.A.

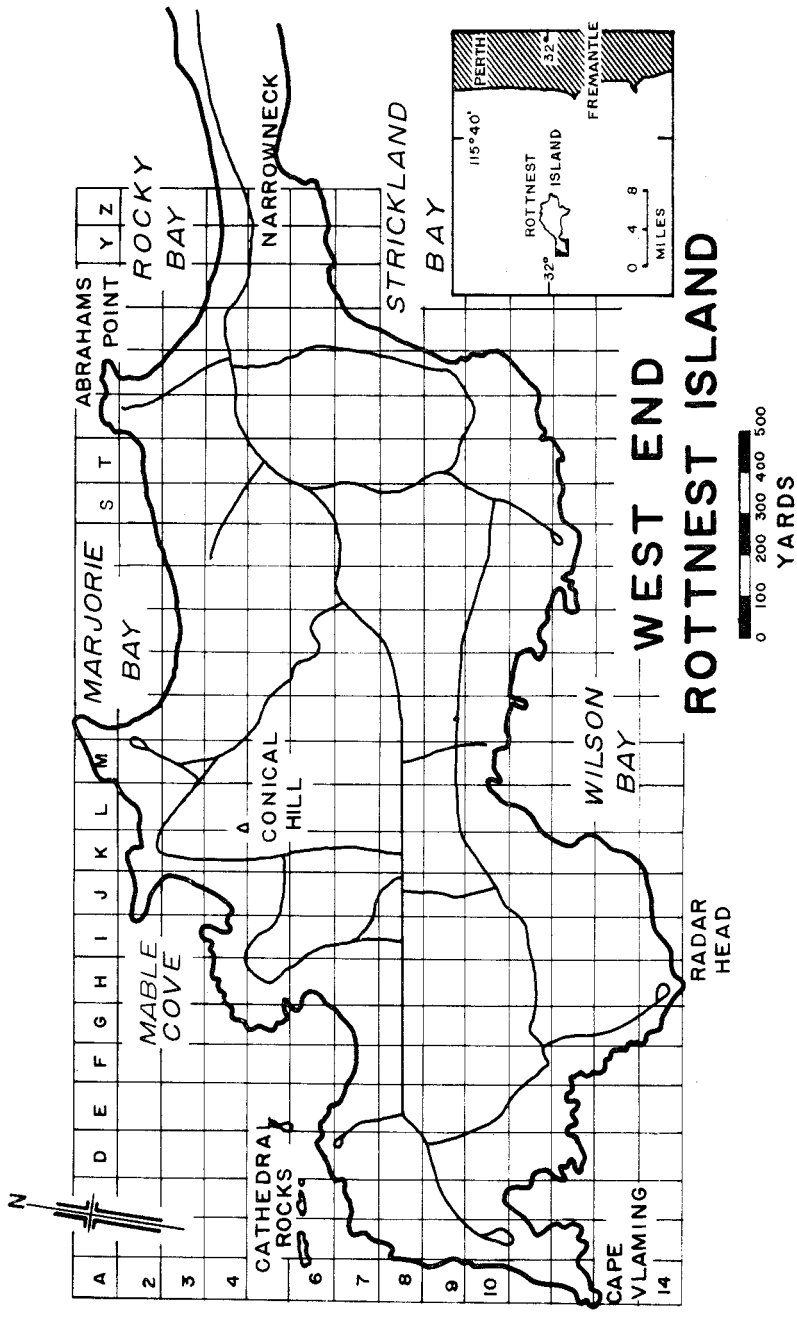

Fig. 1.—The West End of Rottnest Island showing the distribution of roads and the 100-yd sq. grid used for location reference.

Stabilized sand dunes cover the north-eastern third of the West End. Along the north coast, particularly near Marjorie Bay, moving dunes are encroaching on the plateau. The remainder of the West End is relatively flat except for a series of limestone ridges. Fresh water and drainage systems are completely absent because the sandy soil is so porous that even after heavy rains water does not remain on the surface.

