STUDIES ON MARSUPIAL NUTRITION

IV. DIET OF THE QUOKKA, SETONIX BRACHYURUS (QUOY & GAIMARD), ON ROTTNEST ISLAND, WESTERN AUSTRALIA

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Summary

The Rottnest quokka loses condition towards the end of summer, which is a season of marked drought. The diet of the quokka was studied to see if the reason for this decline could be ascertained.

Dry matter intake by adult males averaged 45 g/day for much of the year; however, during autumn the average dry matter intake was only 32 g/day, which yielded less than their minimal requirements of nitrogen (0·6 g/day). Water intake was also deficient in summer and autumn wherever succulent herbage or seepage water was scarce or absent.

I. Introduction

The discovery by Moir, Somers, and Waring (1956) of ruminant-like features in the digestion of the quokka has stimulated experimental work on comparative nutrition in marsupials. It has also strongly influenced nutritional and related studies on Rottnest I., although the motivation of these studies has largely come from elsewhere.

All workers on Rottnest I. soon become aware of its tremendous deterioration as a habitat in late summer—the island is then most parched and palatable herbage least plentiful. A concurrent decline is equally obvious in the condition of the quokkas, which become increasingly thin and verminous towards the end of summer. In its lack of competitors and predators, the quokka population seemed to be limited only by the food supply on Rottnest I.; in such an ecologically simple situation it was hoped that knowledge would quickly accrue on how a natural population of mammals was controlled. In practice, however, it has been anything but simple to establish the precise cause of mortality and its effect on population.

The examination of hundreds of skulls of animals that had died naturally has confirmed, at least for juveniles, the expectation that mortality was highest in late summer; but the difficulty in finding moribund animals or animals which have recently died has precluded direct determination of the cause of death (Shield 1959). It has alternatively been assumed that the cause of death was also the cause of late summer debility. Attempts have therefore been made, by variously depriving them of nutrients, to reproduce in experimental animals the haematological and clinical characteristics of Rottnest quokkas in late summer. In such a way, trace-element deficiency, dehydration, and starvation-induced disease have all been proposed, tested, and proved irrelevant to the general summer debility of Rottnest quokkas (Main, Shield, and Waring 1959). All the available evidence indicated

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that semistarvation was primarily responsible for the seasonal decline in condition and, presumably, in its severest form, for late summer mortality in Rottnest quokkas. A survey of the diet of the quokka was therefore undertaken by the present author.

This paper deals with the seasonal fluctuations in four Rottnest habitats of (1) the food items in the diet; (2) the nitrogen and water content of these items; and (3) the daily intake of dry matter, nitrogen, and water (from herbage). In the final discussion these estimates of intake are compared with what is known of the quokkas' requirements.

II. The Environment

Rottnest I. is situated 12 miles west of Fremantle and has an area of $7 \cdot 4$ sq. miles, including the several salt lakes in its eastern half (Fig. 1). It is composed of limestone which is covered to a varying depth with calcareous sand. The topography is generally undulating, consolidated dunes occurring everywhere except in the vicinity of some of the lakes. There are no watercourses, and fresh water is restricted in summer to low-level seepages round parts of the lakes and, more rarely, along the coast.

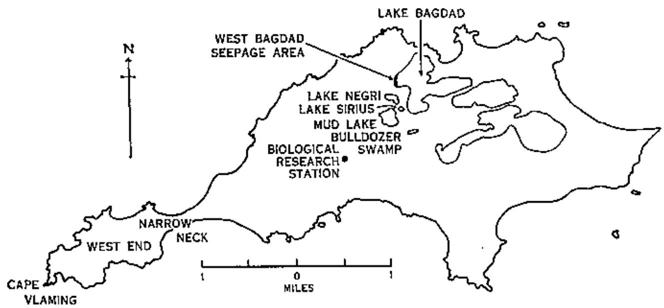

Fig. 1.—Map of Rottnest I., W.A., showing localities mentioned in the text.

The wet season begins about the end of April or early May, and throughout the winter a period of a fortnight without substantial rain is rare. Of the 29 in. received per year, only 2 in. fall in the period November–March.

