ECOLOGY OF THE KOALA, *Phascolarctos cinereus* (Goldfuss), ON FLINDERS CHASE, KANGAROO ISLAND

A thesis submitted for the degree of Doctor of Philosophy

I. H. EBERHARD

B.Sc. (Adelaide)

Department of Zoology

The University of Adelaide

August 1972

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Date . . 21 April 1970 . . Signed

According to one tradition of the Australian aborigines, see Mountford (1965), the first koala came into being following the death of an orphan. This orphan had been cruelly murdered by tribal elders, as punishment for stealing water. However, the theft was forced on him by the tribe's neglect. As compensation, the first koala did not need to drink and this has been true of koalas since (it is often said that the aboriginal name 'koala', means, 'no drink', or, 'I do not drink', e.g., Troughton, 1941; p. 132, but see Stead, 1939). The tradition also indicates that the aborigines are permitted to kill and eat the koala, provided they treat the carcass in a ritual way. That aborigines commonly hunted koalas is testified to by a number of early accounts, extracts of which are given by Waterhouse (1846) p. 260 and Troughton (1941) p. 132.

CONTENTS

PART 1 FIELD STUDIES

INTRODUCTION

1. THE DISTRIBUTION AND ABUNDANCE OF KOALAS

2. BREEDING, GROWTH AND DEVELOPMENT

SUMMARY

The distribution of koalas within Flinders Chase was found to be made up of areas centred on the occurrences of manna gum, *Eucalyptus viminalis*. Some koalas browsed chiefly in trees of other species but there were few animals, if any, that did not feed on the foliage of *E. viminalis* more or less regularly. The composition of populations in several study areas changed from time to time but over as long as three successive years of observation the numbers remained remarkably constant.

The koalas bred in the summer and early autumn, and a high proportion of females successfully raised a single young to independence each year. Growth of the young was rapid over the first three years; it slowed down thereafter and animals reached full size in their fourth and fifth years. Sexual maturity was reached by many females at the end of their second year of growth. Longevity was thought to be at least ten years.

Many animals lived within home ranges. Independent young were faithful to their parental home ranges until their second or third years of growth when they were lost from these areas. These young animals then became members of a nomadic section of the population, composed chiefly of animals of this age group. There was evidence that some of these nomads were ranging very widely. It was inferred that koalas dispersing from the vicinity of manna gums had greatly reduced chances of survival.

The home ranges of mature adults of the same sex did not overlap and there was additional evidence that adults were intolerant of the presence of other koalas. Physical conflict between adults was rarely observed and it was thought that vocalizations and scents were principally responsible for maintaining the security of home ranges and for attracting mates.

Experiments undertaken with koalas held in captivity on their responses to the foliage of various eucalypt species, indicated a degree of relationship between the palatability of a species and its yield of essential oil, as well as an inability to maintain weight when fed an unpalatable species. Consideration of the toxic effects of essential oils and aspects of their production by plants lent support to an hypothesis relating the koalas' responses to different eucalypt species in part to the effects of oil yield and composition on gut flora.

It was concluded that the distribution of koalas on Flinders Chase was governed by a need for manna gum browse and that within the distribution the abundance of koalas was limited by intolerant social behaviour.

DECLARATION

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

ACKNOWLEDGEMENTS

This study was carried out with the permission of the Fauna and Flora Board for Flinders Chase, while I was the holder of an Australian Wool Board Senior Post-Graduate Scholarship.

I was assisted throughout the study by the advice and encouragement of Professor H.G. Andrewartha and Dr. M. Smyth. I was assisted in the experiment on water turn-over rates, reported in Section 6, by the advice and help of Dr. B. Green.

My thanks are also due to the following people:
Mr. W.R. Gasking of the Cleland National Park, for caring for animals used in experiments; Mr. G. Lonzar, Mr. N. Coles, and their families, of Kangaroo Island, and Mr. and Mrs. R. Robins of Crafers, South Australia, for assistance and hospitality.

INTRODUCTION

In the Australian myth collected by Mountford (1965), the 'koala' is called 'koobor'. Stead (1934) lists other additional aboriginal names, Walker (1964) lists others again and Troughton (1955) p.400 gives another. The European colonists of Australia called Phascolarctos cinereus the 'native sloth' or 'native bear'. This last name is still used, but 'koala' is far more common.

The koala, native sloth or native bear weighs up to 30 lb (13 kg). The pelage is thick and short. Its colour is most often grey, but the chin, chest and inner aspects of the fore-limbs are always white, together with the long hair from the inside of the ears. The ears themselves are large and rounded; the eye is small and the snout remarkable for the large amount of naked or near-naked skin associated with the nostrils. The digits of the manus are provided with strong claws; the first and second digits are markedly opposed to the third, fourth and fifth. The second and third digits of the pes are joined together (the marsupial condition of syndactyly); the first digit of the pes is short and broad, it too is opposable in some degree to the others. The pouch has two nipples; it is often said to 'open backwards', but see Pocock (1921). The tail is a mere stub.

The koala is arboreal and nocturnal. It browses on the foliage of the omnipresent Australian genus Eucalyptus, but is reputed to be very selective with regard to species within this genus. The koala does not seek a nest or hollow during the day, but sleeps curled up in a fork. It moves rather slowly and awkwardly on the ground.

The koala's proper Linnaean name is not unequivocal. Recent users, among them, Ride (1970), Walker (1964), Marlow (1962), Simpson (1945), Iredale and Troughton (1934), but also Pocock (1921) and even Forbes (1881), use Phascolarctos cinereus and of these at least Iredale and Troughton, and Marlow give 1817 as the year when Goldfuss first published 'cinereus'. However, generally older users, among them Stead (1934), Wood Jones (1923-25), Lucas and Le Souëf (1909), Ogilby (1892), Oldfield Thomas (1888) (but compare Oldfield Thomas, 1887), and

Waterhouse (1846) use Phascolarctus cinereus and, at least in the case of the latter four, give 1819 as the year when Goldfuss first published 'cinereus'. In the earliest work listed here, Waterhouse is ambiguous. He calls the genus Phascolarctus (but see p. 539), but heads his synonymy with Phascolarctos De Blainville 1816. Calaby (letter dated 19 March 1972) says that his copy of the original description (Blainville, 1816; genus only) reads Phascolarctos, and that Goldfuss published his Lipurus cinereus in 1817. The koala's proper Linnaean name is therefore Phascolarctos cinereus (Goldfuss, 1817).

Phascolarctos has also received various treatments in taxonomic systems, from the time of the initial recognition of the basic unity of the marsupial fauna. The koala's large caecum, foot structure, selenodont dentition and arboreal life have suggested a closest relationship to the group of marsupials known as gliders and possums (and in particular to the genera Pseudocheirus and Schoinobates). However, the koala has a number of unique characteristics, and also shares a good number of peculiarities with the fossorial wombats. Koalas, wombats and the glider-possum group are all syndactylous, diprotodont marsupials. All taxonomists, however, have so far agreed in separating wombats from the glider-possum group at family level. The problem has been to decide whether koalas should be placed in a taxonomic system so as to show a closest relationship to wombats, to glider-possums, or so as to stand equally remote from either. Forbes (1881) in a study of koala anatomy found many characteristics in both organ and skeletal structure to be common only to koalas and wombats. Nonetheless he favoured separating koalas, wombats and glider-possums at family level at least. Pocock (1921), on the basis of external characteristics, separated wombats, koalas and 'phalangeroids' (glider-possum and kangaroo groups) at the level of super-family. On the other hand, Sonntag (1922), in a very careful investigation, found the anatomical evidence overwhelmingly in favour of a closest relationship to wombats. He joined the two in a family, but kept them apart at sub-family level. Notwithstanding, Wood Jones (1923-25), Simpson (1945), Marlow (1962) and Walker (1964) have followed Bensley (1903) in linking Phascolarctos with Schoinobates and Pseudocheirus - Phalangeridae (Phascolarctinae). Iredale and Troughton (1934), on the other hand, followed

Oldfield Thomas (1888) in keeping Phascolarctos apart within a monotypic family (Phascolarctidae). However, evidence continues to accumulate in favour of Sonntag's assessment. Pearson (1949) reported that koalas and wombats differ from other marsupials and resemble each other in that they develop a persistent chorio-allantoic placenta while also showing persistent yolk-sac contribution to the placentation. Sharman (1961) found the chromosomes of Phascolarctos (2n = 16) to be unlike those of any of the Phalangeridae (2n = 14 - 22) and as easily grouped with the Phascolomidae = Vombatidae (wombats); see also Martin and Hayman (1967). Hughes (1965) examined the spermatozoa of 18 marsupial species derived from five families. He reported that the spermatozoa of the koala and wombat, Phascolomis mitchelli = Vombatus ursinus, had a unique, somewhat rat-like morphology which clearly separated them from those of the other marsupials studied. Kirsch (1968), in a comprehensive serological study, found koalas to be most like wombats. Kirsch proposed a new taxonomy for marsupials in which koalas constitute a separate family but are linked with wombats at the level of super-family. Following Kirsch, the koala may be classified as follows:

Superorder	Marsupialia	Illiger, 1811
Order	Diprotodonta	Owen, 1866
Superfamily	Vombatoidea	(Iredale and Troughton, 1939 (1934?))
Family	Phascolarctidae	Owen, 1839
Genus	Phascolarctos	De Blainville, 1816
Species	cinereus	(Goldfuss, 1817)

The animal named Lipurus cinereus by Goldfuss in 1817, came from the vicinity of the Nepean river near Sydney, New South Wales. The type specimen is no longer in existence (Oldfield Thomas, 1888). Oldfield Thomas (1923) separated a Queensland race, which he named P. cinereus adustus. The syntypes for the race came from the Eidsvold district of south-eastern Queensland. They differed in being smaller animals, with shorter skulls, shorter coats and backs more strongly suffused with reddish or tawny. Troughton himself named P. cinereus victor in 1935. The syntypes of this race were a young male from French Island, Victoria and a male number M 5732 in the collection of the Australian Museum, Sydney. These animals, when compared with koalas taken in New South Wales, were distinguished by their more robust bodies, broader skulls with proportionately larger nasalia (though there is an intergradation of dimensions) and in the colour, thickness, length and hairiness of the coat.

Few fossil phascolarctid remains have been found. De Vis (1889) described *Koalemus ingens* of south-eastern Queensland from the distal end of an incomplete right fibula. De Vis estimated the weight of *K. ingens* as 5 cwt! (200 kg). He also referred to *K. ingens* a cranial fragment, though it clearly came from a vastly smaller animal (which De Vis assumed was a juvenile). Bartholomai (1968) considered that *K. ingens* was probably of Pliocene age. He argues that *K. ingens* is better referred to the Diprotodontidae. However, he considers the cranial fragment collected by De Vis to be of undoubted koala origin (though not from a juvenile animal). Bartholomai himself describes a fossil koala, *Phascolarctos stirtoni*, from the Pleistocene of south-eastern Queensland. Stirton (1957) described an Upper Oligocene fossil phalangerid with phascolarctine affinities, *Perikoala palankarinnica* (see also Stirton *et al*, 1967). Stirton *et al* (1961) have described a further fossil koala, *Litokoala kutjamarpensis*, of probable Miocene age. Turnbull and Lundelius (1970) have described *Pseudokoala erlita* from the late Pliocene of western Victoria. Fossil *Phascolarctos* sp. remains of probable Pleistocene age have also been recorded for Kangaroo Island, South Australia (Pledge, pers. comm.) and from the south of Western Australia (Glauert, 1910). In this latter case the remains are attributed to the extant species (see also Bartholomai, 1968). The location of these various finds, together with the locations ascribed to the types for the three races of the extant species, are shown in Figure 1.

The *Phascolarctos* fossils from Kangaroo Island and Western Australia are interesting in that they lie outside the limits considered by Burnet (Sutton, 1934) to make up the range of koalas in Australia at the time of the European colonization (1778). This range is shown by a continuous line in Figure 1. It covers the eastern sea-board of Australia

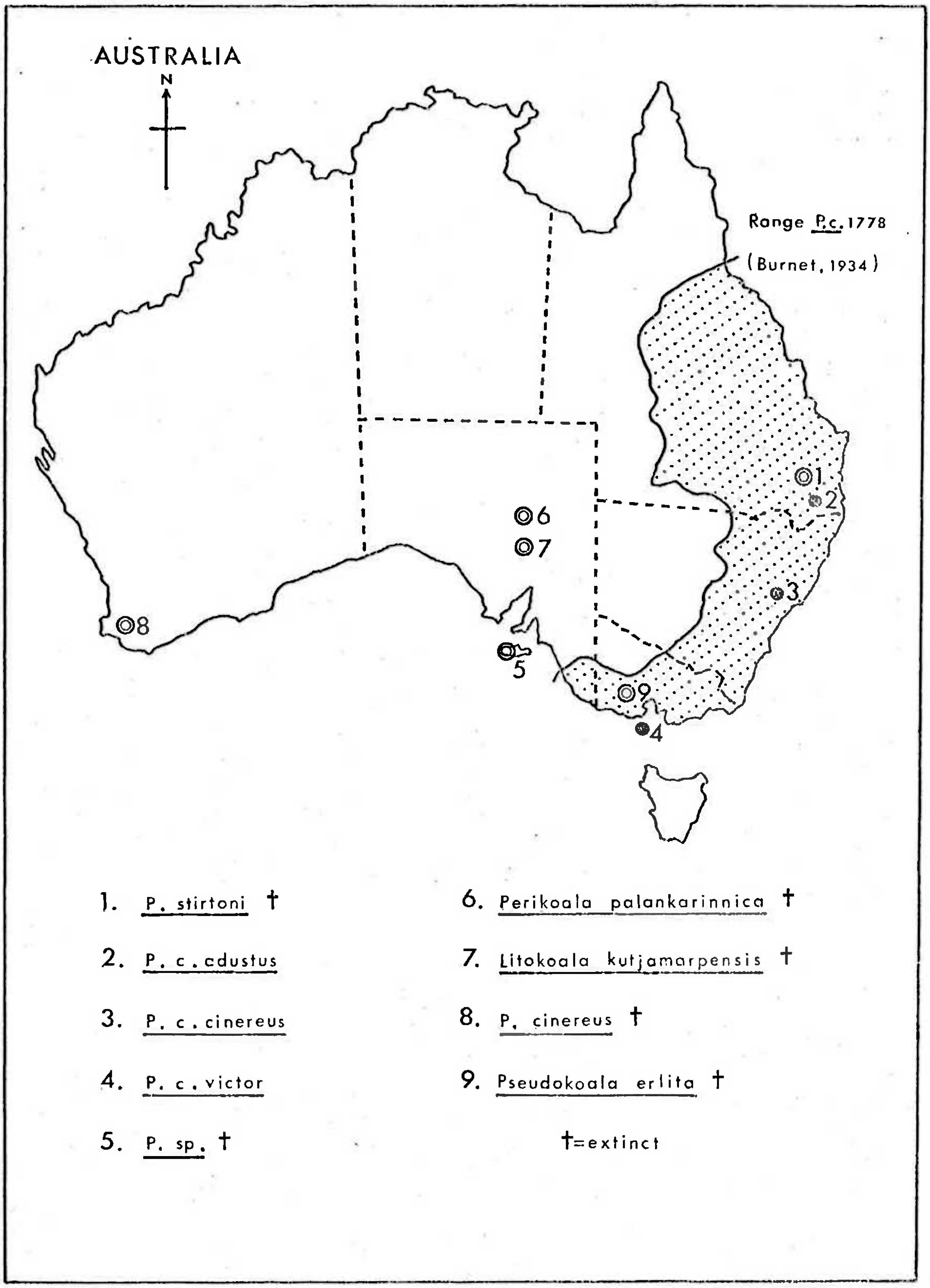


Figure 1 Type localities for extant races of *Phascolarctos cinereus* and geographic range ; sites of fossil finds.

from about Townsville (c. lat. 20°S.) in Queensland to south-eastern Gippsland (c. lat. 38°S.) in Victoria, and round to the extreme south-east of South Australia. It can be inferred (see below) that in parts at least of this range, koalas were very abundant. The present range of koalas is vastly reduced. The clearing of forests has probably been the most important single factor though changing patterns of wildfire, and epidemic disease have also without doubt played a part. Troughton (1941) p. 134 and Stead (1934) record that at times between 1885 and 1903, epidemics involving some form of ophthalmic disease and periostitis of the skull swept away millions of koalas in New South Wales and Victoria. The koalas have further been reduced by the fur trade. Lucas and Le Souëf (1909) reported that in the year 1908, 57,933 koala skins passed through the Sydney market alone. Wood Jones (1923-25) quotes Osborn and Anthony to the effect that in the two years 1920 and 1921, 205,679 koalas were killed for the fur market. Troughton (1941) p. 137 reports that in 1924 the colossal total of 2,000,000 koala pelts were exported from the eastern States (Queensland, New South Wales and Victoria); and that in the last open season on koalas (Queensland, 1927), 10,000 licensed trappers were responsible for an export of 600,000 skins.