Temperature, rainfall, wind velocity, and cloud cover have been recorded at the main lighthouse in the centre of the island for over 80 yr (Bureau of Meteorology, Perth, W.A.). The average annual rainfall is 29·5 in. but usually less than 10% of the total precipitation occurs in the summer months. In some years as little as 1·2 in. have been recorded in the 6-month summer period (October–March). The hottest months, January and February, have an average daily maximum of 78·5°F. July is the coldest month with an average daily maximum of 62·4 and minimum of 46°F. Although it may occasionally get very hot (maximum recorded was 108°F, January 29, 1956), the daily maximum in summer is usually reached fairly early in the day because a cooling sea breeze from the south-west usually comes in about 11 a.m.

Fig. 2.—The vegetation of the West End of Rottnest I. (after Storr 1961*a*).

The length of the drought period, and the number of days of excessive heat no doubt have a greater effect on the quokka than does the total annual rainfall or mean monthly temperature. During the period that the quokkas have been studied population declines occurred only during the summers of 1953–4, 1957–8, and 1961–2 (Holsworth, unpublished data), and only these summers had the following characteristics:

(1) A period of more than 150 days during which time the total rainfall was less than 1 in. (defined here as the drought period);

(2) The drought period extending into April;

(3) More than 136 rainless days during the last 150 days of drought; and

(4) More than 20 days during the summer with a maximum temperature over 85°F.

Other meteorological values such as wind velocity, nights with dew, and cloud cover are no doubt important factors in the quokka's environment, but suitable measures of these factors were not available.

The West End quokka population is effectively isolated from the remainder of the island because the Narrowneck is covered with a dune scrub vegetation not preferred by the quokka. Storr (1961*a*, 1964) describes three major vegetation types for the West End of Rottnest I. (Fig. 2). They are as follows:

(1) The plateau of Cape Vlaming is covered by succulent plants growing in the very friable, guano-enriched soil of a shearwater (*Puffinus pacificus*) colony. The most common succulents are *Carpobrotus aequilaterus*, *Threlkeldia diffusa*, *Rhagodia baccata*, and *Cryophytum crystallinum*. Succulent vegetation also occurs near Cathedral Rocks, and in small amounts at a few other places along the coast.

(2) Coastal scrub vegetation is found along the southern coast of the West End and those portions of the northern coast that are exposed to the north-easterly winds. The most common shrubs are *Scaevola crassifolia*, *Westringia dampieri*, and *Olearia axillaris*.

(3) Steppe, dominated by the shrub *Acanthocarpus preissii* and the grass *Stipa variabilis* covers the large expanse between the two areas of coastal scrub.

Small, dense copses of *Acacia rostellifera* occur only in localities sheltered from the salt-laden winds. The growth and abandance of *A. preissii* reflects very markedly the exposure of an area to wind. In sheltered depressions it forms a dense tangle 2 or 3 ft deep which provides ideal cover for the quokka. In exposed areas it forms small discrete bushes between which grow shrubs of *Thomasia cognata* and *Guichenotia ledifolia*, the grasses *Stipa variabilis*, *Poa caespitosa*, *Polypogon monspeliensis*, *Lagurus ovatus*, and *Bromus gussonii*, and numerous annual forbs.

The three major vegetation types on the West End appear to be edaphic climax types, consequently their distribution is not influenced appreciably by quokka browsing. Within each vegetation type the abundance of some species may be controlled by the quokka but there is no indication that the range has been, or is being taken over by unpalatable species.

IV. Distribution

To show the approximate areas preferred by the quokkas during a period of peak population density, the distribution map shown in Figure 3, was compiled by plotting the location of each animal present in 1961 near its place of first capture. Rather than showing all animals located near the road where they were caught, they are, together with the uncaught portion of the population, shown dispersed over the whole area *pro rata* to their occurrence along the road in each of the various vegetation types. There was no indication that any age or sex group was distributed differently from the population as a whole.

The locations of all animals captured between May 1961 and May 1963 are plotted in Figure 4 to show the seasonal changes in the distribution of the quokkas. Since almost all animals were caught near roads, the direct plot of their capture

locations also indicates the path of the Land Rover. Quokkas were concentrated at Cape Vlaming during the summer of 1962 (January–May 1962), but not during the summer of December 1962–May 1963, nor in the summer of 1964 (not shown), because during the summer of 1962 about 80% of the population near Cape Vlaming died (Holsworth, unpublished data). The trail into the west end of Marjorie Bay was not made until early in 1962 and that accounts for the absence of captures in that area during 1961.