The flora is predominantly sclerophyllous and perennial. Succulents (Chenopodiaceae and Aizoaceae) are plentiful only on the damp saline soils round the lakes and on headlands and islets colonized by seabirds. Annual herbs and grasses were originally a very minor component of the flora, but since the settlement of the island in 1831, scores of alien species have become established, most of them growing in winter (Storr 1962).

(a) *West End Study Area*

This comprises the south-western peninsula of Rottnest I., including the Narrow Neck but excluding Cape Vlaming. There is no fresh water apart from a small coastal seepage.

The interior of the peninsula is an undulating "grassland" interspersed with low thickets of *Acacia rostellifera*. While this grassland consists almost exclusively of monocotyledonous plants, much of it is dominated not by grasses but by the low, pungent-leaved, liliaceous shrub *Acanthocarpus preissii*; elsewhere the perennial tussock grasses, *Stipa variabilis* and *Poa caespitosa*, are abundant. Towards each coast the grassland gives way to dune scrub, a moderately dense assemblage of shrubs 2–8 ft high and including *Olearia axillaris*, *Scaevola crassifolia*, *Myoporum insulare*, *Diplolaena dampieri*, *Acacia cuneata*, and *Westringia dampieri*.

Earlier workers (Shield 1959; Barker 1961) included Cape Vlaming in their West End study area, but its vegetation is very different and the present author has preferred to treat it separately.

(b) *Cape Vlaming Study Area*

The shallow soil above the cliffs at Cape Vlaming is riddled with mutton-bird burrows. Here the dune scrub is largely replaced by succulent herbs and shrubs: *Carpobrotus aequilaterus*, *Threlkeldia diffusa*, *Tetragonia implexicoma*, *Atriplex cinerea*, and *Rhagodia baccata* (which alone of the Cape Vlaming succulents occurs generally on the West End). Many quokkas are attracted to this highly succulent vegetation in summer, but few quokkas are found there in winter.

(c) *Mud Lake Study Area*

This comprises the flats round Bulldozer Swamp, Mud Lake, Lake Sirius, and Lake Negri, and the south-western and north-western shores of Lake Bagdad. Small seepages of fresh water occur here and there round the larger lakes.

Damp saline soils are monopolized by the samphires *Arthrocnemum halocnemoides*, *A. arbuscula*, and *Salicornia australis*. They are replaced on slightly higher ground by the sedges *Gahnia trifida* and *Scirpus nodosus*, among which are scattered bushes of *Rhagodia baccata* and *Atriplex paludosa*. Between the sedge zone and the prevailing grassland and *Acacia* scrub there is often a narrow belt of tea-trees (*Melaleuca pubescens*), under which thickets of *Solanum simile* afford the quokkas good daytime shelter.

(d) *West Bagdad Study Area*

The strip of land between the *Gahnia* and the far western shore of Lake Bagdad is irrigated throughout summer by a copious seepage of fresh water. The sward, dominated by the couch-like *Sporobolus virginicus*, is dense and green but apt to be grazed and trampled low by the hordes of quokkas drinking there on summer evenings. Most of these quokkas spend the day under nearby tussocks of *Gahnia*.

The author's West Bagdad and Mud Lake study areas together comprise the "Lake Bagdad" of previous workers.

III. Composition of the Diet

(a) *Materials and Methods*

During monthly visits to Rottnest in 1958, 511 quokkas were captured in the evening, mostly by hand-netting: 208 at West End, 103 at Cape Vlaming, 155 at Mud Lake, and 45 at West Bagdad. The animals were placed singly in chaff bags and kept overnight at the Biological Research Station. On the following morning they were released at their place of capture. A sample of faeces was taken from each bag and, after preparation, examined microscopically (Storr 1961).

(*b*) *Results*

Mean seasonal percentage (dry weight basis) of the various plants comprising the diet in each study area are set out in Tables 1–3.

(*c*) *Comments*

The diet at Cape Vlaming was overwhelmingly dominated by succulents, particularly *Carpobrotus*. Herbs and grasses were understandably unimportant in summer: fertilized by mutton-bird excreta they grow luxuriantly in winter and spring but, after flowering, die off quickly on the exposed plateau.