In view of the blood-letting implied by these statistics, it may be thought surprising that the koala has come to be regarded by most of the Australian public as a very special animal, and one deserving complete protection. Fortunately, this is so, and in those Australian states where they occur in the wild, koalas are listed on the schedules reserved for wildlife requiring complete protection. Grave public fears formerly held for the survival of the species seem now to be groundless. Although koala numbers in New South Wales and Queensland may have further declined, despite protection (Kikkawa and Walter, 1968), their range in Queensland is still very extensive, while koala numbers in Victoria have increased strongly. McNally (1960) reported that, in this latter state, some 7,000 koalas had been taken from French and Philip islands (to which they had been introduced and where they had greatly multiplied) and liberated on the mainland. At this time, 1960, some 50 areas had been re-stocked, 6 with more than 500 koalas. The present range of koalas in Australia,

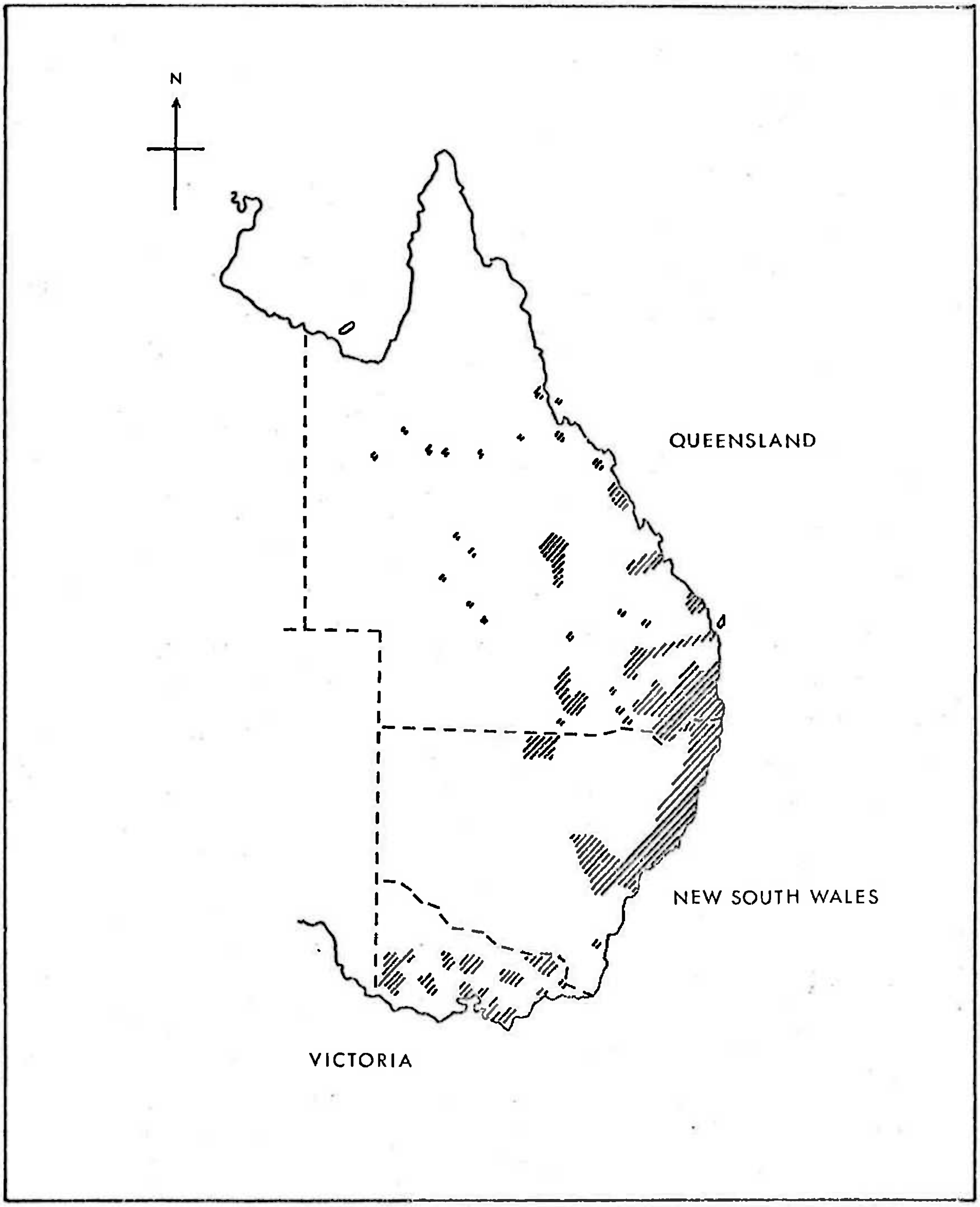


Figure 2 Distribution of *Phascolarctos cinereus* in Australia (1972)

as it is known, is shown in Figure 2. Data for Queensland is from Kikkawa and Walter (1968); for New South Wales is from the National Parks and Wildlife Service of that state, and for Victoria is from the Native Fauna Conservation Society of that state. It remains, of course, uncertain if particular places presently inhabited were so formerly.

The popularity of the koala in Australia is now such that one item of folk-lore is almost universally held: that is that koalas can eat the leaves of only a few of Australia's many different (c. 500!) species of 'gum trees' (*Eucalyptus* sp.). The literature on koalas is, in fact, not extensive and koalas remain one of the least well understood of Australian marsupials.

A study of the ecology of a population of koalas living on Kangaroo Island, South Australia, was first suggested to me by Professor H.G. Andrewartha. [Koalas, of course, are not native to this part of South Australia; this present population originated in the introduction of a number of animals in 1923. At the time the suggestion was made, (1966), it was believed that the population numbered a little over one hundred animals and was entirely confined to several relatively small areas where manna gum, *E. viminalis*, grew. This, coupled with the fact that koalas may be found during the day by the inspection of trees, suggested that the population could be studied in unusual detail (provided the problem of catching animals could be overcome). In fact, this assessment was soon proved to be inaccurate. However, additional reasons for pursuing the study were:

a. the need for a properly founded management programme: in some places it seemed clear that koalas were defoliating and killing the trees on which they apparently relied.

b. the view that it was timely to undertake field studies of an animal in which there was a great deal of public and scientific interest, but about which very little was really known.

The target I set myself in this study was to explain the distribution and abundance of koalas, in terms at least at the level of the important 'factors of the environment'. I expected this to lead me to want some information at least on just about all aspects of koala whole-animal biology, so I began to collect information and make observations even as I set out to document the distribution and abundance. I found that working on a broad front made for many problems: but I liked the larger view it gave me of the animal.

The basis for my field studies was largely -

(1) the capture and examination of koalas,
(2) the release of marked animals and the recapture of selected ones,
(3) systematic searching to gather data on numbers, movements, dispersion etc.

The field studies were supplemented by some observations and experiments, mostly to do with browse preferences, on confined animals.

This thesis is in two parts. The first reports my field studies; the sections into which it is divided are meant to follow one another as a progression in analysis. The second part reports the observations and experiments on confined animals.

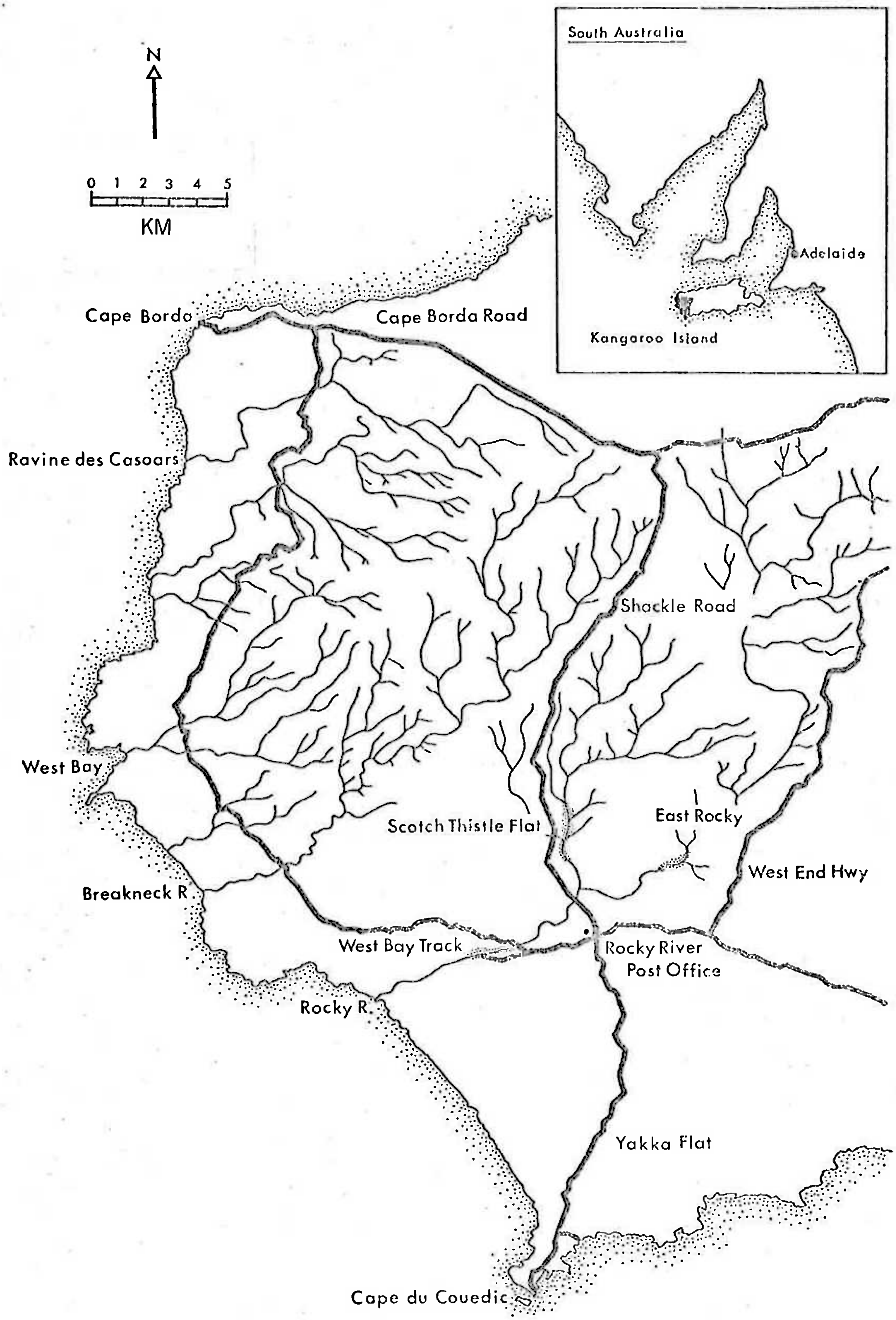


Figure 3 FLINDERS CHASE KANGAROO ISLAND

PART 1 FIELD STUDIES

0. INTRODUCTION

0.1 Kangaroo Island

Kangaroo Island lies off the South Australian coast in latitude 36° South and longitude 137° East. It is some 90 miles (145 km) long, east to west, and 25 miles (40 km) wide, with a total land area of 1680 sq. miles (4,351 km^2).

At the time of its charting by European navigators, the island was not inhabited by Australian aborigines. The European settlement of the island has been followed by the usual extensive husbandry of the land for pastoral purposes, and much of the native vegetation has been destroyed. However, some quite extensive tracts remain; the largest and most important of these is the Flinders Chase Flora and Fauna Reserve, which occupies some 220 sq. miles (570 km^2) of the western end. The island flora, and its relationship to mainland floras has been studied by Wood (1930) while Bauer's (1959) extensive geographical study gives accounts of the geology, pedology and climatology, among other matters.

The central part of Kangaroo Island is a low (highest elevation c. 950' or 290 m) dissected plateau, formed of ancient, complexly metamorphosed sediments. The surface is made up of the weathering products of these basement rocks which gives an infertile podsol containing, in places, much lateritic gravel. In a few places there is a very superficial covering of younger deposits. The plateau and its marginal slopes account for some 58% of the total surface area. The rest of the island is largely a coastal province of Pleistocene-Recent calcareous aeolianites. The island was separated from, and rejoined with, the mainland a number of times during Pleistocene-Recent times.

Kangaroo Island weather is mediterranean. The circulation is controlled by pressure systems moving from west to east, with their centres usually well south of the island. Temperatures are moderate. Rainfall is also moderate but dependable and distinctly seasonal - some 65% falls between May and September. In Table 1 I have given mean maximum, minimum and mean monthly temperatures for Cape Borda and in Table 2 I give the average rainfall for successive fortnightly periods throughout the year, also for Cape Borda. These data are based on 60 years of records and come from Bauer (1959).

TABLE 1 Cape Borda, Kangaroo Island: mean daily maximum, mean daily minimum and mean daily temperatures for each month of the year (60 year average).

MONTH	Mean Max. Temp.		Mean Min. Temp.		Mean Temp.	
	°F	°C	°F	°C	°F	°C
Jan	73.4	23.0	56.7	13.7	65.1	18.4
Feb	74.3	23.5	57.6	14.2	66.0	18.9
Mar	70.4	21.3	55.9	13.3	63.2	17.3
Apr	65.3	18.5	53.9	12.2	59.6	15.3
May	61.2	16.2	52.2	11.2	56.7	13.7
June	57.8	14.3	49.6	9.8	53.7	12.1
July	56.5	13.6	48.1	8.9	52.3	11.3
Aug	57.0	13.9	48.0	8.9	52.5	11.4
Sept	59.1	15.1	48.6	9.2	53.9	12.2
Oct	62.8	17.1	50.1	10.1	56.5	13.6
Nov	67.4	19.7	52.4	11.3	59.9	15.5
Dec	70.9	21.6	54.4	12.4	62.7	17.1
Annual	64.7	18.2	52.3	11.3	58.5	14.7

TABLE 2 Cape Borda, Kangaroo Island: average rainfall over successive 14 day periods throughout the year for 60 years.

period	Average fall		period	Average fall	
	pts.	mm.		pts.	mm.
Jan 1-Jan 14	25	6	Jul 2 -Jul 15	208	53
Jan 15-Jan 28	35	9	Jul 16-Jul 29	178	45
Jan 29-Feb 11	23	6	Jul 30-Aug 12	179	46
Feb 12-Feb 25	46	12	Aug 13-Aug 26	138	35
Feb 26-Mar 11	33	8	Aug 27-Sept 9	130	33
Mar 12-Mar 25	32	8	Sept 10-Sept 23	114	29
Mar 26-Apr 8	74	19	Sept 24-Oct 7	82	21
Apr 9-Apr 22	79	20	Oct 8-Oct 21	68	17
Apr 23-May 6	90	23	Oct 22-Nov 4	65	17
May 7-May 20	161	41	Nov 5-Nov 18	54	14
May 21-June 3	157	40	Nov 19-Dec 2	38	10
June 4-June 17	216	55	Dec 3-Dec 16	41	10
June 18-July 1	208	53	Dec 17-Dec 31	34	9
			Jan 1-Dec 31	2508	637

0.2 Flora and Fauna of Flinders Chase

The poor soils and seasonal distribution of rain favour a dense, low, prickly scrub dominated by Eucalyptus, Acacia, Melaleuca, Hakea, Banksia, Xanthorrhoea, Grevillea, Casuarina and Leucopogon. Ten species of eucalypts have been reported from Flinders Chase. They dominate the flora everywhere.