A comparison of the distribution of quokkas and the distribution of vegetation types shows that the quokkas are most abundant on the steppe and least abundant on the coastal scrub. Maps of the distribution of animals caught at different seasons show that the concentration of animals on the succulent mat of Cape Vlaming occurs only in late spring and during the summer. The distribution of animals on the steppe shows little seasonal change, but there appears to be a strong positive correlation between the density of quokkas and the density of grasses (cf. Figs. 3 and 5).

Fig. 3.—The distribution of the quokka during a period of peak abundance in 1961–62 on the West End of Rottnest I. Total population about 800.

Although the quokkas were fairly evenly dispersed over the West End they did not move at random over the area. Repeated captures of individuals showed that the quokka is sedentary, and probably, like most mammals, it has a home range (Burt 1943). Since most methods for calculating home range size have been worked out for studies where traps are placed on a grid, some modifications were necessary in this study. Since I already had the study area divided by a 100-yd square grid (Fig. 1) it was convenient to plot the location of each quokka captured on the grid. For purposes of analysis the capture location was considered to have been at the centre of the grid square, and the home range to be represented by the polygon formed by connecting the outermost grid squares in which the animal was recorded. This method corresponds closely to the method for determining the "maximum estimate" of home range size (Blair 1942).

An average home range size for quokkas was determined by considering two groups of animals. The first group consisted of animals caught as adults prior to 1960 and still alive in 1963. The second group included adults, juveniles, and yearlings first caught in 1961 and subsequently caught at least five times by May 1963. Six

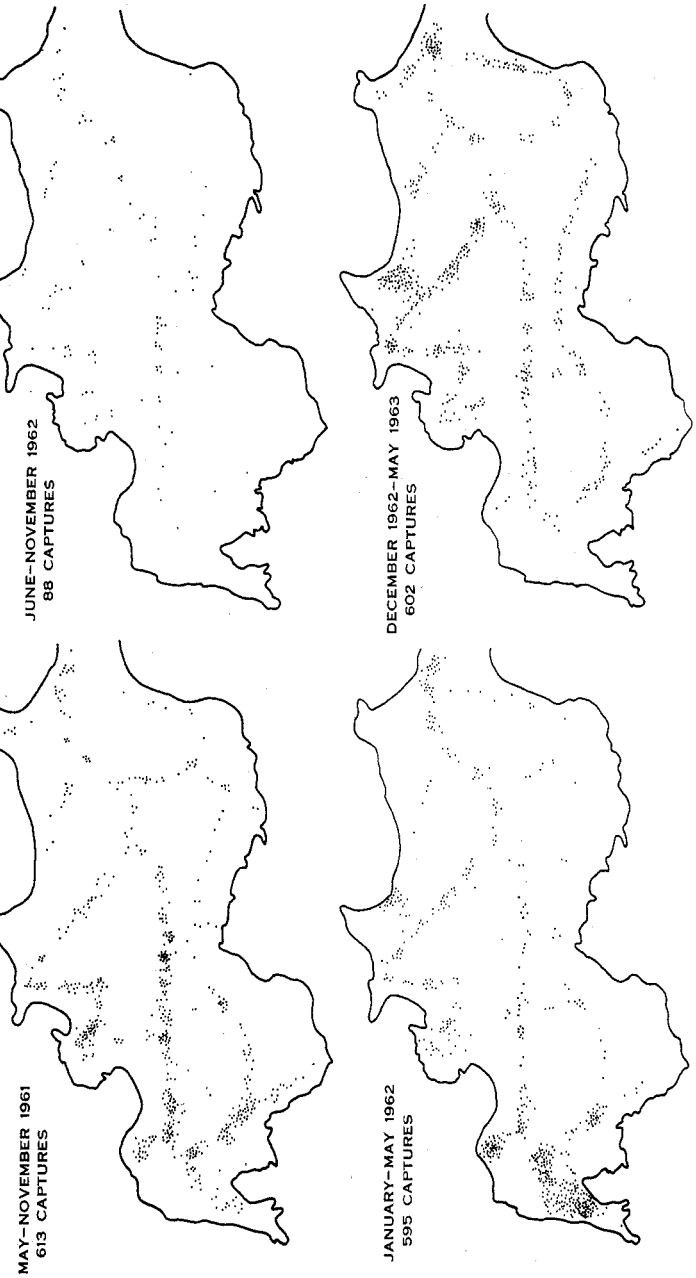

Fig. 4.—The distribution of the quokka at different seasons is shown. Since most animals were caught near the roads their distribution follows the path of the Land Rover.