TABLE 1

CAPE VLAMING: ITEMS IN FOOD

Values given as percentage dry weight

Food Plants	Jan.–Mar.	Apr.–June	Oct.–Dec.
Succulents			
Carpobrotus aequilaterus	69	80	52
Rhagodia baccata	27	13	26
Threlkeldia diffusa	1	Trace	1
Shrubs			
Acacia rostellifera	—	1	—
Frankenia pauciflora	—	Trace	—
Olearia axillaris	Trace	—	Trace
Scaevola crassifolia	1	2	1
Westringia dampieri	1	—	9
Forbs	Trace	3	Trace
Grasses	1	1	11

In the West End study area succulents accounted for slightly less than 50% of the diet in summer; *Rhagodia* was the principal item (the scarcity of *Carpobrotus* away from Cape Vlaming being confirmed by these data). Following the opening rains in late April the proportion of succulents in the diet fell sharply, while that of shrubs rose to nearly 50%. Winter and spring saw no change other than increased consumption of grass.

The diet at Mud Lake also varied with the seasons, though not so markedly as at West End. Consumption of succulents was similarly greatest (77%) in summer, but at no time did it fall to much below 50%. This indicates the superior palatability of the samphires as compared to *Carpobrotus*, which is apparently ingested mainly for its water.

In all seasons, and especially in winter, woody shrubs contributed relatively little to the diet at Mud Lake. Despite its greater abundance here, *Acacia rostellifera* provides less forage than at West End. In sheltered situations it grows into a small tree with most of its foliage inaccessible to quokkas; whereas it occurs at West End mainly in low wind-pruned thickets. Another factor contributing to the greater consumption of shrubs at West End was the scarcity of alternative foods. The peninsula had not been burnt for many years, hence much of the grassland was overrun by tangled masses of *Acanthocarpus*. In contrast, recent burning of the country round the lakes had favoured the tussock grasses over the slower-growing *Acanthocarpus* and provided more space for annual herbs and grasses and for such short-lived shrubs as *Solanum simile* and *Guichenotia ledifolia*.

At West Bagdad only half as much samphire was eaten in summer as at Mud Lake, but three times as much grass and sedge. These differences can be explained partly by reference to the relative availability of the plants and partly to the water requirements of the animals. Palatable grasses, especially *Sporobolus*, are much more plentiful at West Bagdad, while samphires are relatively scarce, and although *Gahnia* is particularly abundant in the vicinity of the seepages, it is certain that in summer only animals with no water problems could eat large quantities of this tough, dry sedge.

TABLE 2

WEST END: ITEMS IN FOOD

Values given as percentage dry weight

Food Plants	Jan.–Mar.	Apr.–June	July–Sept.	Oct.–Dec.
Succulents				
Atriplex cinerea	—	—	Trace	—
Carpobrotus aequilaterus	1	6	—	Trace
Rhagodia baccata	47	18	19	43
Threlkeldia diffusa	Trace	—	—	1
Shrubs				
Acacia rostellifera	21	35	36	30
Diplolaena dampieri	—	1	3	—
Guichenotia ledifolia	—	—	Trace	—
Olearia axillaris	Trace	1	1	Trace
Scaevola crassifolia	6	12	10	11
Solanum simile	1	—	—	—
Westringia dampieri	—	—	Trace	1
Forbs	6	16	9	4
Grasses	17	11	22	10

IV. Water and Nitrogen Content of Food

(a) *Materials and Methods*

Terminal foliage (20–40 g dry wt.) was taken monthly in 1958 from at least five different individuals of each food plant. The samples were collected on the last day of each field trip, wrapped in polythene, weighed immediately on returning to Perth, and again after oven-drying for 36 hr at 100°C. The material was then ground and analysed for nitrogen by the method of Willits, Coe, and Ogg (1949).

(b) Results

Mean seasonal water content (percentage *wet* weight of foliage) and nitrogen content (percentage *dry* weight of foliage) are set out in Table 4 for each food plant. These values have been applied to the dietary data in Tables 1–3 to give the water and nitrogen content of total ingested water; seasonal means of these values are shown in Table 5.

(c) Comments

Almost without exception, growth is restricted in Rottnest I. plants to the rainy season; hence the nitrogen and water content of forage is generally much higher at the end of winter than at the end of summer.