On the plateau area of Flinders Chase occur Eucalyptus remota, E. diversifolia, E. obliqua (stringy-bark), E. baxteri (brown stringy-bark) and E. cosmophylla (cup or bog gum). These trees are stunted, or of a mallee growth form with a large lignotuber and a number of main stems. In places the 'mallee' is under 9' (2.7 m) in height. This plateau comprises most of Flinders Chase, except in the south and south-west, where the Rocky River divides the plateau from the coastal province (extensive areas of consolidated sand dunes which run to the coast). The dunes of this coastal province are mostly covered with a thick, low mallee scrub of E. diversifolia and E. rugosa. However, along the large creeks and the rivers, and in other areas of better soil, occur stands and various associations of E. cladocalyx (sugar gum), E. fasciculosa (pink gum), E. ovata (water/swamp gum) and E. viminalis (manna gum). All these species grow only in tree form and specimens of E. cladocalyx and E. viminalis are very large, reaching 90' (27 m) and more in height. E. viminalis and E. ovata are restricted to the Rocky River and a small part of the 'corridor' between the plateau and the coastal province. The other species are all widespread and abundant. Some photographs of several kinds of eucalypts are presented at the end of this introduction (Figs. 5 - 9). *

The mammal fauna of Flinders Chase is summarized in Table 3. It is noticeable that it does not include any animal likely to prey on koalas. Indeed, the only conceivable predator of koalas on Kangaroo Island is the wedge-tailed eagle Aquila audax. However, these

---

* In parts of the text it is necessary to refer repeatedly to particular species. I have generally used common names since they are more easily read.

eagles are rather infrequently observed and then either soaring at great heights, or attending to the abundant carrion (road kills of wallaby and goanna, Varanus gouldii), so there are reasons for thinking that they do not constitute a menace to koalas. The only other non-mammalian fauna associated with koalas is the tick Ixodes tasmani, which is very occasionally found on them. Koalas in general are remarkably non-verminous animals, though they may carry the intestinal cestode parasite Prototaenia obesa, and were the host carrying the parasite responsible for the nomen nudum Taenia geophiloides (Mackerras, 1958).

TABLE 3 Flinders Chase, Kangaroo Island: Mammal Fauna

Mammal	Abundance	Authority
Tachyglossus aculeatus (echidna)	+	Obs.
Ornithorhynchus anatinus (platypus) X	+	Obs.
Macropus fuliginosus (kangaroo)	++	Obs.
Wallabia eugenii (wallaby)	+++	Obs.
Trichosurus vulpecula (possum)	+++	Obs.
Cercatetus sp. (possum)	?	Obs.
Phascolarctos cinereus (koala) X	+	Obs.
Isoodon obesulus (bandicoot)	?	Obs.
Dasyurus viverrinus (native cat)	?	Wood Jones (1923-25)
Rattus fuscipes (bush rat)	+++ (1967-69)	Wheeler (pers.comm.)
Rattus lutreolus (swamp rat)	?	Wheeler (pers.comm.)
Arctocephalus sp. (seal)	+	Obs.
Order Chiroptera (bat)	+++	Obs.
Felis catus (cat) X	?	Obs.
Sus scrofa (pig) X	++	Obs.
Capra hircus (goat) X	+++	Obs.
Mus musculus (mouse) X	+++ (1972)	Augee (pers.comm.)
Rattus rattus (rat) X	?	Augee (pers.comm.)

X = 'introduced'

+++ = very abundant

+ = common

Koalas were first introduced to Flinders Chase in 1923, when, according to local report, six pairs were brought from Victoria and kept in an enclosure containing water gum, E. ovata; close by the site of the present Rocky River Post Office and Rangers' cottages. These animals are said to have escaped and made their way to the nearest stand of manna gum, E. viminalis, some two miles (3.2 km) distant and on the Rocky River. Gosse (1939) says that the original introduction was of six animals and that these were followed in 1925 by twelve more.

In any event, it seems that over the last thirty years koalas have been seen in considerable numbers in this manna gum stand and in another area of manna gums some four miles upstream.

0.3 Philpott's study

Philpott (1965) searched likely areas in Flinders Chase for koalas and manna gum. He found that the manna gum was restricted to three areas along the Rocky River and that koalas were present in all three places. Many of the manna gums were severely defoliated which he attributed to the browsing of the koalas.

The three areas along the Rocky River where Philpott found and counted manna gums and koalas are shown by shading in Figure 3. The area due north of the Rocky River Post Office is known as Scotch Thistle Flat. The area to the west which extends downstream from where the West Bay track crosses the Rocky River, I refer to as the West Bay Track, while the area on the eastern branch of the Rocky River, to the north-east of the Post Office, will be called the East Rocky.

Table 4 gives the number of manna gums, the percentage of these trees showing severe or extreme defoliation and the number and density of koalas from Philpott's data. The figures for the numbers of trees and koalas along the East Rocky are much more of a minimum than the others; Philpott thought that in this area he might have seen only half the total number of trees. However, Philpott's total of 111 koalas is in remarkable agreement with an estimate of 100 koalas made by Gosse twenty-six years previously.

In Table 4 there is a very evident difference between Scotch Thistle Flat and the other areas in the density of koalas. This difference, however, is greatly reduced if the total numbers of trees (i.e. counting trees of all species) in these areas are considered. Scotch Thistle Flat is an almost pure stand of manna, whereas pink and sugar gums are common in the West Bay Track and sugar gums and stringy-barks are common along the East Rocky. Koalas are quite often seen in these trees when they occur within the confines of the manna gums.

TABLE 4 Flinders Chase, Kangaroo Island:
The numbers of Koalas and Manna Gums
(Philpott, 1965)

	West Bay Track	Scotch Thistle Flat	East Rocky	Total
Number of Manna Gums	771	2,852	503	4,126
Percent of Manna Gums with Severe or Extreme Defoliation	65	6	43	
Number of Koalas	45	36	30	111
Number of Manna Gums per Koala	17	79	17	

There is little difference in the density of koalas relative to area. The West Bay Track and Scotch Thistle Flat are roughly comparable in size. However, another difference between these places may be important in relation to the density and this will be discussed later (text 1.2 p. 36).

The striking incidence of severe or extreme defoliation of manna gums in the West Bay Track is probably only partly due to the browsing of the koalas. It was noteworthy that some trees showing extreme, severe or even only moderate defoliation were in almost continuous use but responded vigorously to the summer growing season, whereas other comparable trees, though not browsed to any great extent, responded weakly. I think it likely that such trees were overmature and stressed in some additional way.

Philpott did not find any koalas apart from these areas, though he noted that there had been very occasional reports of isolated animals far from the Rocky River. He considered them to be survivors of a dispersal, brought about by social pressures, from the only areas really suitable for koalas - those places where manna gum was available as food.

This report agreed well with local opinion on the distribution and abundance of koalas and also with a long-standing popular view that koalas are able to live on only a few of the hundreds of species of Eucalypts; among which manna gum is prominent as the alleged staple diet of koalas in Victoria.

In addition to the manna gums of the main areas, there are also odd trees in other places. Philpott counted thirty-four between Scotch Thistle Flat and the confluence of the East and West Rocky River branches. He considered such trees to be important in the original colonization of this area. There are also four manna gums in the vicinity of the Rocky River Post Office, the original point of release, and two small plantations have been established here recently by the Ranger, one of which is still in the sapling stage. Koalas live here too, but were not counted by Philpott.

0.4 An initial appraisal to establish methods

The East Rocky is very difficult to reach and work in, because of the swampy nature of much of the ground and impenetrable thickets of Prickly Acacia, Acacia armata. The West Bay Track is less physically uniform than Scotch Thistle Flat and so easier to navigate in, but since I intended to work equally in all areas, it was chance that I began to make observations and catch animals in the West Bay Track. The manna gums

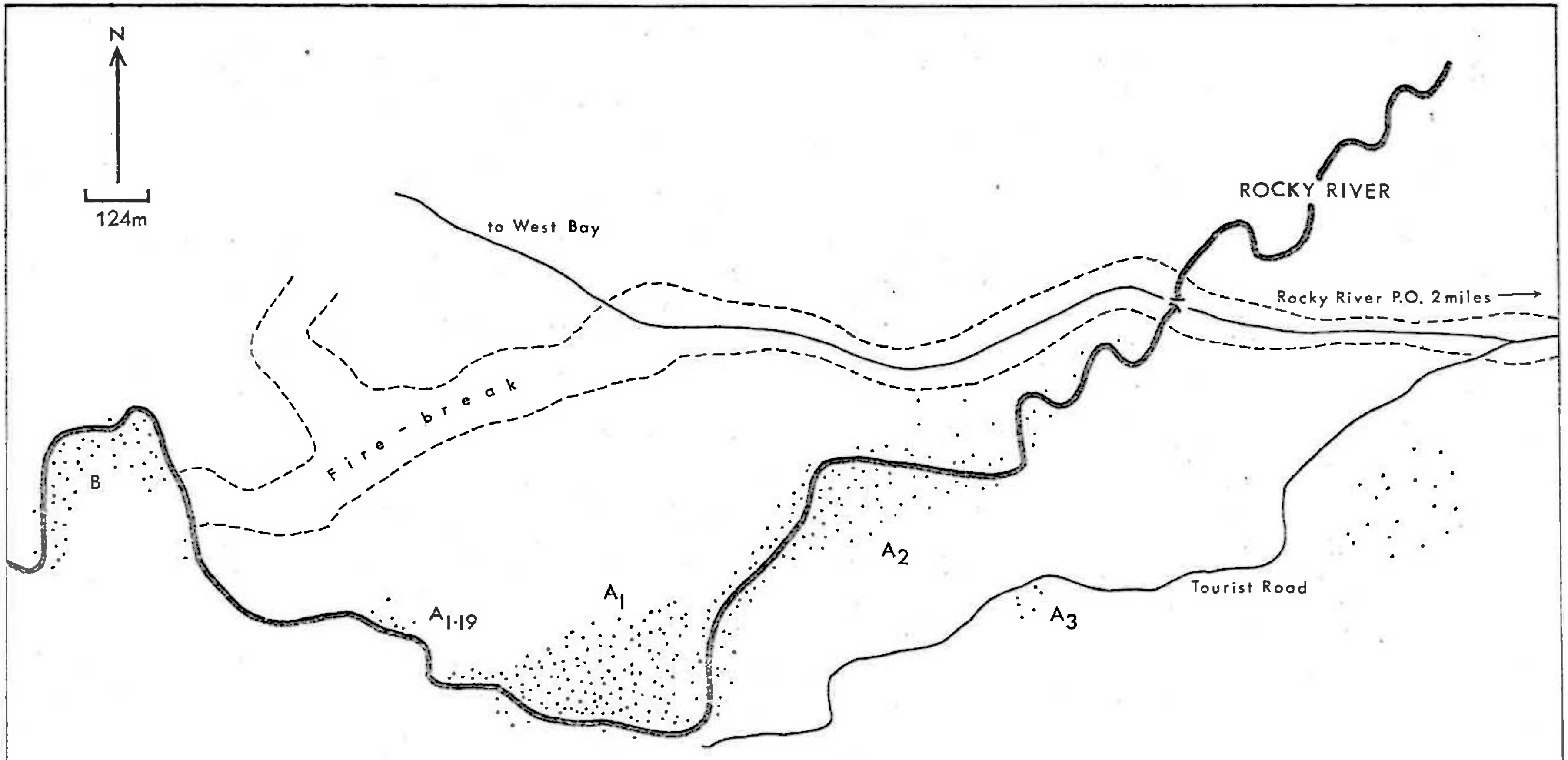


Figure 4 The West Bay Track – distribution of Manna gums & study areas

in this area grow together with many pink gums and some trees of other species in a series of flats along a mile stretch of river. * The area came to be divided into various sub-areas, designated A_1, A_2, etc., with further sub-divisions $A_{1.1}$, $A_{2.1}$, etc. The relationship of the sub-areas referred to later in the text, and then simply by their designation, is shown in Figure 4. Part of A_1 was commonly visited by tourists.

In April of 1966 I caught and marked seventeen animals. Twelve of them were from A_1 and three were from A_3. In May - June of 1966 I searched A_1 on six consecutive days and, a short time later, for another three consecutive days. Of the twelve marked here in April, eleven were seen during these searches. However, no animal was seen on every occasion, and four were seen three or less times. Similar caprice was shown by the nine animals caught during this visit. Area A_3 was searched on nine consecutive days. All three animals marked here in April were seen but no animal was present on every occasion.

Since it was characteristic that when marked animals were seen they were always found close to, and quite often in the same tree where they had been caught and marked, it seemed unlikely that their absences were brought about by movements up and down river within the belt of manna gums, beyond the extent of my searches. Instead, it seemed more likely that many animals were moving away from and returning to the river and the manna gum belt.

This conclusion was provoking, however, in that I had not seen any koalas outside the manna-pink gum belt, despite many searches. I had in particular examined the margins of the area where other species grow, and also those nearby stands of sugar and pink gum which, because of the size of the trees, seemed most likely to harbour koalas. I found evidence in the form of faecal pellets, but this could be attributed as easily to a slow accumulation from a process of dispersal or occasional exploration, as to regular, local movement. This conclusion was also,

---

* In the text, 'manna gum areas', 'manna gum belt' and 'river flats' are used interchangeably.

of course, completely counter to Philpott's assessment and to established local opinion.

During subsequent field trips I began using radio-transmitters to track animals. These transmitters were modified versions of the telemetry devices described by Tester, Warner and Cochran (1964). The signal was intermittent and gave a maximum range of about 200 yards (183 m). The transmitters were built into collars.

The koalas paid no attention to the collar and I saw no attempt to remove it, though most animals that were not recaptured within a few weeks sooner or later rid themselves of it. One animal did carry a collar for five months until it was taken off.

At various times during the period between August 1966 and December 1967, transmitters were put on a total of thirteen animals. Data were not easily obtained. The range was inadequate for the scale of overnight movement which varied from a few chains (40 m) to a quarter mile (400 m) or more. Some of the transmitters functioned unreliably after a short while for a number of reasons. However, the data gained is summarized in Table 5.

TABLE 5 Radio-tracking koalas: movement of individual koalas out of manna gum areas and back again.

No. of days spent in successive periods during which animal was 'in', and 'out' of, the manna gum area.
(R = release; ? = day on which animal not found.*)

ANIMAL	In	Out	In	Out	In	Out	In	Out	Total days
(1)	R	1?1	1	2	1	6	1	1	14
(2)	R	1?1?	1	1	1	3	1		12
	R2	5	2?2	1					
(3)	R?1	1	2	1	1				
(4)	R	2???1	1	2	2				
(5)	R1	1	3	1					
(6)	R2	3	4	1?					
	R5	1	5						
(7)	R6	1	5						
(8)	R???1	4	1						
(9)	R	10??1							
(10)	R1	1?							
(11)	R6								
(12)	R5								
(13)	R5								

?= out

in	out
4	12
2	5
7	7
6	3
4	8
5	2
7	5
18	7
13	
3	7
1	13
2	2
7	
6	
6	
92	69

---

* When animals were not found, they were more likely to have been 'out' than 'in'.