captures appeared to be sufficient to determine the size of the home range; more than six captures produced only an insignificant increase in home range size. Maps of typical home ranges are shown in Figure 6.

From the first group, males and females caught six or more times had home ranges of 17·8 and 19·4 ac, respectively (Table 1, group 1). This estimate of home range size is probably too large because all animals in the category were included and no allowances were made for those individuals that apparently changed location, or for possible inaccuracies in interpreting pre-1961 capture locations.

The second group consisted of 34 males with an average home range of 10·1 ac and 15 females with an average home range of 10·5 ac (Table 1, group 2). The estimated average home range size of about 10 ac is smaller than for the first group, not only because of the shorter time period involved, but also because, excluded from the data were those quokkas which made frequent excursions of 400–800 yd to Cape Vlaming, or made extensive extra-territorial sorties.

Fig. 5.—The distribution of grasses on the West End of Rottnest I.

It was found that if a quokka was not caught quickly it would head towards a region having good escape cover. However, if it could be forced into a different region of escape cover it would become confused, try to run through non-existent tunnels, jump over imaginary objects, and usually end up against an impenetrable bush. It was also observed that all quokkas from one area would use the same escape routes and escape cover. In addition, there appeared to be certain boundaries they would not cross. Similarly, the animals in nearby areas would have their own escape areas and would respect the boundaries of other groups. This behaviour was most often observed in the densely populated regions near the western end of the island where a limestone ridge marked the boundary between two areas. It was almost impossible to chase an animal along the road where it cut through the limestone ridge, and they never ran over the top of the ridge into the neighbouring area.

Since it appeared that the home ranges were not scattered at random over the West End but were dispersed in well-defined groups, the home ranges of all the quokkas caught more than once between 1954 and 1963 were plotted to see if they fell into distinct groups. The data suggested that there were at least 15 distinct groups. These areas are shown in Figure 7 and will be referred to as area 1, area 2, area 3, etc.