TABLE 3

MUD LAKE: ITEMS IN FOOD

Values given as percentage dry weight. Data from West Bagdad in brackets

Food Plants	Jan.–Mar.		Apr.–June	July–Sept.	Oct.–Dec.
Succulents					
*Arthrocnemum halocnemoides**	70	(32)	41	47	47
Atriplex paludosa	2	(3)	Trace	—	—
Rhagodia baccata	4	(7)	5	4	4
Suaeda australis	Trace	(—)	1	—	Trace
Threlkeldia diffusa	1	(Trace)	1	—	1
Shrubs and trees					
Acacia rostellifera	—	(—)	—	3	1
Guichenotia ledifolia	2	(Trace)	5	4	9
Hemichroa pentandra	Trace	(1)	1	—	—
Melaleuca pubescens	1	(—)	2	1	4
Samolus repens	Trace	(5)	—	—	Trace
Solanum simile	8	(12)	5	1	2
Forbs	1	(4)	9	8	3
Sedges					
Carex preissii	—	(—)	2	—	—
Gahnia trifida	4	(15)	2	1	2
Grasses	7	(21)	26	31	27

* Includes *Salicornia australis* (the epidermis of these samphires is frequently indistinguishable).

The summer diet was poorest in nitrogen at Cape Vlaming, owing to the abnormally low nitrogen content of the principal food item, *Carpobrotus*. It was richest at West Bagdad, where seepage water produced a relative abundance of green grass. Over most of the island, as indicated by the similar values obtained at West End and Mud Lake, the nitrogen content of the diet ranged from 1% in late summer to 2·5% in late winter.

Summer food contained most water at Cape Vlaming where the quokkas subsisted almost exclusively on succulent herbage. Because of the comparative scarcity of succulents at West End, there was considerably less water in the food, though twice as much was obtained by selective feeding than if the animals had grazed at random.

TABLE 4

WATER AND NITROGEN CONTENT OF FOOD PLANTS ON ROTTNEST I.

Collections made at Cape Vlaming and West End indicated by asterisk, all other collections from the lakes. Values given as percentage wet weight for water and percentage dry weight for nitrogen

Food Plants	Jan.–Mar.		Apr.–June		July–Sept.		Oct.–Dec.	
	Water	Nitrogen	Water	Nitrogen	Water	Nitrogen	Water	Nitrogen
Succulents								
Arthrocnemum halocnemoides	82	1·1	83	1·2	93	2·9	87	1·7
*Atriplex cinerea**	74	1·3	78	1·3	86	3·5	71	1·7
Atriplex paludosa	77	1·5	78	1·8	86	2·7	80	1·9
*Carpobrotus aequilaterus**	88	0·8	89	0·9	93	2·0	90	1·1
*Rhagodia baccata**	76	1·0	79	1·2	88	2·4	83	1·9
Rhagodia baccata	71	1·8	74	2·0	85	3·3	76	2·2
Salicornia australis	84	1·0	84	1·0	94	2·7	88	1·4
*Threlkeldia diffusa**	85	1·7	84	2·0	91	3·1	82	1·9
Shrubs and trees								
*Acacia rostellifera**	67	1·2	65	1·2	75	2·4	73	2·0
Acacia rostellifera	63	1·3	63	1·4	74	2·1	71	1·6
*Diplolaena dampieri**	49	1·2	53	1·3	68	1·5	57	1·3
*Frankenia pauciflora**	36	0·7	35	0·9	56	1·8	47	1·1
Guichenotia ledifolia	38	0·8	40	1·1	58	1·9	46	1·2
Melaleuca pubescens	59	1·5	55	1·5	66	1·9	63	1·7
*Olearia axillaris**	36	0·9	53	1·1	66	1·7	45	1·2
Samolus repens	48	1·3	50	1·2	76	1·6	65	1·4
*Scaevola crassifolia**	70	0·9	75	1·0	83	1·6	79	1·3
Solanum simile	79	2·7	84	2·8	85	4·5	77	3·3
*Westringia dampieri**	28	0·5	30	0·5	54	1·2	38	0·8
Forbs								
Average of 11 species	75	2·1	86	3·0	86	2·9	78	2·3
Sedges								
Carex preissii	—	—	75	2·6	69	2·0	29	1·1
Gahnia trifida	31	0·9	38	0·9	40	0·9	36	0·8
Grasses								
*Poa caespitosa**	35	1·2	41	1·4	67	1·8	50	1·4
Sporobolus virginicus	53	1·7	52	1·7	72	2·5	65	2·5
*Stipa variabilis**	31	1·5	38	1·8	60	2·3	44	1·9
Stipa variabilis	41	1·6	41	1·6	53	2·1	42	1·7
Average of five annual species	62	1·2	77	2·6	81	2·6	66	1·5