It is clear from these results that most of the animals tested with radio-transmitters showed a more or less regular pattern in which they moved to and from the manna gum areas. The coincidental, but mainly in January 1967, release of many more marked animals (which, in many cases, were also sighted discontinuously in circumscribed parts of the manna gum areas) indicated that local movement to areas outside the manna gum flats was quite general.

Estimates of the distance from the manna gum areas reached by these animals varied from a few hundred metres to a kilometre or more. Of course, in a dense tree scrub such movement amounts to a wide dispersion of animals. This is one reason why this movement had hitherto escaped attention.

Other contributing reasons were, at least for those animals going in to the mallee scrub:

(1) much of the mallee scrub is difficult to penetrate,

(2) koalas were often completely hidden in the heavy head of leaves that in the mallee surround the only forks in which koalas can sit,

(3) it had been natural to assume that mallee, because of its dwarf size, was unsuitable for koalas.

These results, then, confirmed the conclusion I had drawn as a result of marking koalas in the river flats. They also implied:

(1) the restriction of some koalas to very circumscribed parts of the river flats was not due to lack of mobility,

(2) animals could live for short periods of time at least on species other than manna gum. (koala (9) in Table 5 did so for at least ten days),

(3) there were many more animals utilizing the manna gum flats than Philpott and others had previously thought, since only a proportion of the population was to be seen within these areas on any one day.

It followed from (3) that it would be necessary to reduce the scale of my study. I chose to work mainly in A_3 and B.

0.4.1 Special Study Areas

Area A_3 is a group of 14 manna and 14 pink gums, isolated from the river flat by a sandhill some 200 yards (183 m) through at the base and without trees for the most part on its near face, and, at the back, separated by a short stretch of open ground from a line of pink gums and large E. rugosa which are the margin of the mallee scrub on the succeeding rise.

Area B is a river flat holding 131 pink, 106 manna, 2 water gums and 19 E. rugosa, some 50 chains (1 km) downstream from the main flat, A_1. The area is roughly a 300 yard (274 m) square and is bounded on three sides by the river and sugar-pink gums while the fourth side is a steeply rising sandhill clad mostly in E. diversifolia - E. rugosa scrub except for those places cleared as part of a fire-break system.

These areas were mapped with the position of every tree plotted using both aerial photographs and ground survey. The koalas found in these areas were caught and marked. Area B was searched on seven occasions from July 1967 to July 1968 for 7, 8 or 9 consecutive days and again in January and June of 1969. Area A_3 was searched on 8 occasions from May - June 1967 to June - July 1968 for from 11 - 18 consecutive days, and from September 1968 to June 1969 every month for 7 or 9 days. Koalas present in trees within these areas were recorded on maps each day during the search.

These searches were most exact. Initially, all trees were examined from every aspect but as I grew familiar with each individual tree, I came to know from whatever position I was in which parts of the tree were visible and which were not, so I was able to move more freely through these areas. This care is necessary, for although in areas occupied by koalas many are easily seen, some are always very difficult to see. Since I was often in these areas for reasons other than searching, I had plenty of opportunities to check the morning's search in part and on the very few occasions when a koala was noticed that had not been recorded, I usually had reason to believe it an example of infrequent movement during the day.

While I continued to systematically search these areas, I made effort to catch any unmarked animals seen within them. This was mostly done, and on those few occasions when it was not possible, I observed the animal with particular care, so that from my opinion of its age, sex and individuality, I could possibly recognize it again.

I also took any opportunity to search other parts of the West Bay Track, though this was mostly done with less rigour.

0.4.2 Catching: Examination: Marking

Koalas were caught by slipping a noose over the head, using a long pole which had a hook at one end on which the noose could be hung. Almost always the tree had to be climbed and I used climbing irons or spikes and a belt of the kind made by the South Australian Woods and Forests Department. Once noosed the animals were persuaded to enter a large bag, or in some cases, simply pulled off the branch and lowered to the ground. A certain flexibility in technique is needed, however, in order to consistently succeed. Catching animals was easy or difficult according to the kind of tree, weather and altitude. It was never dull.

Koalas differed in their reaction to attempted capture. Animals which were accustomed to the presence of people and had not been hitherto molested, often showed little apparent agitation until a near approach had been made, when their attempts at escape into neighbouring trees or on to branch extremities were often belated. Animals unused to people reacted more quickly while those that had been captured before showed by micturition, tremor and various vocalizations, extreme agitation and made determined efforts to escape and resist capture, even to the extent on several occasions of making leaps for adjacent trees at hopeless distances. Several falls of 40 to 50' (12 to 15 m) or more were not attended with physical injury to the animal, such is the robustness of the body.

Animals were taken to the field station for examination. They were weighed to the nearest 50 grams, and sexed. The length between the occipital crest and the most anterior part of the snout was measured. The amount of wear on the premolar and the first molar was judged into one of five progressive categories, and in young animals the state of molar eruption was noted. The pouch and nipples of females were inspected and the size and activity of the male sternal gland was noted. The examination also recorded the colouration, appearance and physical condition of the animal. Initially, pouch young were removed and examined but this was discontinued as females with young reacted strongly to interference with the pouch and I found the job of reintroducing young to the pouch hazardous for all. The non-examination of pouch young, and the subjective method of assessing tooth wear were forced on the study by two reasons:

(1) most animals were caught because they appeared in areas where I attempted to keep all koalas marked, or because, having been caught and marked, their re-capture could provide useful data on growth, breeding, seasonal variation in condition etc., i.e., catching was not something I could order.

(2) this made the unaided catching, examination of, marking and release of koalas an even more time-consuming job than it would have been otherwise, and one necessarily to be kept as simple as possible.

For the same reasons it was desirable to economize on the number of different measurements that were taken. Early in the study fore-limb, hind-limb and crown-rump measurements were recorded. The eighteen animals for which these additional measurements were available, varied from several less than 12 months old to some of the largest taken. Over this wide range there was no evidence of differential growth (all measures correlated highly with the others but with the best correlation going to head-length and body-weight) so it was thought that nothing was lost when these measurements were discarded in favour of head-length, the most easily taken measurement. For each animal handled, at least two independent measures of head-length were always taken.

Koalas were marked with specially made tags consisting of two laminated plastic discs, 33 x 18 x 1.5 mm, on which was engraved a number or letter, which appeared on the face of the tag in a different colour. Five different colour combinations were used, the discs being held in the ear by Verdict plastic interscrews, with araldite as a thread-filler. A tag was placed in each ear, giving four opportunities of identifying the animal. These tags could be read at a considerable distance with 10 x 50 binoculars. I never failed to identify a tagged animal surely, though this was not always immediate. Tags were not infrequently lost, but in many cases at least one tag was retained throughout the course of the study. From June 1967 on, numbered fingerling tags were placed in one or both ears in addition, enabling, on their recapture, recognition of individuals that had lost the principal tags. I recorded only one loss of a fingerling tag. I also successfully marked some animals with Durafur Black R dye, which was prepared as described by Rowley (1956).

I examined and marked koalas without recourse to drugs or special holding devices. Animals did struggle vigorously at times but attempts at aggressive clawing and biting were infrequent. Large females when with pouch young were the most difficult to handle.

Animals were mostly released on the same day and into the same tree from which they were taken. They usually climbed with alacrity, though they would often pause every five feet or so, when animals low down would sniff at the bark. It was also usual for koalas to appear to settle down very readily, but occasionally, and with an increasing probability after the animal had been caught more than once, they would climb to the top of the tree and vocalise in a very characteristic manner. This vocalization I term the distress call and the only occasions on which I heard it were when I released captured animals, or, less frequently, when I attempted recaptures. It is a loud sound and may be continued for some time - as long as one and one half hours on one occasion. It is often accompanied by shivering and slavering on a small scale and is best described as a series of high-pitched yelps interspersed with a chattering sound. It is striking to witness such a response from an animal that has remained quiet during handling and has exhibited little indication of distress.

It is just as striking that such a response seems to elicit little interest from animals nearby - though on one occasion when I released two animals into adjacent trees, one of which was already occupied, and both the released began to call, the resident animal joined in. This suggests that distress can induce a sympathetic response.

The effect of the capture and release of an animal on its subsequent movements and those of its neighbours was not clear. It did not follow that such animals would always shift their ground, though I formed the impression that this was rather more likely than in the absence of interference. However, such movement was always within the animal's normal range.

Koalas have keen senses. Their vision may be relatively poor during the day, but their hearing is very acute and it is difficult to approach animals in remote areas without being detected. The importance of their olfactory sense will be inferred in other sections.

It is intriguing that some among those koalas which are completely unused to people will engage in surprisingly effective cryptic behaviour. Animals on the trunk of a tree may keep themselves on the side opposite the intruder. They can be moved in any direction at will by circling the tree. Other animals surprised out on a thin limb will incline the body away from the observer and fail to present an outline or silhouette. There are variations on these forms of behaviour and perhaps the immobility of many patently alert animals is one. They are seen also in animals that have been recently caught, though all animals will quickly adapt if their area is much visited.

In view of the non-universality of such behaviours, it is tempting to consider them behaviour patterns selected for in less secure times but no longer vital. I know of no natural predators of koalas.

A similar argument might explain why the koalas' vigorous and determined efforts to escape restraint do not incorporate that element of hysteria which distinguishes, for instance, the response of the smaller, ground-foraging brush-tailed possum, Trichosurus vulpecula.

0.5 Results

In the general introduction to this thesis, I said that a large part of the field study of koalas was based on:

(1) the capture and examination of koalas

(2) the release of marked koalas and the re-capture of selected animals

(3) systematic searching of particular areas or for particular koalas

In fact, 140 koalas were caught a total of 249 times, and 2,136 sightings were made of marked animals. In addition, 28 koalas were caught for the stocking of several public and private fauna collections. These animals were selected on the basis of age and sex. On the other hand, the 140 animals, though caught over a number of years, were 'chosen' either because they came to the particular areas where I attempted to keep all koalas marked, or because they happened to be present when I visited other places for the purpose of catching koalas. They can therefore be regarded as a randomly selected sample of the koala population. In Table 6 I give the sex composition and age-structure (in terms of three classes, 1 year, 2 years and 'mature') of this sample. For this purpose I have assumed that koalas may live to the age of 12 years (Section 2.3 discusses growth, ageing and longevity in koalas). In the figure and table, one animal of the one year class, for which gender was not recorded, is omitted: the total number is therefore 139 rather than 140. The one year class is also very probably under-represented since it does not include any of the 21 pouch and 5 belly-carried young which were too small to mark, but which belong to this age-class and were caught with the initial capture of a mature female. An unknown proportion of these may have been caught and marked later on, so all have been omitted.

TABLE 6 Sex composition and Age structure (in terms of three classes) of a sample of 139 koalas.

Class	1 year	2 years	'mature'	Total
Male	17	5	40	62
Female	13	16	48	77
Total	30	21	88	139

The table and figure indicate

(1) a prolifically breeding population (the under-represented, see above, 1 year class, male and female, is 62.5% of the 'mature' female class: this clearly is prolific breeding if the assumption about longevity is warranted).

(2) a very considerable loss (these figures suggest a value of 71%) of males during the second year of growth, which again, is possibly an underestimate.

(3) an even sex composition in the 'mature' part of the population.

The distribution of sightings of marked animals is shown in Table 7. In itself, with the assumption that the places where animals were caught and released were all searched regularly, it suggests an enduring localization of some animals and a rapid turnover (via death or migration) of others (of 149 marked animals, 74 or c. 50% were seen 3 or less times, while 3 were seen more than 100 times). The figure in this table is 149, rather than 140, since nine animals which had lost tags when caught a second time could not be identified: in this table they are therefore doubly represented.

TABLE 7 **The distribution of sightings of marked koalas**

Sightings	No. of koalas	Sightings	No. of koalas	Sightings	No. of koalas
0	32	21	0	49	1
1	15	22	1	50	1
2	15	23	2		
3	12	24	1	54	1
4	6	25	1		
5	6	26	0	64	1
6	2	27	1		
7	2	28	0	73	1
8	3	29	0		
9	3	30	0	77	1
10	2	31	0	78	1
11	2	32	0		
12	2	33	1	80	1
13	3	34	2	85	1
14	8	35	0		
15	1	36	0	92	1
16	1	37	1	97	1
17	1	38	0		
18	2			115	1
19	3	42	2	120	1
20	2			126	1

Σ 123 12 14 49

The distribution of captures is shown in Table 8 and the amount of time actively spent doing field work in Table 9.

TABLE 8 The distribution of captures

No. of captures	No. of koalas	Total captures
1	94	94
2	16	32
3	13	39
4	7	28
5	5	25
6	4	24
7	1	7
Totals	140	249 *

* An additional eight captures not counted in this were associated with the removal of collars bearing radio-transmitters, and an additional 28 captures with the stocking of several private and public fauna collections.

TABLE 9 Field work: Number of trips and total time

Year	No. of trips	Time spent (weeks)
1966	3	6
1967	6	15
1968	8	12
1969	6	6
1972	1	1
Total	24	40

Figure 5

Mallee scrub – Stringy-bark (E. obliqua) in foreground.

Figure 6

Sugar gum (*E.cladocalyx*) forest.

Figure 7

Manna gum (E.viminalis) showing severe defoliation.

Figure 8

E.viminalis defoliated by koalas and showing maintenance of a secondary crown through the development of epicormic shoots.

Figure 9

Dead and dying *E.viminalis*.

THE DISTRIBUTION AND ABUNDANCE OF KOALAS

1.1 The distribution of koalas

The finding (text p.19) that many koalas were moving between the manna gums and other eucalypt associations and, in fact, were spending the larger proportion of their time in trees other than manna gums, suggested the possibility of koalas living permanently away from the river flats. This in turn implied that manna gum was not essential for the survival of koalas which fixed attention on the possible bases for the association between koalas and manna gum. There seemed to be four logical possibilities:

(1) The apparent direct relationship was spurious. Something else made certain river flats favourable to, or necessary for the survival of, both koalas and manna gums. This hypothesis could not be entertained. For one thing, the 'something else' remained inconceivable; for another, if it were true, there should not have been a differential use within the river flats of manna, pink and sugar gums, strongly in favour of manna gum (in B, where pink gum was slightly more abundant than manna gum, of a total of 1,024 sightings of koalas, 872 were of koalas in manna gum).

(2) The apparent direct relationship was real, but depended on an interaction between manna gums and some other component of the environment, e.g., manna gums might be free of some insect pest etc. This hypothesis likewise could not be put into terms of real things in Flinders Chase.

(3) The apparent direct relationship was real, and depended on an intrinsic property of the manna gums, which was something other than the quality of the food which the manna gums provided. In real terms the property might have been the accessibility of foliage, the number of suitable forks to rest in, the size of the tree, the shape and size of the leaves, the bark and wood type (determining the ease with

which the tree is climbed) etc. However, in all these properties the eucalypts are rather similar and the small species-differences that can be detected seem totally inadequate to explain the differential use documented in (1). It may be added that most of these properties are covered by the term 'growth form', and as such are determined by accidents of light, prevailing wind, competition from other plants, physical trauma, etc. So pink gums and manna gums growing side by side tend to have very similar growth-forms indeed. Furthermore, foliage on the manna gums, as a result of intensive koala browsing, was often far less abundant than on neighbouring trees of other species. In this respect therefore, manna gums should be less attractive than other species.

(4) The apparent direct relationship was real, and depended on the quality of browse provided by the manna gums. This view was unshakable. It did, however, admit two alternatives with respect to the distribution of koalas.