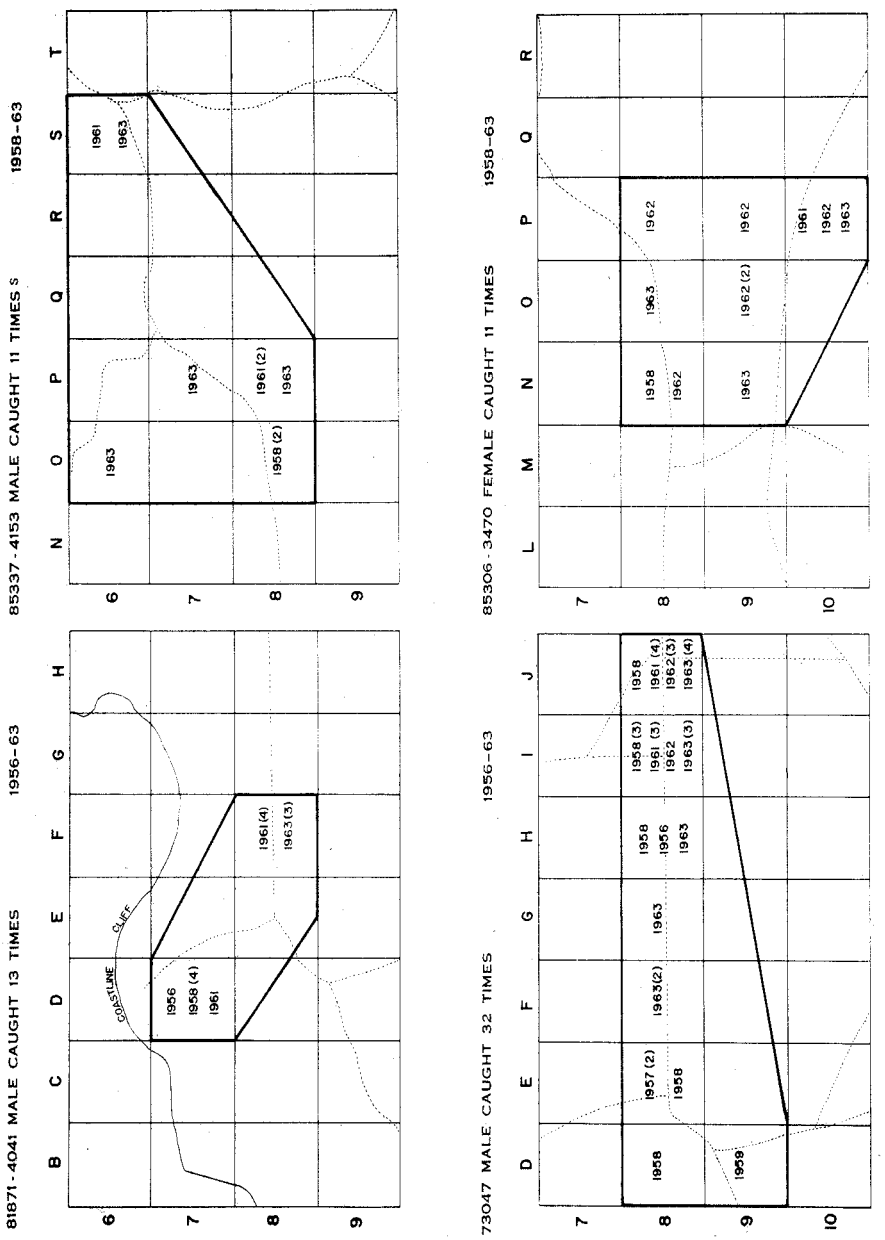

Fig. 6.—Maps of four typical home ranges of quokkas calculated after the method of Blair (1942).

If the quokkas of one group avoid the area occupied by a neighbouring group because that area is defended, then that area fits Noble's (1939) definition of a territory. Since no territorial defence behaviour was actually observed, the term

TABLE 1

SIZE OF THE HOME RANGE OF THE QUOKKA AS MEASURED BY A METHOD MODIFIED FROM BLAIR (1942)

Period	Number of Times Caught	Males		Females	
		Number of Animals	Average Size of Home Range (ac)	Number of Animals	Average Size of Home Range (ac)
Before 1960 to 1963 (group 1)*	4 or 5	3	8·0 (4–14)‡	6	16·6 (8–20)
	6 or more	8	17·8 (8–26)	7	19·4 (4–56)
1961–63 (group 2)†	5	15	8·4 (4–16)	5	9·4 (4–20)
	6 or 7	11	11·8 (4–18)	6	10·5 (6–16)
	8 or more	8	10·8 (6–24)	4	11·8 (4–16)

* Group 1 includes all animals caught before 1960, recaptured at least three times, and known to be alive in 1963.

† Group 2 includes only those animals that were caught at least five times between 1961 and 1963, and were adult by 1963. Animals that apparently changed home ranges or territories, animals that made extra-territorial excursions, and animals from Cape Vlaming have been omitted. Group 2 does not include any animals that were included in group 1.

‡ The average size for the class is followed by the range of size in parentheses.

"territory" cannot be used in its classical sense. However, Pitelka (1959) suggests that the term should be used without regard to the mechanism, behavioural or otherwise, by which exclusiveness is maintained. Therefore, the areas occupied by the 15 groups of quokkas will be called group territories according to Pitelka's criteria.

The following tabulation shows the approximate size of the group territories:

Group area No.	Territory size (ac)	Group area No.	Territory size (ac)
1	40	9	10
2	25	10	15
3	35	11	15
4	10	12	10
5	20	13	10
6	25	14	30
7	25	15	25
8	30		

Each group territory occupies 10–40 ac (average 22 ac). The boundaries between some of the group territories are imperfectly known but between others the divisions could be plotted quite precisely, especially where limestone ridges or other geographical features served as boundary markers. Many territorial boundaries did not coincide

with any observable topographic or vegetative feature of the habitat, but neither did all major geographic features coincide with territorial boundaries. For example, in recent years area 7 has been divided by a large sand "blowout" but the quokkas continue to cross the bare sand and scramble up the steep sides.