The problem, long recognized by agriculturists, of sampling herbage as "grazed" is especially acute on Rottnest I., where the vegetation is much less uniform in palatibility and nutritive value than in artificial pastures. Also, the quokka is a more fastidious feeder than domestic livestock; it eats slowly, cropping with its incisors or plucking with its hands small pieces of plants which may be rejected after tasting. The level of nitrogen and water in the food could therefore have been substantially underestimated.

TABLE 5

WATER AND NITROGEN CONTENT OF TOTAL INGESTED MATTER FROM FOUR LOCALITIES OF ROTTNEST I.

Values given as percentage wet weight for water and as percentage dry weight for nitrogen

Localities	Jan.–Mar.		Apr.–June		July–Sept.		Oct.–Dec.	
	Water	Nitrogen	Water	Nitrogen	Water	Nitrogen	Water	Nitrogen
Cape Vlaming	86	0·8	88	1·0	—	—	86	1·3
West End	71	1·2	77	1·5	81	2·3	78	1·8
Mud Lake	79	1·2	77	1·5	89	2·5	80	1·7
West Bagdad	72	1·3	—	—	—	—	—	—

TABLE 6

DAILY LOSS OF DRY MATTER FROM THE STOMACH OF ADULT MALE QUOKKAS

Date	Locality	No. in Sample	Mean Body Weight (kg)	Mean Dry Weight of Stomach Contents (standard deviation in brackets) and Time of Killing for Dissection				Daily Loss of Dry Matter from Stomach (g)
				First Subsample		Second Subsample		
				Weight (g)	Time (a.m.)	Weight (g)	Time (p.m.)	
6. ii.62	West Bagdad	11	3·23	82·6 (16·8)	3·00	62·4 (14·5)	9·00	26·9
7. ii.62	South Coast	11	3·05	90·2 (17·7)	2·00	56·5 (17·4)	8·00	44·9
8. ii.62	Mud Lake	11	3·26	89·2 (9·8)	2·15	52·6 (5·0)	8·15	48·8
1. v.62	South and west coasts	18	2·89	84·3 (13·0)	2·30	58·7 (10·5)	10·30	30·7
2. v.62	Mud Lake	18	3·10	86·9 (12·9)	3·00	59·1 (11·4)	11·00	33·4
29.viii.62	Eastern half	22	3·44	67·4 (15·0)	2·30	30·4 (6·4)	10·30	44·4
–. xi.60	Eastern half	41	3·05	—	—	—	—	44·7

V. DAILY INTAKE OF DRY MATTER, NITROGEN, AND WATER (FROM HERBAGE)

(a) *Materials and Methods*

It has been assumed that the amount of dry matter ingested per day is equal on average to that lost from the stomach. In November 1960 loss of dry matter from the stomach was found to be linear with respect to time, the rate being 44·7 g/day in adult males and 33·4 g/day in adult females (Storr 1963).

To check whether the rate was seasonally constant, the work was repeated for adult males in February, May, and August, 1962. Smaller samples than in the earlier work were adequate (as stomach loss was known to be linear, only two subsamples were required for each determination). The animals were caught between midnight and 2 a.m., half the sample being killed soon after, the remainder either 18 or 20 hr later. Stomach contents were extracted, dried, and weighed, as in 1960.

(b) *Results*

Mean dry weights of stomach contents in early morning and in the following evening, and the extrapolated daily losses of dry matter, are shown in Table 6 for each field trip in 1962 and, for comparison, the rate obtained in November 1960. Daily intake of dry matter had been equated to these rates and applied to the data in Table 5 to give (in Table 7) the daily intake of nitrogen and water from herbage. For the

TABLE 7

DAILY INTAKE OF NITROGEN AND WATER FROM HERBAGE OF ADULT MALE QUOKKAS FROM FOUR LOCALITIES OF ROTTNEST I.