(4a) Manna gum is needed by koalas (in the stochastic sense that in its absence they have a greatly reduced chance of survival). In this case, the distribution of koalas should be confined to the vicinity of manna gums.

(4b) Manna gum is favoured by koalas, but is not needed for survival. With respect to the distribution of koalas, this in turn admits two possibilities.

(4b1) All other species are equivalent - koalas must have spread by now to continuously occupy Flinders Chase: they would certainly be living in forest and scrub relatively close to the manna gum areas.

(4b2) All other species are not equivalent - in this case the distribution over Flinders Chase would be patchy. However, since all species that occur on Flinders Chase

> are represented within a short distance of the manna gum areas, then it should have been possible to find koalas living entirely without manna gum, close to the manna gum groves.

It was clear from this analysis that a possible vastly increased area of koala distribution within Flinders Chase, and the concomitant non-requirement of manna gum for survival, could be tested by observation within relatively short distances of the manna gum areas. Of course, I did not neglect to search the trees for living koalas and the ground for koala droppings wherever I was within Flinders Chase. Like Philpott (1965) I searched other parts of the Rocky River, the Breakneck River, the West Bay Creek, the Ravine des Casoars and parts of the plateau accessible from the West Bay Track or Shackle Road (see Figure 3), amongst other places, without finding any trace of a koala population isolated from the groves of manna gum. I also canvassed local opinion. This negative evidence can be considered in conjunction with more positive evidence gained closer to the river flats which also indicated a distribution restricted to the vicinity of manna gums. This evidence was accumulated by searching for koalas in the areas surrounding A_3 and B up to a distance of about 800 metres from the margins of A_3 and B. In the area surrounding B all eucalypt species occurring in Flinders Chase, except water gum, E. ovata, were well represented. In A_3 and B any unmarked animals were caught and marked; if they remained they became part of the marked population on subsequent field trips. But unmarked animals found outside the study area were not caught. Clearly, if there had been any koalas living permanently in the surrounding bush, isolated from the groves of manna gum, then this would have led to the sighting of relatively fewer marked koalas in such places. Data are given in Tables 10 and 11. I have not included observations made on animals with transmitters nor observations made subsequently from a knowledge of where these animals might be found. The totals do include observations made on the same animal during different field trips but not multiple observations made during the one field trip. In the case of observations within A_3 and B I have recorded only those that were found, at one time or another, in both places i.e., I have excluded those animals that remained permanently domiciled in the manna gum areas. I have also considered only those field trips during which successful searches were made outside A_3 and B.

TABLE 10 A_3 and Surrounding Areas, July 1967 - June 1969: Numbers of Marked and Unmarked Koalas.

	Marked	Unmarked	Marked/Total
Observations Within A_3	24	2	0.92
Observations Without	8	1	0.89

TABLE 11 B and Surrounding Areas,* July 1967 - June 1969: Numbers of Marked and Unmarked Koalas.

	Marked	Unmarked	Marked/Total
Observations Within B	113	21	0.84
Observations Without	18	5	0.78

* In the data from B which, unlike A_3, is not surrounded by a stretch of open ground, I have excluded from the sum of observations made without the area, seven made only just beyond the margin. All were of marked animals.

The ratios within each of the tables are very similar. This suggests that there were no animals living permanently away from the river flats.

There is support for the above conclusion in the results of a search for faecal pellets in the area surrounding B. In this survey a number of lines were followed out from the margin of the river flat and at successive distances of approximately 40m six trees were arbitrarily selected and the ground underneath searched for pellets. Data are given in Table 12 where the values refer to the number of trees under which faecal pellets were found. The numbers have been pooled for lengths of approximately 200m. When the full 200 metres was not covered and the number of trees under which searches were made was therefore less than thirty, a ratio is given.

TABLE 12 The Number of Trees (out of thirty, except where indicated) under which Faecal Pellets were found at Various Distances from the Margin of B. *

Distance Out (metres)	0 - 200	200 - 400	400 - 600	600 - 800
South-West	8	3	1	1
West 1	19	8	1/18	
West 2	20	11	0/12	
East	6	0		
North	19	3/18		
South	0	0/24		

* Faecal pellets are abundant under all trees within B.

This table shows that although koalas may wander a considerable distance from the river flat, there is a rapid fall off in the abundance of sign which is consistent with the idea that there are no koalas living permanently away from the manna gums. The greater abundance of sign to the West, and its absence to the South may be partly explained by the distribution of manna gums within the river flat. Most of the manna gums in the area are on the western side while the southern margin is bordered by numerous pink gums and E. rugosa. However, the results may also be influenced by, or may even largely derive from, the types of eucalypt associations through which the various lines passed. Those to the East and South-West passed mostly through stands of sugar gum while that to the North passed through a sugar-pink gum association and some stringy-bark. The line to the South passed entirely through an association dominated by the mallees E. rugosa - E. diversifolia, while those to the West went through sugar-pink gum and brown stringy-bark-cup gum associations. The preferences that koalas show for particular species of eucalypts are examined in Section 8. Evidence given in this section suggests, for example, that associations including brown stringy-bark would be more attractive to koalas than the others named here.

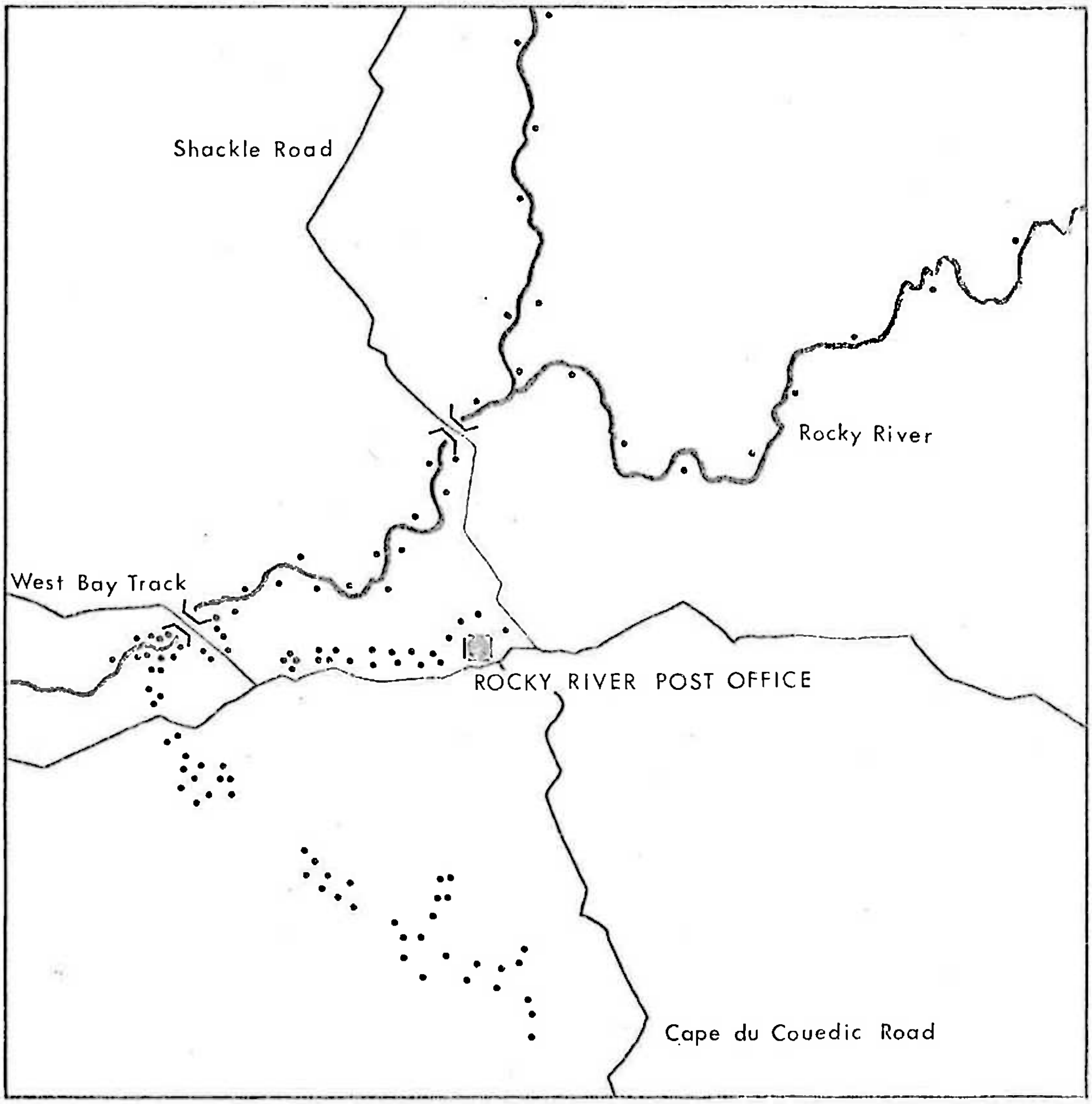


Figure 10 The distribution of water gum, *E. ovata*, in Flinders Chase.

Area B is a very representative area with regard to the composition of the surrounding associations. Nine of the ten species present in Flinders Chase occur near here in fair abundance, and I think my findings on the distribution of koalas about B and A_3 are probably true for all manna gum areas in the Chase. The one species that does not occur in the immediate vicinity of either A_3 or B is E. ovata, the water gum. This species occupies a special position as the one into which koalas were originally released and presumably by means of which, from an occurrence linking the site of release to the Rocky River, they colonized the manna gums. The evidence I have on the koalas' utilization of this species is rather ambiguous and it is therefore discussed elsewhere as a special case (text 5.2). However, its distribution (shown in Figure 10) is very restricted and its stands are nowhere far from manna gum, so whatever its status as a habitat for koalas, it has little influence on the present distribution and abundance of koalas. The distribution of koalas in Flinders Chase, if understood to refer to those places where numbers of koalas can be consistently found, is made up of areas centred on the occurrences of manna gum along the Rocky River. This conclusion, from the analysis given at the beginning of this section, required that manna gum was not only attractive to koalas, but also needful.

1.2 The abundance of koalas

In Tables 13 and 14 I have presented data from A_3 and B to show the number of different animals seen during a particular search period, the average number seen per day and the range in numbers.

These counts span the intervals of time over which A_3 and B were studied; they come from 22 such counts made in A_3 and 11 in B.

TABLE 13 A_3: Numbers of Koalas

	No. of Days	No. of Koalas	Mean No. Seen	Range
May - June 1966	12	4	3	2 - 4
Jan. 1967	3	5	3	3
May 1967	14	4	3	1 - 4
Jan. - Feb. 1968	13	6	3	0 - 5
May 1968	10	4	3	2 - 4
Jan. 1969	9	5	2	1 - 5
June 1969	12	6	4	1 - 5

There are 14 manna and 14 pink gums in this area. The average number of koalas seen per day over all search periods in Table 13 is three. This gives an average density of about one koala per five manna gums.

In B there are 106 manna gums and 152 pink gums and other trees. The average number of koalas seen per day over all search periods in Table 14 is 10. This gives an average density of about one koala per eleven manna gums, which is about one half of that in A_3.

TABLE 14 B: Numbers of Koalas

	No. of Days	No. of Koalas	Mean No. Seen	Range
July 1967	7	14	7	3 - 9
Jan. 1968	8	20	10	4 - 13
July 1968	8	22	12	11 - 15
Jan. 1969	8	19	11	9 - 14
June 1969	8	18	10	7 - 13

There may be many factors involved in this difference between two areas so disparate in size and physical situation but one which I think may be important concerns local movement into adjacent eucalyptus associations. Area A_3 adjoins a mallee scrub dominated by *E. rugosa* - *E. diversifolia* with some pink gums. Area B on the other hand has close-by associations including stringy-bark, brown stringy-bark, cup gum, sugar and pink gum as well as *E. rugosa* and *E. diversifolia*. My data on the distribution of faecal pellets, as well as my observations of animals outside this area, show that these other species are used more readily than the sandhill mallees. I suggested that on the basis of evidence presented elsewhere (Section 8) this, in part at least, reflects a preference for some species. I do not have unequivocal evidence that the presence of a more favoured species (of the other-than-manna gum group) bordering the manna gums reduces the frequency with which an animal uses the manna gums, but I find this suggestion plausible.

This is the difference referred to in a discussion in the early part of this section on the difference in density between the West Bay Track and Scotch Thistle Flat indicated by Philpott's counts. Scotch Thistle Flat is surrounded by a belt of pink gums and stringy-bark, which in many places quickly gives way to a brown stringy-bark-cup gum association more robust than that near B. The central and largest part of the West Bay Track, areas A_1 and A_2, have on the one side open ground and E. rugosa - E. diversifolia, and, on the other, some large sugar gums but mostly very slender-stemmed or whipstick E. diversifolia mallee.

There is a suggestion in the data for B that there was a significant increase in the number of animals using this area from July 1967 to January 1968, but apart from this, the numbers in both areas are noteworthy for their constancy.

In Table 15 I have presented counts made in A_1. These counts are derived from searches that were made with less rigour than those made in A_3 and B. Nonetheless, they serve to illustrate the abundance of koalas in this area during the study.

TABLE 15 A_1: Numbers of Koalas

	May-June 1966	Jan. 1967	Dec. 1967	July 1968	Jan. 1969
No. Days	8	3	1	1	1
No. Koalas Seen	18 - 24	25	33	29	24

In this table the values for May - June 1966 are the range; in January 1967 25 animals were seen on each of the three days that the area was searched.

It was apparent from counts such as these and others, taken in conjunction with data on local movement away from the manna gums, that the West Bay Track alone supports more than the 111 koalas that Philpott counted in the whole of Flinders Chase.

In the absence of any censuses other than those reported in this study, I have no objective basis for assessing the status of the population during the years before 1965. It is likely, however, that in recent years the population of koalas in the West Bay Track has been increasing to some extent following a reduction in numbers brought about by the removal of 47 koalas in 1964 as a management procedure. This may be the explanation for the apparent increase in numbers in B from July 1967 to January 1968, since this was a favoured catching site.

The removal of koalas on this occasion in 1964 has been the only attempt at management since the koalas were introduced to Flinders Chase in 1923. It was stimulated partly by concern at the extreme condition of many trees in A_1 and A_2 and partly by an interest in introducing koalas elsewhere on Kangaroo Island as protection for the species following the very severe bush-fire of 1958 which threatened to burn the river flats. The finding on local movement suggests that this fire may well have had some effect on the population, though the rapid recovery of eucalypts from fire damage and the security of the river flats, and at least some of the adjacent areas, suggest that it would have been transient.

From local report it seems quite likely that the distribution and abundance of koalas and the condition of the manna gums have been for many years much as I found them over the period of study.

The relative constancy of the numbers of koalas during the study was clearly not to be explained simply as the relationship between mortality and natality within the study areas. Only two dead koalas were found within the manna gum areas of the West Bay Track, while the composition of the population in any place varied from time to time. And it was clear from the presence of young koalas on the bellies and then the backs of the females in the spring and summer that most adult females were breeding and successfully rearing young. It seemed that the birth rate was balanced not by deaths in the groves of manna gum but by emigration. Because there was no evidence of a persistent population isolated from the groves of manna gums, it must be presumed that most of the emigrants died without reproducing, in places remote from the groves of manna gum where they had originated.

BREEDING, GROWTH AND DEVELOPMENT

2.1 Breeding

The juvenile koalas carried on the backs of females in the summer months differ considerably in size, indicating an extended seasonal breeding period. The weights of twenty-seven young caught in January of 1967, 1968 and 1969 ranged from 850 g to 3,250 g.

In Table 16 I have presented the percentages of females, excluding juveniles, carrying pouch young at various times during the summer and autumn. The number caught is included in brackets.

TABLE 16 Females with Pouch Young (%). Number caught in brackets.