Where geographical features mark boundaries, evidence suggests that territories do not overlap. Elsewhere, the overlapping of boundaries suggested by the data may be an artifact introduced by inaccuracies in recording capture locations. There is a possibility that roads could be used by the quokka as avenues of travel and could determine the shape of the group territories. Many quokkas were caught at both ends of the sausage-shaped territory of area 14 (Fig. 7) which suggests that they were moving up and down the roads. However, if roads really do influence the shape of territories then it is difficult to explain why no animals from area 14 have been caught at the extremities of the roads in areas 10, 12, or 13.

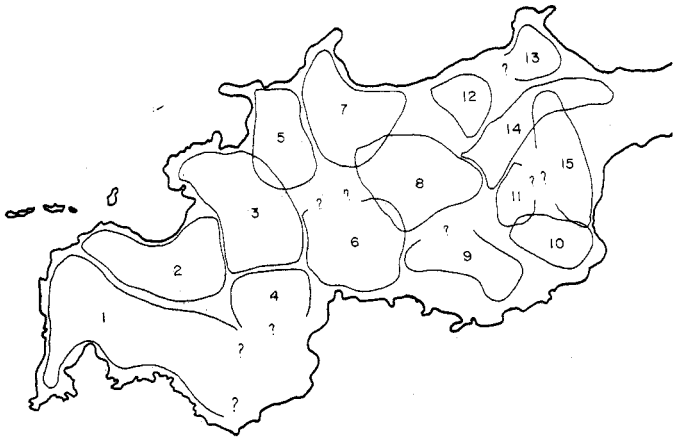

Fig. 7.—The 15 group territories (designated area 1, area 2, etc.) were determined by plotting the distribution of the home ranges of all quokkas caught on the West End of Rottnest I.

The verification of the existence of the proposed group territories demands some measure of the fidelity of the quokkas to their group territory. Any expression of faithfulness to a territory should consider both the time interval between first and last capture and the number of times the animal was caught. To obtain a meaningful expression is difficult because the relationships between the number of times an animal is caught, its frequency of occurrences in foreign territories, and the time interval, are probably not linear. For example, animals caught most frequently were usually caught almost on the same spot each time, but most of those found outside their home territory were caught less than four times. Because of these difficulties, two expressions of fidelity are given in Table 2; the number of animals moving per 100 captures, and the number moving per 100 animal years. For the purposes of calculation, 1 animal year equalled 1–12 months, 2 animal years equalled 13–24 months, etc.

To determine the fidelity of the quokka to its birth place and to use a standard reference point for all animals, each animal when first captured was considered to be in its natal territory, and all shifts in location are recorded with reference to this assigned territory.

Since only those quokkas caught more than once could be used to determine the boundaries of each group territory, data on 709 animals were available in 1963. Data on the distribution of animals caught in December 1963, and January, February, and April 1964 were not available when Table 2 was compiled, but subsequent analysis has shown them to be entirely consistent with the following interpretation of the data.

TABLE 2

FREQUENCY OF CAPTURE AND MOVEMENT BETWEEN GROUP TERRITORIES

Group Area No.	Number Caught 2 or more Times	Number of Captures	Number Changing Territories	Number of Moves per 100 Captures	Average Number of Years Between First and Last Capture	Number of Moves per 100 Animal Years
1	197	657	8	1·22	2·52	1·62
2	97	319	12	3·76	2·52	4·90
3	93	353	18	5·10	2·78	6·98
4	12	36	2	5·56	1·66	10·00
5	51	195	8	4·10	2·52	6·25
6	45	151	7	4·64	2·47	6·36
7	44	133	8	6·00	1·48	12·30
8	33	112	5	4·46	2·12	14·00
9	11	34	1	2·94	2·00	4·55
10	21	59	0	0·00	2·81	0·00
11	7	30	1	3·33	3·14	4·50
12	12	27	0	0·00	2·50	0·00
13	5	11	0	0·00	1·00	0·00
14	67	251	8	3·19	2·72	4·40
15	14	36	1	3·03	1·50	4·78
Totals	709	2404	79	3·34*	2·46*	4·50*

* Average.