Localities	Nitrogen (g)				Water (ml)			
	Feb.	May	Aug.	Nov.	Feb.	May	Aug.	Nov.
West End	0·5	0·5	1·0	0·8	110	120	190	160
Mud Lake	0·6	0·5	1·1	0·8	180	110	360	180
West Bagdad	0·3	—	—	—	70	—	—	—
Cape Vlaming	$<0·4$	$<0·3$	—	$<0·6$	<270	<230	—	<270

purpose of these calculations two assumptions were made: (1) that mid-seasonal level of nutrients in the food was similar to the mean of the whole season; and (2) that daily intake of dry matter was the same at West End as on the similarly vegetated west and south coasts of the main island.

(c) *Comments*

In view of the high variability (*c.* 20%) in dry weight of stomach contents, the estimates of daily losses were surprisingly consistent. There were only two departures from an average loss of about 45 g/day, viz. (1) in May when it was generally about 32 g/day; and (2) at West Bagdad, where it was 27 g/day in February.

The general slowing down of digestion at the end of summer is almost certainly due to a decline in "ruminal" microorganisms. Counts of bacteria and protozoa in the rumen of sheep grazing at Perth were highest in November when the herbage was green and rich in nitrogen; and lowest in April when it was dry and nitrogen deficient (Moir 1951).

There is no ready explanation for the low rate at West Bagdad (which was confirmed by a similarly low rate in a sample of adult females taken at the same time); but possibly contributing to it are the following factors:

(1) Abnormally high density of quokkas—the population of drinking animals was estimated to be 600 in January 1958 (Dunnet 1963);

(2) The relatively high infestation of the gut nematode *Austrostrongylus thylogale* (Barker 1955);

(3) The presence of fresh water—prolonged drinking may be detrimental itself to digestive processes, or indirectly detrimental through neglect of feeding.

Even at its best, the dry matter intake of Rottnest quokkas is much lower than that of captive quokkas feeding on relatively dry food. For example the daily intake of adult male quokkas fed by Calaby (1958) on three different diets was 112–138 g of lucerne chaff, 108–120 g of a 3 : 1 mixture of lucerne chaff and sheep nuts, and 44–74 g of equal parts of oaten and lucerne chaff and sheep nuts. It would seem that, as in ruminants (Dodsworth and Campbell 1952), the dry matter intake of quokkas is depressed when their food is highly succulent.

Various circumstances have prevented the determination of dry matter intake at Cape Vlaming. Because of the extremely low nitrogen content of the food and its equally extreme succulence, it will undoubtedly prove lower than at West End. The estimates of nitrogen and water intake at Cape Vlaming (based on south coast dry matter intakes) should therefore be considered maximal.

VI. Discussion

(a) *Nitrogen Requirements compared with Intake*

Recent work by Brown (1964) indicates that the minimum nitrogen requirement for an adult male quokka to remain in nitrogen balance is 0·6 g per day. Disregarding possible differences in protein digestibility, the comparison of this estimate with those of nitrogen intake on Rottnest I. (Table 7) suggests a large nitrogen surplus in winter and a varying deficit in late summer. At West End and Mud Lake the apparent deficit is small and of the same order as experimental errors. Nevertheless many animals could well be deficient in nitrogen in summer, e.g. juveniles and lactating females (whose requirements would be relatively greater than those of adult males) and all quokkas in such inferior habitats as dune scrub dominated by *Westringia dampieri*.

The deficit is much larger in the other study areas and there is accordingly little doubt that nitrogen is grossly deficient at Cape Vlaming and West Bagdad, owing to the low nitrogen content of the food at Cape Vlaming, and to the small dry matter intake at West Bagdad.

(b) *Water Requirements compared with Intake*

The minimal water requirements of non-growing, non-lactating (i.e. adult male) quokkas are, in effect, equal to the losses sustained in renal function, defaecation, salivation, and thermoregulation. What is known of these losses is entirely due to Bentley (1955) and Sadleir (1959).