	Jan.	Feb.	Mar.	Apr.	May	June
1966			60(10)		83(6)	
1967	17(29)				80(5)	
1968	33(9)	80(5)				
1969	0(5)	75(4)				64(14)
1972		45(11)				
Total	19(43)	55(20)	60(10)		82(11)	64(14)

This table shows that some females have pouch young in January and suggests that the majority of births have occurred by about March. One pouch young was seen in late December and very small pouch young were seen in January, February and March. Births therefore occur between late December and April, with a peak in February. In Eastern Australia the mating season for koalas is generally said to extend from September to January in New South Wales and from November to February in Victoria; so births occur during much the same season as in South Australia.

In the absence hitherto of observations on marked animals, it has remained uncertain whether koalas in the wild breed in successive years. Females in Flinders Chase commonly did so, and of four marked mature females which remained under observation over four successive years, two carried young each year and two carried young in three of the four years.

Only one young is produced each year as a rule, though I have one record of twin pouch young. Since there are only two nipples in the pouch, such an occurrence depends on a female missing the previous breeding season or breeding very late, for there can be no chance of a new born young attaching to the greatly enlarged teat which persists for some time after the weaning of the previous young.

Asdell (1946) quotes Semon for the statement that the koala is monoestrous, but one female from which I removed a dead pouch young early in the breeding season carried a young later in the year, and another female carried a comparatively small young on her back when she had been recorded with a pouch young early in the breeding season, suggesting that this first pouch young had been lost and replaced late in the season. Koalas may therefore be more typically polyoestrous. This conclusion is supported by Briese (1970) who examined vaginal smears taken regularly from eleven koalas for periods ranging from 37 to 58 days. He found in three animals successive peaks of cornified epithelial cells at 27 - 30 day intervals, suggesting an oestrous cycle of that period (of the remaining eight koalas, four showed no cyclic events and four showed cell fluctuations of 26 - 29 day intervals, but successive oestruses could not be positively established).

2.2 Pouch Young

Before parturition and then with growth of the young, the pouch undergoes considerable development and becomes a large, thick-walled structure with a muscular sphincter. The gestation period is reported by Troughton (1941) and Pollock (pers. comm.) to be about 35 days. Troughton also quotes Burnet for a birth weight of about 5.5 gr. (0.36 g). The smallest pouch young I encountered weighed about 0.70 g.

A birth weight of about this value or less would be consistent with the known range for marsupials which includes 0.01 g for Dasyurus viverrinus (Hill and Hill, 1955) and 0.90 g for Megaleia rufa (Sharman, Frith and Calaby, 1964).

The birth of very immature young is one characteristic of marsupial reproduction. It is not entirely satisfactory to attribute this to a very short gestation period since Waring, Moir and Tyndale-Biscoe (1966) have noted that some marsupials have gestation periods equalling or exceeding those of their eutherian counterparts. Tyndale-Biscoe (1968) has postulated that, relative to total gestation, the period of active embryo-genesis in all marsupials is short, is determined by limitations of the intra-uterine environment and is preceded by an obligatory period of diapause. This hypothesis, he points out, is very relevant to consideration of the known phenomenon in the Macropodidae of lactation-controlled delayed implantation or embryonic diapause. In this group the gestation period is, typically, nearly equal in length to the oestrous cycle; parturition is followed by an oestrus and the fertilized ovum develops to the blastocyst stage, but no further, while the pouch young continues to suckle. The phenomenon differs from delayed implantation in eutherians in that, typically again, it is lactation-controlled and the blastocyst remains totally dormant. In the continuously breeding red kangaroo, Megaleia rufa, the blastocyst resumes development following premature loss of the pouch young or the completion of pouch life at any time of the year. In the seasonally breeding quokka, Setonix brachyurus, females carrying a pouch young enter anoestrus and the blastocyst degenerates. However, in the tammar Macropus eugenii, the onset of seasonal anoestrous does not result in the degeneration of the blastocyst which is carried over dormant but viable (Berger, 1966 and 1970). So, in this species, embryonic diapause is partly independent of lactation.

So far as is known, this kind of embryonic diapause is restricted to the Macropodidae. Clark (1967) found that the pigmy possum, Cercatetus concinnus, has a post-partum oestrus but concluded that since blastocysts recovered from the uteri increased in size with age of the pouch young, embryonic diapause of the former kind does not occur. Within the Macropodidae there are some exceptional species. In the grey kangaroos, *Macropus giganteus* and *M. fuliginosus*, gestation periods and oestrous cycles are rather variable; gestation can overlap with the oestrous cycle, but a post-partum oestrus does not occur. Sharman, Calaby and Poole (1966) postulated the secretion of a hormone to prevent this oestrus. Nevertheless, embryonic diapause of a kind does occur in the eastern grey kangaroo, *M. giganteus*, since a small part of natural populations have fertile matings later during the life of the still-suckling pouch young, though the blastocyst produced may never become completely quiescent (Clark and Poole, 1967). The whiptail wallaby *Macropus parryi* also does not apparently undergo a post-partum oestrus (Calaby and Poole, 1971). In the swamp wallaby, *Wallabia bicolor*, the gestation period exceeds the oestrous cycle. However, females undergo a pre-partum oestrus and embryonic diapause occurs. Sharman, Calaby and Poole (1966) recognized four patterns of reproduction in Australian diprotodont marsupials. They are as follows:

GROUP 1	Gestation shorter than the length of one oestrous cycle; delayed implantation does not occur. Example *Trichosurus vulpecula* - oestrous cycle 26 days, gestation 17½ days (Pilton and Sharman, 1962).
GROUP 2	Gestation nearly equal in length to, but shorter than one oestrous cycle; delayed implantation does occur. Example *Megaleia rufa* - oestrous cycle 35 days, gestation 33 days (Sharman and Calaby, 1964).
GROUP 3	Gestation exceeds the length of one oestrous cycle, but pregnancy does not prevent the return to oestrus at the expected time and delayed implantation does occur. Sole example *Wallabia bicolor* = *Protemnodon*

bicolor - oestrous cycle 32 days, gestation 35 days (Sharman, Calaby and Poole, 1966).

GROUP 4 Gestation and the length of one oestrous cycle overlap; post-partum oestrous does not occur, but a kind of embryonic diapause can occur later during the pouch-life of the young. Sole example *Macropus canguru* (but now *M. giganteus* and *M. fuliginosus*, see above) - oestrous cycle 32 - 55 days, gestation 29 - 38 days (Sharman *et al.*, 1966).

Most non-macropod marsupials so far studied are like *Trichosurus vulpecula* in Group 1. The most recent and detailed information on the lengths of cyclic reproductive processes in kangaroos is tabulated by Calaby and Poole (1971).

Briese (1970) suggested that the measures of oestrous cycle and gestation period for koalas reported here should not be accepted unreservedly. However, should they be confirmed then they would seem to ally the koala with the swamp wallaby in Group 3 of Sharman *et al*'s classification. It must be noted, though, that there have been no reports from captive colonies of koalas of delayed parturition, i.e. the birth of young to females isolated from males since the mating that produced a previous young, which would indicate the occurrence of a lactation-controlled embryonic diapause. There is no information on the length of cyclic reproductive processes in wombats, the marsupials which recent work (Hughes, 1965; Kirsch, 1968) suggests are most closely allied to koalas.

The sex ratio among neonatal koalas is probably close to unity. Fifteen small pouch young were examined and seven of these were male, eight female.

It is a commonly held opinion that very small pouch young cannot be removed from the nipple without damaging the tissues of their mouths. I have removed a young koala weighing only 5.0 g which successfully re-attached and grew to independence. Merchant and Sharman (1966) have reported that marsupial young at all stages of development may be removed by gentle traction without damage to tissues of mother or young.

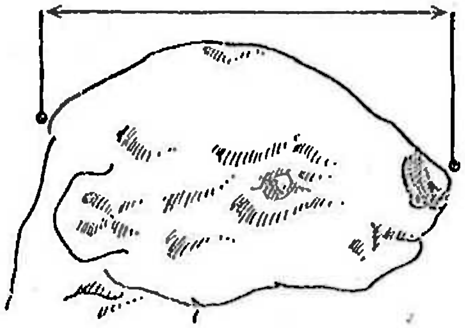
As indicated before, I terminated the examination of pouch young before the process of removing and returning them unaided to the pouches of unaesthetized females was refined to the point where proper observations and photographs could be taken. However, I have presented for their intrinsic interest photographs of two preserved pouch young in Figures 11 and 12. The young in Figure 11 is male. It weighed 15.0 g when freshly dead and had a head-length of 23 mm. The body is hairless but there are a few tiny bristles around the mouth, which is open at the sides. The eyes are closed and the palmar surfaces of manus and pes, as well as the snout and tips of the pinnae are pigmented. The young in Figure 12 is of undetermined sex. It weighed about 0.7 g when freshly dead with a head-length of about 0.8 cm. The pinnae and hind-limbs are little more than buds. The eyes are represented by tiny pigment spots. The mouth is closed at the sides and a considerable degree of cranial flexure is obvious. The epitrichial talons on the manus are remarkably developed and the region of the snout is very prominent. In Table 17 I have summarized some of the development, in obvious external characteristics, apparent from the examinations of pouch young that were made. The characteristics are listed against the pouch young in which they were first observed. The technique of measuring head-length in small pouch young differed from that used with larger animals in which the occipital crest was developed and used as a limit. In pouch young head-length was measured between the most anterior part of the snout and the mid-point of an imaginary line between the ears. 'Elbow-wrist' was measured between the olecranon process of the ulna and the external lateral surface of the carpal joint (pisiform carpal bone?). 'Ankle-knee' was between the patella and the external, lateral surface of the tibia-astragalus. The several measures of body size are illustrated in Figure 13.

<u>Figure 11</u>

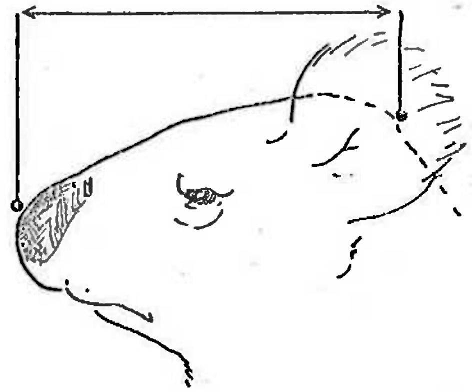
Pouch-young weighing 15.0g.

Figure 12

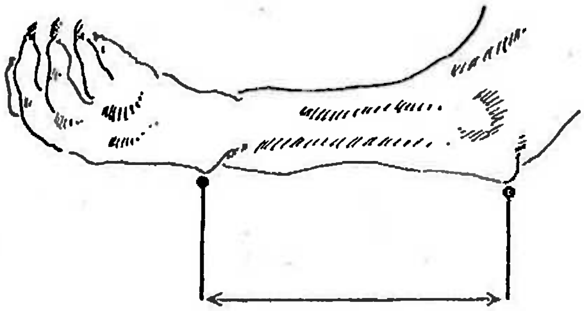
Neonatal pouch-young weighing 0.7g.



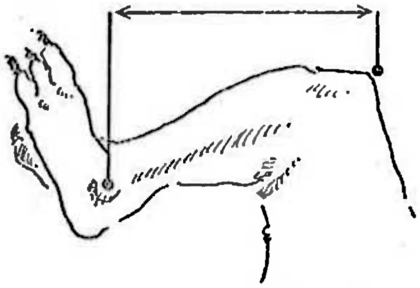
HEAD LENGTH
Pouch-young



HEAD LENGTH
Adult



E.W. LENGTH



A.K. LENGTH

Figure 13 Body-measurements recorded for pouch-young and adult koalas.

TABLE 17 Development in Pouch Young

Wt. (g)	H.L.cm	E.W.cm	A.K.cm	Schedule of first appearance of some obvious external characteristics.
0.7	0.8	0.4	1.7	Claws on manus.
4.7	1.6	-	-	Pouch apparent, claws on pes, pinnae separate from head, eyes evident, pigment on snout, pinnae, manus and pes.
5.0	1.2	1.0	-	
15.0	2.3	1.6	1.2	Scrotum apparent, mouth open at sides (i.e. no longer round).
30.5	2.8	1.9	1.8	
47.1	3.4	2.6	-	Active, squeals, bristles around mouth.
48.5	-	-	-	Pinnae lying back against head, not forward.
50.6	3.2	2.6	1.6	Defaecation and micturition.
59.3	3.6	2.9	-	
65.5	-	-	-	Eyes open, some fine long hairs on body.
82.5	3.6	2.7	2.4	Grasping reflex well developed.
84.5	3.9	2.5	-	
92.5	4.0	3.2	-	
96.5	4.0	3.2	-	
128.5	5.0	3.7	-	Down on head.
145.5	4.7	3.8	3.3	
180.0	-	-	-	Fine, long hair on body.

H.L. = head-length

E.W. = elbow-wrist length

A.K. = ankle-knee length

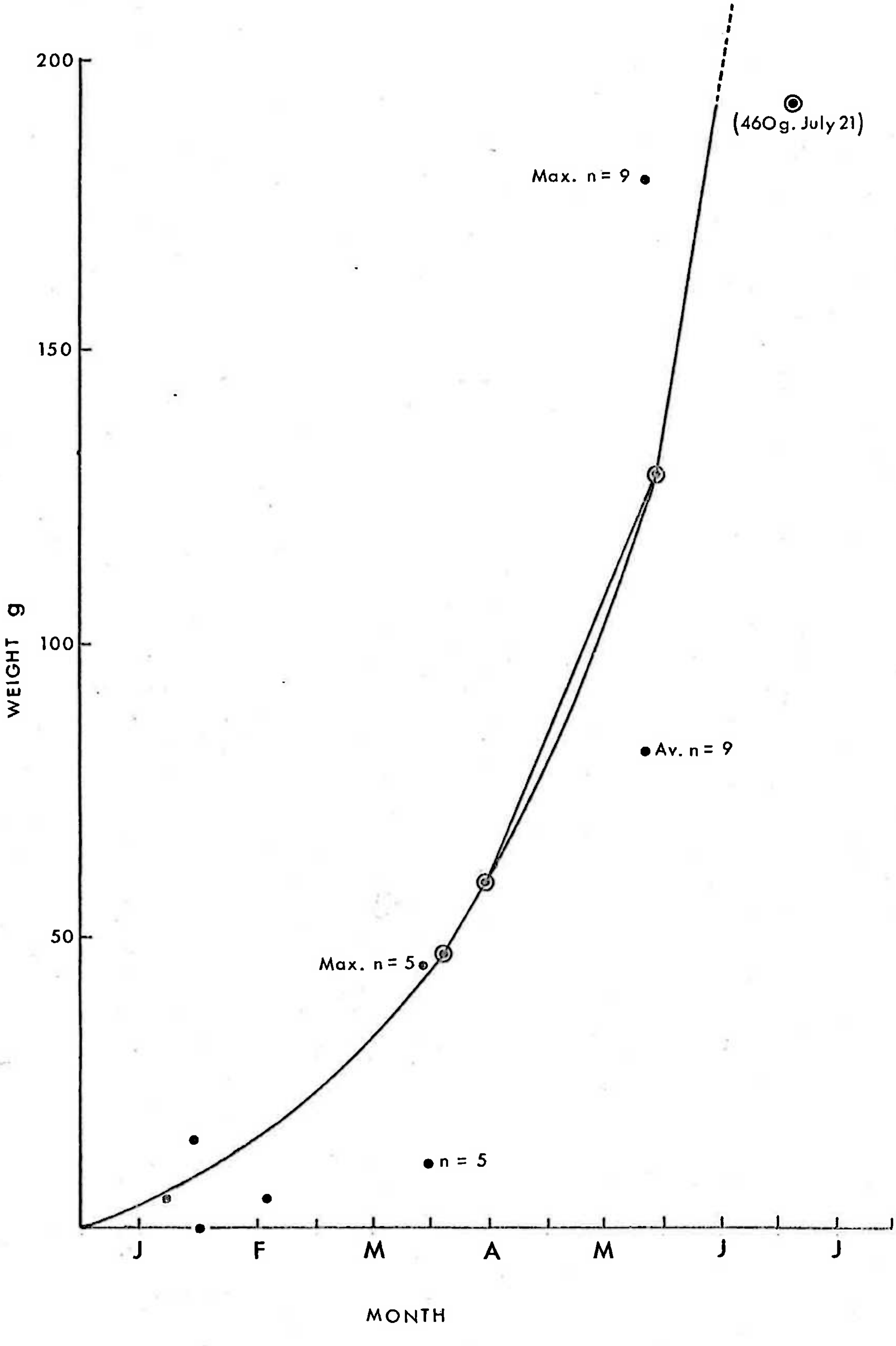


Figure 14 Weights of pouch-young by month; ◎ weight gain for one pouch-young, and a growth curve for the first four months of life.