The 709 animals included in Table 2 were caught 2404 times, or an average of 3·4 times each. The time between first and last capture was in some cases more than 7 yr, but the average time was 2·46 yr (based on the actual period, not animal years). Altogether 79 animals (11%) were found outside their natal or assigned territory which gives an average of 4·5 moves per 100 animal years or 3·34 moves per 100 captures. Of those animals recorded as having been caught outside their natal territory, most (74%) were caught only once in a foreign area. Table 2 shows that most of the exchanges involved animals in areas 2 and 3. When the data were originally plotted it was observed that most of these exchanges actually took place between areas 2 and 3 and areas 3 and 5.

The best evidence supporting the hypothesis that the group territories are real entities is shown by the movements of quokkas from area 1. Fortunately, the area is richly endowed with place names so that few errors in recording locations have occurred, and it is separated distinctly from area 2 by a limestone ridge. From a tagged population of 327 animals 197 were caught more than once, and only eight of these were recorded outside area 1. Four of the eight were caught in area 2, the others were caught at various locations on the West End as far east as Narrowneck.

It might be expected that yearlings or juveniles would move out of their territory with greater frequency than adult animals. Many yearlings were first caught and tagged when they were still following their mothers and consequently they were properly assigned to their true natal territory. Neither these animals, nor animals tagged at a later age, showed a higher rate of shifting to new territories. When the sex structure of the animals that moved into a foreign territory was examined, males and females were equally represented.

There are several reasons why an animal may have been outside its natal territory. No doubt temporary excursions into strange territories are engaged in by the quokka just as they are in other territorial mammals (Burt 1943). There was an indication of a true change in territorial affiliation by a small number of quokkas. These animals, after having been caught several times in one locality, suddenly appeared in a new area and remained there. True changes in territory were recognized in not more than eight instances. Some of the 79 animals that were recorded in foreign territories may represent errors made in interpreting the capture location statements recorded prior to 1961 when the grid pattern was established.

Changes in location were probably increased by the action of the several researchers working on the West End during the past 10 yr. Between 1961 and 1964 I know that I accidently released at least five animals in the wrong location. Three of these, a male and a female with a yearling at heel, were later recaptured in their home territory. A lone yearling took up residence in the foreign territory into which it was released. No doubt errors occurred in recording or transcribing data that would account for some of the 79 shifts in location.

V. Discussion

Proper interpretation of the relationship between the distribution of quokkas and the distribution of the vegetation requires detailed knowledge of the quokka's food habits. Storr (1961*b*, 1964) estimated the food habits of the quokka on the West End by examining 311 samples of faeces collected at monthly intervals during 1958. His results show that the diet of the quokkas caught at Cape Vlaming consisted almost entirely of *Carpobrotus aequilateris* and *Rhagodia baccata*, and only during the October–December period did the proportion of all other food exceed 20% in the animals on Cape Vlaming. In other areas of the West End, *R. baccata* also accounted for 18–47% of the diet of quokkas. *Acacia rostellifera* was almost of equal importance but other shrubs never amounted to more than 14% and grasses and forbs together not more than 31% of their diet at any season. Most of Storr's data came from animals caught along the road through the centre of West End, around Mable Cove, and on Cape Vlaming.

Only the distribution of the unpalatable shrubs *Acanthocarpus preissii, Thomasia cognata*, and *Guichenotia ledifolia*, and the highly palatable and nutritious grasses (Storr 1962) corresponds with the distribution of the quokkas. This indicates that grasses might form the major portion of the quokka's diet and that their importance has been underrated by Storr (1964). Moreover, only the grasses and the associated forbs occur in sufficient quantity to provide adequate food. During the period 1961–64 there was not enough *A. rostellifera* and *R. baccata* on the area to feed the animals at the rate suggested by Storr (1964), and those species do not occur at all over much of the West End. In most areas *A. rostellifera* showed only slight browsing and in many areas it did not appear to be eaten at all.