The amount of urine excreted by quokkas on Rottnest I. has been measured by Bentley; in winter it averaged 25 ml/hr in animals that had been feeding on succulent herbage, a value similar to those observed in captive quokkas supplied drinking water *ad libitum* in cool weather. In December and January, animals caught 2 miles from the nearest free water were excreting 3 ml, or less, per day of highly concentrated urine. As Sadleir obtained rates of 2·9 and 2·3 ml/hr in quokkas kept at 30 and 40°C but given unlimited water, a high proportion of winter urine is clearly excess water. From 60 to 70 ml/day would probably suffice for the elimination of dissolved wastes—perhaps more in winter when protein intake is higher (consumption of water and urine flow were observed by Sadleir to vary with the protein content of the diet).

The water content of quokka faeces on Rottnest I. was found by Bentley to be 65% in winter and 50% in summer. Allowing a dry-matter digestibility of 63% (the average rate in Brown's low-protein trials), faecal output would be 16 g/day, resulting in a daily water loss of 30 ml in winter and 16 ml in summer.

The saliva secreted during a meal can be disregarded, for most of it would be re-ingested with the food. The copious salivation induced by high temperature (Bartholomew 1956) is best considered with loss by evaporation, from which it cannot be distinguished in practice.

Water loss by evaporation varies with the temperature, the mean rate in adult males kept by Bentley at 21, 29, and 40°C being respectively 5·5, 8·7, and 17·8 ml/hr. These data cannot be fully exploited as little is known of the temperatures experienced by quokkas on Rottnest I. Only one of their microhabitats has been studied, namely a daytime shelter beneath a *Gahnia* tussock at West Bagdad. Here the daily maxima measured by Sadleir on a hygrothermograph were 5–12°C higher than official readings at the lighthouse a mile away. Since the daily maximum temperature at the lighthouse averages 25·5°C in January–March, the quokkas at West Bagdad evidently endure temperatures of more than 30°C on many summer days. Considerably lower temperatures are to be expected in the few places where the vegetation is relatively tall and the canopy dense and continuous; but over most of the island, and at West End in particular, conditions would approximate to those at West Bagdad. The adoption of official shade temperature should therefore give conservative estimates of loss by evaporation, viz. 6·0 ml/hr in February and 3·3 ml/hr in August, when the mean temperatures are respectively 22·4 and 14·5°C.

Thus estimates of mean daily water loss for adult male quokkas for February and August are, respectively, 65 and 75 ml by renal function, 15 and 30 ml by defaecation, and 145 and 80 for thermoregulation. For their comparison with actual intake, 10 ml of metabolic water should be added to the water ingested with herbage (Table 7) remembering that this is augmented at the lakes with seepage water in summer, and everywhere in winter with rain and dew. As all these estimates are subject to errors of unknown magnitude, they must be regarded as very approximate. Nevertheless, they suffice to indicate a large water surplus at Mud Lake in winter, and the great dependence of West Bagdad quokkas on seepage water in summer. The apparent surplus at Cape Vlaming and deficit at Mud Lake in summer are both too small to be considered significant. The apparent deficit at West End in summer is much larger (*c.* 100 ml/day) and may be taken as evidence that water is deficient there and in other parts of the island where succulent vegetation and seepage water are similarly scarce or absent.

Whether or not the quokkas individually receive enough water, the inability of ordinary vegetation to provide adequate water has profoundly affected the nutrition of Rottnest quokkas. In summer thirst impels them to search for succulent herbage or to congregate at seepages, both of which are apt, as at Cape Vlaming and West Bagdad, to result in serious deficiency in other nutrients. In contrast, mainland quokkas inhabit densely wooded swamps and enjoy lower than shade temperatures, and have no water problems. In the Darling Range, they apparently maintain good condition throughout the year despite a diet that can be little richer in nitrogen than that of the Rottnest quokka in summer (Storr 1964). The effect of the low nitrogen content of Rottnest herbage in summer therefore would be much less serious if it were not coupled with an abnormally low intake of dry matter. If this low intake is due to the quokkas' insistence on succulent food, then their late summer debility could be caused as much by the prevailing absence of free water as by the seasonal deterioration of the herbage.

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