In Figure 14 I have drawn an approximate growth curve for the first four months of life. The curve is based on:

(1) some weight increases of a pouch young in captivity (these are graphed).

(2) the assumption that the maximum weights in the two samples of 5 and 9 pouch young examined in March-April and May-June respectively come from koalas born at the very beginning of the birth-season (December 15 to January 1); and that the averages of these samples represent weights of young born at the peak of the birth season in mid-February.

(3) the weights of five other pouch young viewed in relation to the birth-season.

There is a dependence between Figure 14 and Table 17 in that the weights given for the five pouch young caught in March-April were estimated from their head-lengths and the weights of young with similar head-lengths caught in January, February or May-June. These March-April young were examined while still in the pouch and were not removed for weighing. This method, however, did not prove a simpler alternative to the removal of pouch young.

Fleay (1937) reported that the young of a koala held in the Melbourne Zoo was completely independent of the pouch at five months, while Troughton (1941) quotes Burnet for a total pouch life of eight months. Fleay, however, did not indicate how accurately the date of birth was determined and Minchin (1937) reported a koala still using the pouch when at least six months of age. The earliest I have seen females in the wild carrying young on their bellies was late July while some females were not seen with young until as late as November. With a birth season from late December through to March and possibly into April, this suggests a total pouch life of about seven months.

It is at about the end of pouch life that there takes place the coprophagic phase of weaning reported by Minchin (1937) and Fleay (1937) in which over a period of up to six weeks, the young feeds regularly from the female's cloaca on material passed from higher up in the digestive tract. This habit may be, as has been suggested, vital in view of the relative toughness of eucalyptus leaves as food and the presence of toxic substances in the essential oils. It may also serve to inoculate the young with micro-organisms from the parent's caecum, the principal site of digestion. I have not seen koalas clean the pouch or groom the young in any way.

These dependent young are often carried and suckled up to the time when the female breeds again. I have one record of a female with a pouch young on one nipple while the other large teat was still lactating, but all other females with pouch young were dry in the other teat and the young were not carried, though they remain closely associated with the female often well into the second year of growth. Weaning is therefore complete by the time the young koala is twelve months' old.

Growth is rapid in the latter part of the first year. One captive young weighed 460 g at an age thought to be between six and one half and seven and one half months. Two and one half months later it weighed 1,150 g. Five young carried on the belly in September and October ranged in weight from 300 g to 841 g, while the average weight of ten female young caught in January of 1967, 1968 and 1969 was 2,050 g and that of seventeen males was 2,300 g. The heaviest female weighed 2,750 g and the heaviest male 3,250 g, which indicates that in their first year of growth koalas may reach about 3,000 g. In Figure 15 I have:

(1) arrayed the weights of dependent young (i.e. young in the first year of growth) by month of capture (seven young are represented both in May-June and January),

(2) graphed the weight increases for two dependent young caught at intervals,

(3) drawn in a growth curve for the first year of life, on the basis of (1) and (2) coupled with birth-season limits and data on subsequent weight gains during the second year of growth.

A high 'breeding-rate' (i.e. a high proportion of females conceiving young each breeding season) does not, of course, necessarily mean a high rate of increase. This depends on fecundity (the number

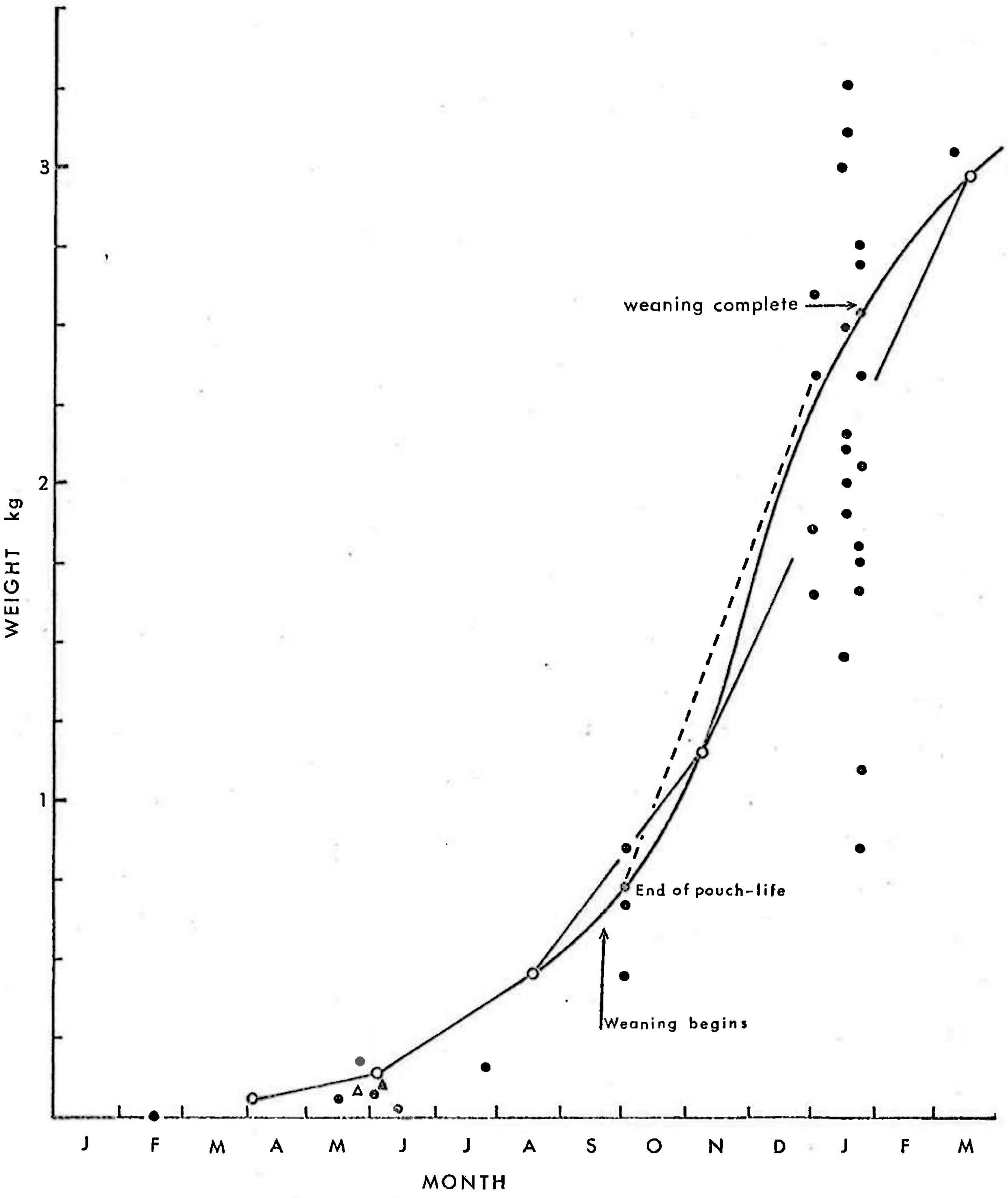


Figure 15 Weights of dependent young arrayed by month; weight gains for two dependent young ●--● ○—○ and a growth curve.

△ n = 4

▲ n = 3

of young produced by each female), speed of development - and age-specific, survival-rates (also expressed as life-expectancies and death-rates). For the purpose of estimation of age-specific survival-rate, it is often assumed that the population under study has an age distribution which remains stable over time, so that a knowledge of this age-structure, i.e., the relative numbers belonging to successive year classes, permits calculation of survival-rates. Such estimates, in studies of large mammals, are usually associated with killing animals, since many of the more useful indicators of age - annuli in teeth, bones or ear ossicles; corneal weight; baculum shape; ossification of long-bones; cranial morphometrics etc., cannot be measured in the live animal. The alternative method for studies of rare fauna or intensive studies where it is not possible to slaughter animals, is to measure survival-rates directly, through continued observation or trapping of marked animals. The great difficulty of this method hinges on the word 'continued'. In this study, an attempt to directly measure the survival-rate of pouch young to the stage of dependent juvenile and of dependent juvenile to the stage of independence, was one reason for pursuing so intensively searches for marked animals. It required:

(1) Searches for females, which had been caught and marked when carrying <u>very small</u> pouch young, at a time (+ 7 months) when their young would have just begun a permanent ex-pouch life.

(2) Searches for females, which had been caught and marked when carrying <u>newly-emerged</u> pouch young, at a time (+ 4 months) just prior to complete weaning.

Data is given in Tables 18 and 19. The young which were seen at both the stages indicated in either (1) or (2) are referred to in the Table headings as a 'cohort'. Their numbers are inevitably small, but they suggest a considerable survival of young in their first year of growth.

TABLE 18 Survival-rate of pouch young over period from birth to permanent emergence.

No. in cohort	No. to survive	Survival-rate
14	11 *	0.79

* In fact, twelve of the fourteen females carried young, but the size of one dependent juvenile indicated that the first pouch young had been lost.

TABLE 19 Survival-rate of dependent young over period from first permanent emergence to just prior complete weaning.

No. in cohort	No. to survive	Survival-rate
13	12	0.92

These direct measures can be compared with the indication given by the total number of young in the one year class of the 'random sample' (30) of koalas described in the introduction to Part 1, the number of females over one year old in this same sample (64), and the proportion (0.70) of females over one year old likely to breed, suggested by the data given in Table 22. These figures suggest a survival-rate of 0.67. A true value of between 0.67 and 0.73 is therefore quite likely.

2.3 Growth, Ageing and Longevity

Thirty-four koalas were caught as dependent juveniles or as just independent young; the season of the birth of these animals was therefore known. Two were caught again during their second year of growth and five others were each caught a number of times over several subsequent years.

The variability in the growth shown by these animals indicated that koalas could not be reliably aged on the basis of body weight or size after their first year. However, characteristics of the dentition and appearance of these young koalas meant that animals two years old, or thereabouts, could be so recognized.

The dental formula is

$$\text{I.}\ \frac{3-3}{1-1}.\qquad \text{C.}\ \frac{1-1}{0-0}.\qquad \text{P.M.}\ \frac{1-1}{1-1}.\qquad \text{M.}\ \frac{4-4}{4-4}$$

The third molar erupts toward the end of the first year of growth and the fourth molar erupts in the latter half of the second. Molar progression does not occur and there are no deciduous teeth. The amount of wear on the teeth was judged into one of five progressive categories (I - V). These were termed, 'nil' (I), 'slight' (II), 'moderate' (III), 'considerable' (IV), and 'extreme' (V). The judgments were subjective and depended on the fact that in young animals the lophs are very sharp while in the older ones the surfaces may be very nearly quite flat. I have presented in Figures 16, 17 and 18, photographs of the premolar and first two or three molars in the right upper jaws of three koalas. The pre-molars represent the classes II, III and V, respectively: the first and second molars in both the first two plates show slight wear (II) while in the third plate, the first molar falls into class V, and the second molar into class IV. None of the seven animals known definitely to be in their second year of growth were considered to show any tooth wear, and this was also true of most animals caught at about the same weight range. However, four captured during their third year of growth were all judged to show slight wear on the premolar and the anterior lophs of the first molar and one at the end of its third year was judged to have class III wear, as did two of the three caught in their fourth years. Few animals of a body weight greater than that reached by these animals in their third year did not show at least class III wear so it was thought that the absence of tooth wear was characteristic only of animals up to the end of their second, or early in their third year of growth.

Koalas about two years old or less can also be recognised by their silver-grey pelage, the completely pigmented snout and the thickness and shortness of the fur on the outside of the pinnae. These characteristics begin to change in the third year of growth. In addition, the pouch of females remains undeveloped and the nipples recessed until they breed for the first time, while the sternal gland in males is only evident by the end of the second year of growth and remains small for some years.

Figure 16

Right upper jaw of a koala showing Class II wear of the pre-molar and the first and second molars.

Figure 17

Right upper jaw of a koala showing Class III wear of the pre-molar and Class II wear of the first and second molars.

Figure 18

Right upper jaw of a koala showing Class V wear of the pre-molar and the first molar and Class IV wear of the second molar.

In Figures 19, 20, 21 and 22, I have presented in graphical form the gains in weight and the increases in head length with age for males and females separately of those animals which were caught a number of times and which at the time of their first capture were of known age. The successive points for three females which were recaptured at considerable intervals are plotted but not graphed. Measures of various parts of the body were related linearly to each other over a wide range but head length was the most easily taken, though even so, as the values for BLUE H suggest, it may be difficult to avoid error under field conditions. It is apparent from these figures that growth may continue to be rapid in the second, third and fourth years but there are considerable differences between individuals.

On the basis of these data the following criteria were used to classify animals into 1 and 2 year classes for Table 6:

2 year class: males $\leqslant$ 5100 g or between 5100 g and 6600 g if caught between Jan 1 and Feb 15.
Females $\leqslant$ 4400 g or between 4400 g and 6400 g if caught between Jan 1 and Feb 15.

1 year class: males $\leqslant$ 3000 g or between 3000 g and 4100 g if caught between Jan 1 and Feb 15.
Females $\leqslant$ 2800 g or between 2800 g and 3200 g if caught between Jan 1 and Feb 15.

With age, tooth wear becomes more evident, the fur on the outside of the pinnae becomes long and sparse and, particularly in males, unpigmented areas develop on the snout. The silver and dark grey colour of the young becomes lighter and, particularly in females, a reddish colouration of the pelage on the crown, back and flanks may develop. The sternal gland area of males becomes large and is often nearly naked.
In Table 20 I have given the means and the ranges of body weight and head length for twenty-five females and seventeen males which had significant tooth wear (teeth judged to be in classes IV or V) and otherwise the appearance of fully mature individuals.