The food habits of the quokkas in different areas play an important part in determining their survival rate. Storr (1964) found that although the quokka has a great surplus of dietary nitrogen in the winter, during the summer it is severely deficient. Quokkas on Cape Vlaming experience a greater nitrogen deficiency than those in other areas because their diet of succulent vegetation results in a very small dry matter intake.

In addition to the shortage of nitrogen, Storr calculated that an adult male quokka will lose 240 ml of water per day during the summer and, since its food on the steppe provides it with only 120 ml per day, dehydration is inevitable. On Cape Vlaming, however, succulents provide a superabundance of water. Contrary to what might be expected the abundant water in summer is probably responsible for the deaths of many animals on Cape Vlaming.

The digestive system of the quokka resembles that of ruminants in that it uses bacteria to digest cellulose and starch (Moir, Somers, and Waring 1956). Recent evidence indicates that the animal is also able to re-cycle nitrogen (Kinnear and Brown, personal communication). If this is true, then it is reasonable to expect that, like the ruminant, when it is on a low nitrogen diet its ability to re-cycle nitrogen will increase if at the same time it is deprived of water (Livingstone, Payne, and Friend 1962). Consequently, quokkas eating succulents on Cape Vlaming probably re-cycle nitrogen less efficiently than those elsewhere on the West End because they have a high water intake, and this probably accounts for their lower survival rate during hot, dry summers (Holsworth, unpublished data).

The quokka is ideally suited for a nomadic existence because it neither burrows nor makes a nest, and even the female is not tied to a particular locality while raising her young. In spite of this, the quokka spends most of its life in an area of less than 12 ac with a group of 25–150 other quokkas that confine themselves to a group-territory of less than 30 ac.

The home ranges of individual quokkas in the smaller group territories appear to occupy the whole of the group territory, but the larger territories are about two or three times the size of the home ranges. In area 1 there is a suggestion in the data that the home ranges are distributed into three groups: a small group occupying Radar Head, another group remaining close to area 2, and between them, residing a third group which consistently goes to Cape Vlaming during the hot summer evenings.

It is not known if the home range has precisely marked or indefinite boundaries, nor is it known what determines the limits of a quokka's explorations. McNab (1963)

suggests that the home range size bears a close relationship to the weight or metabolic rate of a mammal. The estimate of 10 ac for the home range of a 4-kg quokka fits McNab's predicted home range size very closely in spite of the fact that marsupials have a metabolic rate only half that of placentals (Brown and Kinnear, personal communication). This suggests that the basis for McNab's predictions is incorrect and the correlation between his prediction and the size of the quokkas home range is spurious.

No doubt, far more interesting and important than the size of the home range are the other attributes of home range such as: Which parts of a home range does an animal use most? Where home ranges overlap, how does the use of each part by different animals compare? Until the activity of these animals is studied using nearly continuous monitoring of attached radio transmitters, some of the important questions regarding the relation of the quokka to its home range will remain unanswered.

The extent of a group territory does not increase or decrease with changes in population density. After the reduction of the quokka population in area 1 during the summer of 1962 there was no influx of immigrants of any age from the adjacent area 2, nor from any other group territory. The territorial boundary between areas 1 and 2 was respected by the animals in area 2 even though there were very few animals in area 1 to defend it. The apparent stability of area 7, even after half of it had been turned into a sand blowout, suggests that the group territories and their boundaries are, somehow, quite permanent, possibly fixed by tradition.

Topographical features coincide with the divisions between some group territories, but how the quokkas mark the boundaries is not known. Male quokkas have large paracloacal glands (Holsworth, unpublished data) similar to those described for other marsupials (Bolliger and Whitten 1948; Broek 1904, 1910; Green 1963). One pair of glands, presumably scent glands, have ducts leading to the outer edge of the cloaca. The contents of these glands consist of an odorous cream-coloured liquid which could be deposited on the faeces or passed with the urine. Many other mammals use scent as territorial markers (Hediger 1949; Mykytowycz 1965; Tarasov 1960; Wynne-Edwards 1962, p. 104 et seq.) and probably the quokkas are no exception.

Territories occupied by a group have been described for many other mammals but none of them are closely similar to the group territories described here for the quokkas. The occupancy of a group territory by a large number of non-gregarious animals with equal representation of sexes, with all age classes, and with overlapping home ranges appears to be unique.

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