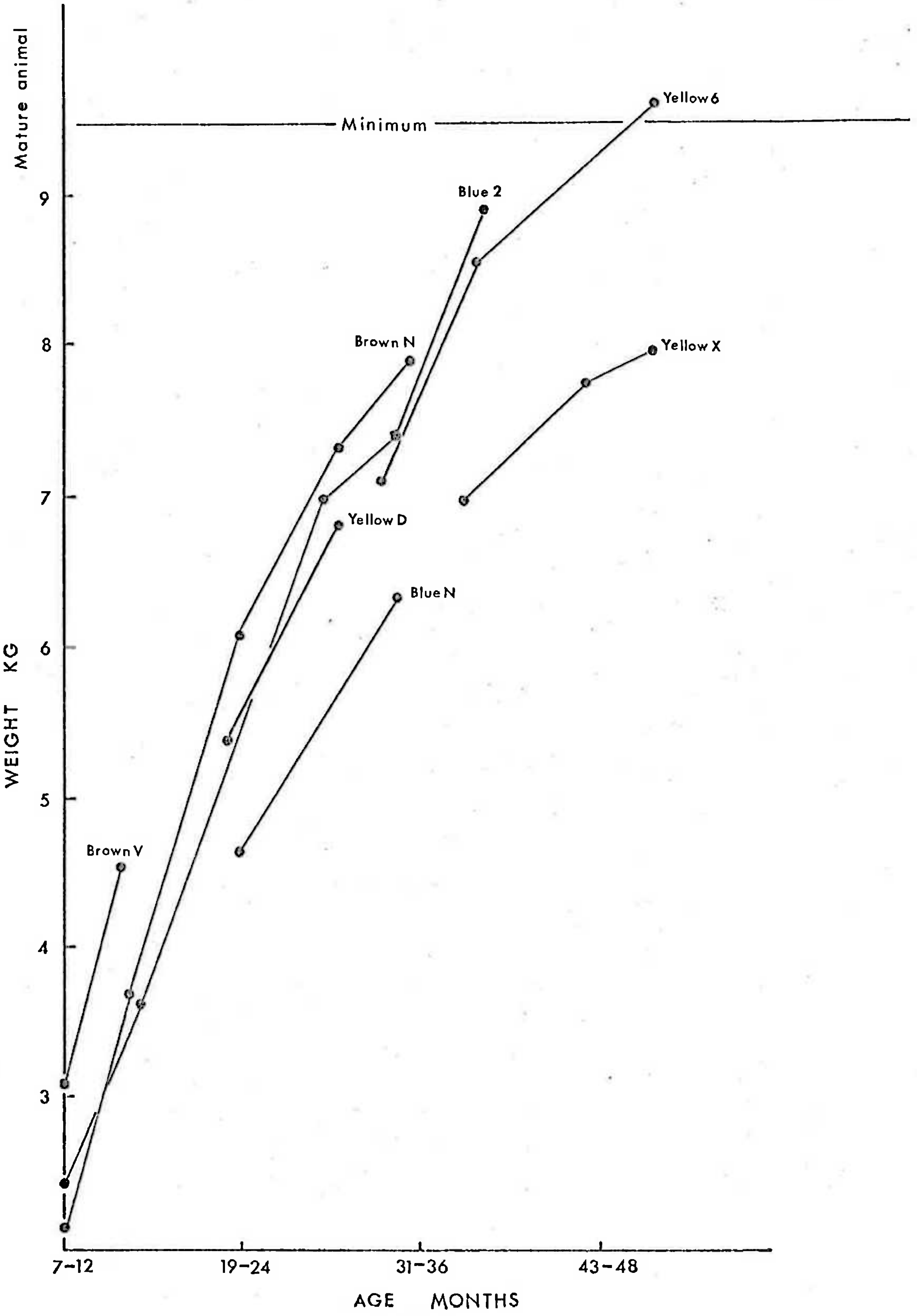


Figure 19 Weight gains with age ♂

Mature weight scale from Table 20.

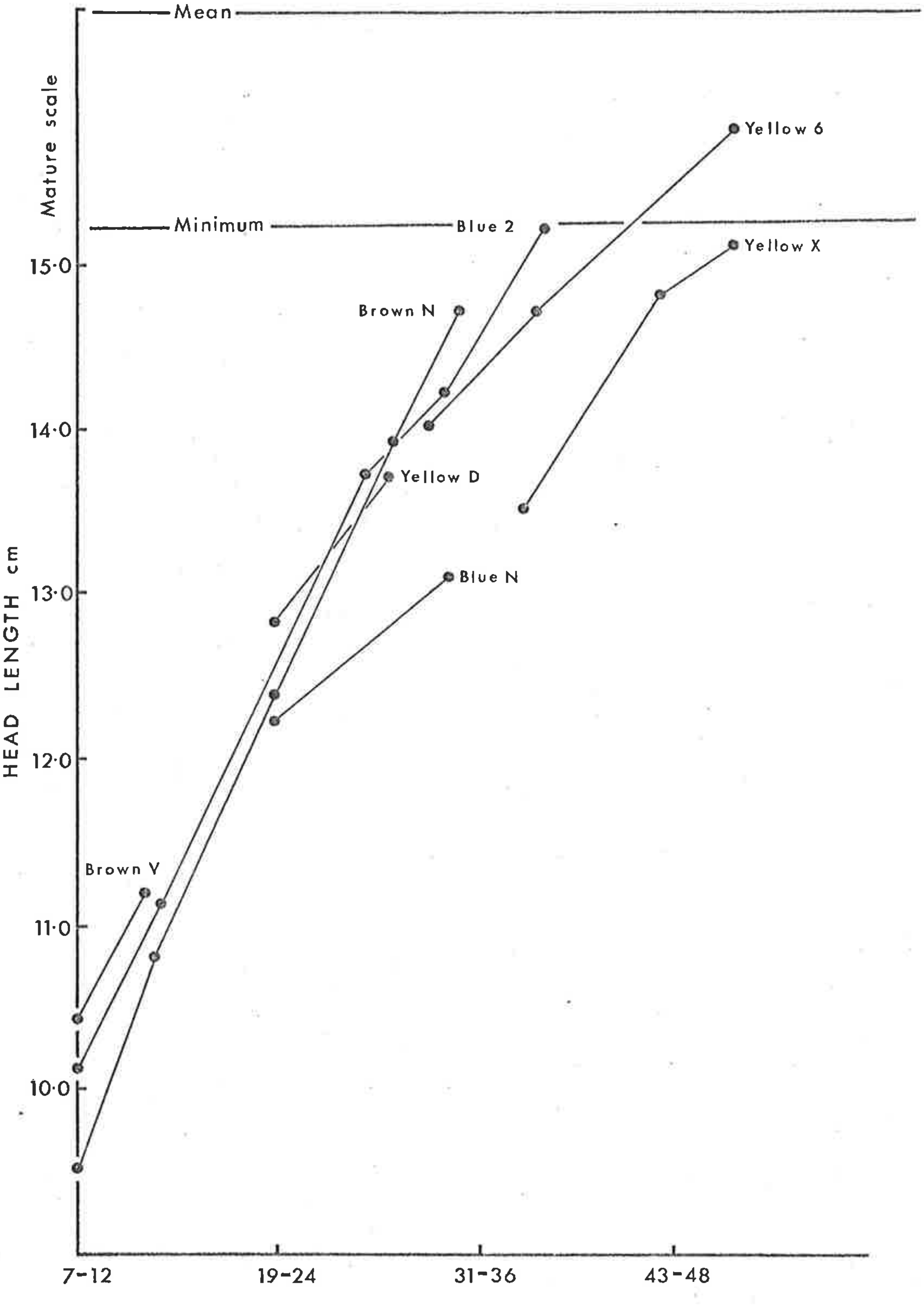


Figure 20 Increases in head length with age ♂

Mature head length scale from Table 20.

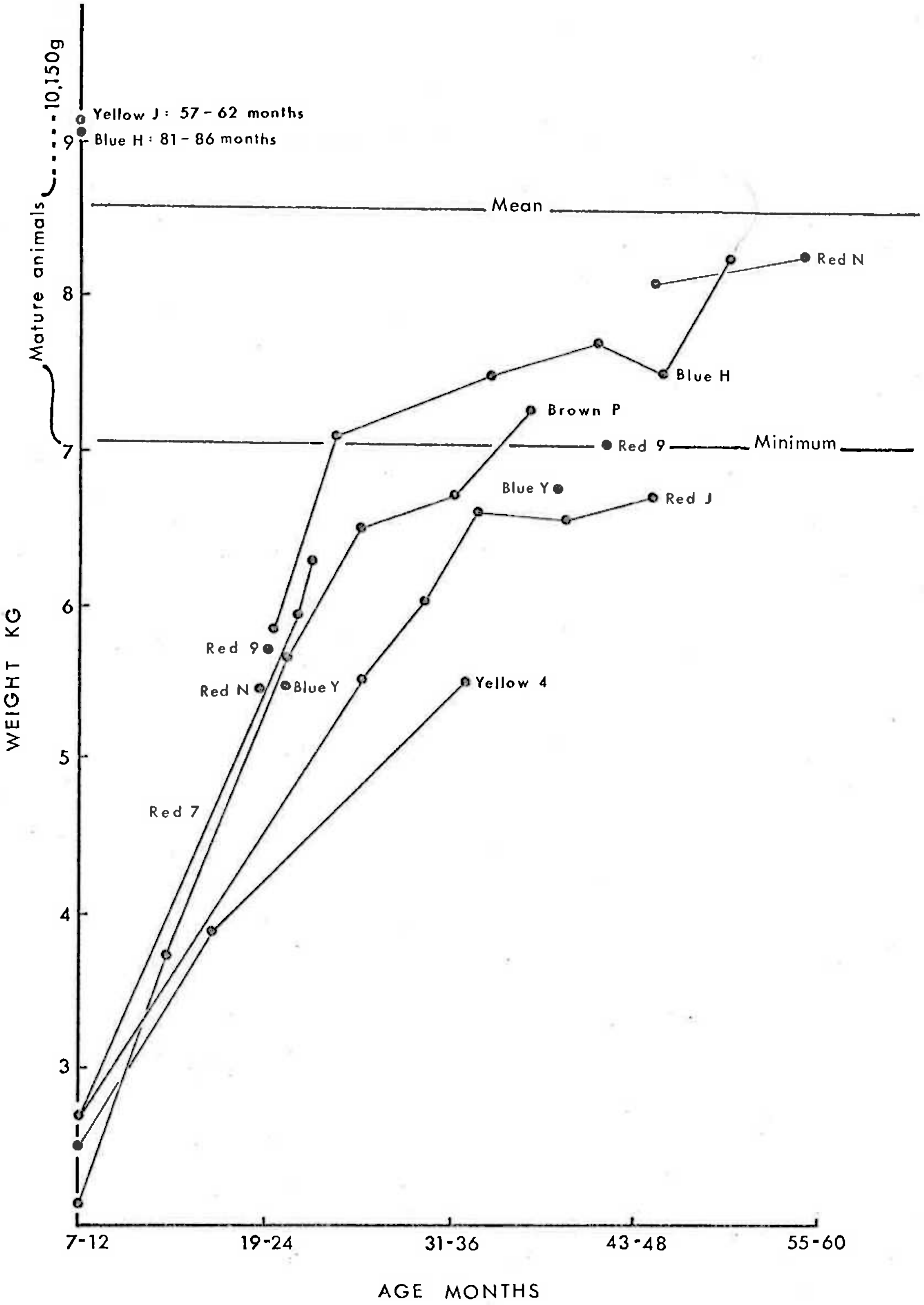


Figure 21 Weight gains with age ♀

Mature weights scale from Table 20.

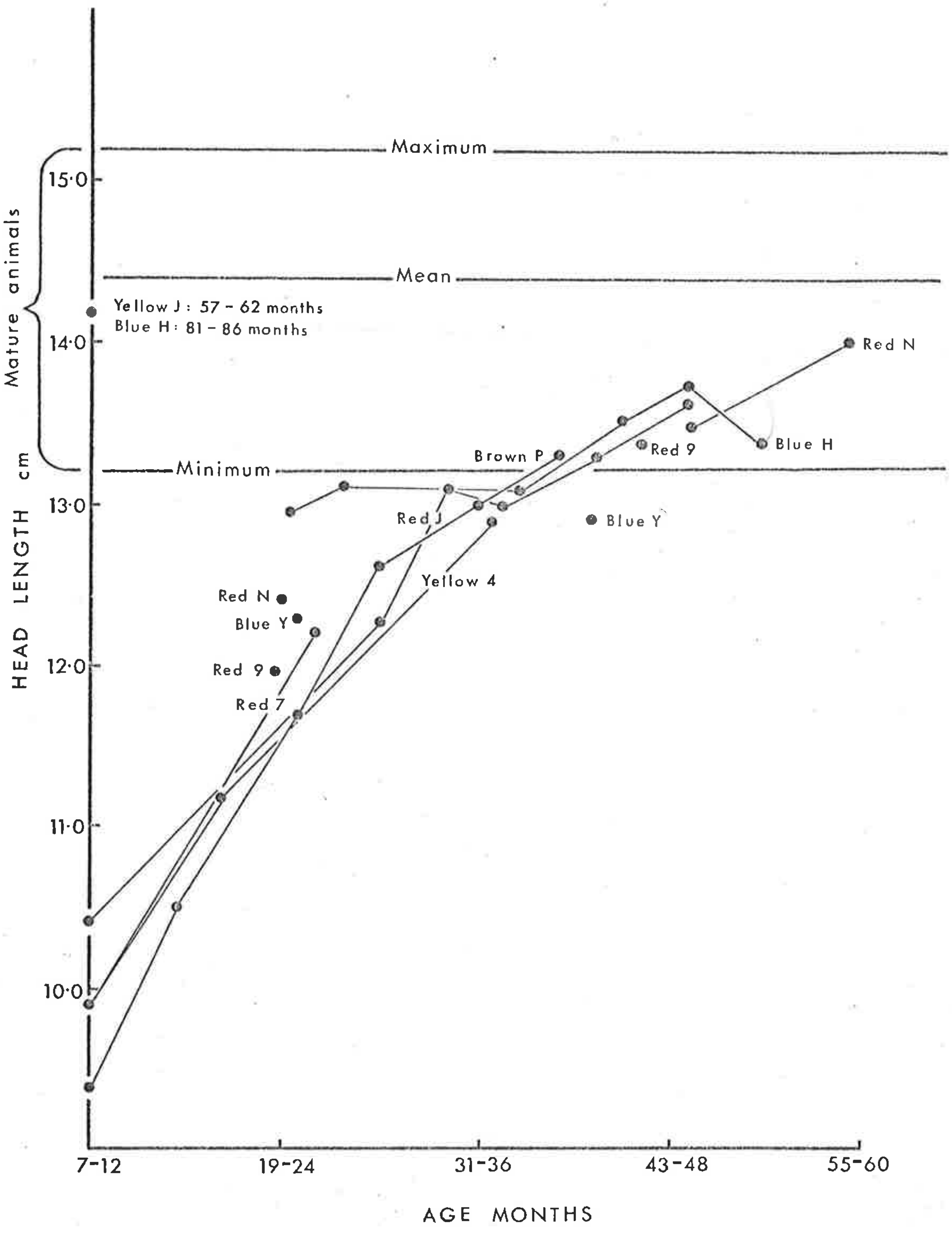


Figure 22 Increases in head length with age ♀

Mature head length scale from Table 20.

TABLE 20 Head Length and Weight of Adult Koalas

		17 Males	25 Females
Weight	Mean	11,250 g	8,600 g
	Range	9,500 - 13,050 g	7,050 - 10, 150 g
Head Length	Mean	16.5 cm	14.4 cm
	Range	15.2 - 18.1 cm	13.2 - 15.2 cm

BLUE H reached a size and weight within the range for females in her fourth year of growth and YELLOW J, at about the end of her fourth year of growth, was just below the mean head-length for females in Table 20 and just above the corresponding mean weight. YELLOW 6, on the other hand, did not reach a size and weight within the range for males until his fifth year. It is likely then that females are not fully grown until some time after their fourth year and males until some time after their fifth year.

Koalas are popularly supposed to live in captivity for up to twenty years (Faulkner, 1922; Troughton, 1941). If males and females are not of a mature weight, size and appearance until their fifth year at least, then one male and four females, caught as fully mature animals at the beginning of the study and which were present at the end (1969), were then at least eight years old and probably more. Two of these were known to have maintained weight over the four years of study. Three other females were caught again in 1972. One of these had been marked as a dependent young, another as a young about two years old, and the third as a rather young-looking adult. Some statistics on these animals are given in Table 21. It is apparent from these data that longevity in the wild may easily exceed ten years. Of course the average life-expectancy will be less than this. Indeed, it is apparent from the data given in Section 3 that the average life-expectancy may be as little as two or three years.

TABLE 21 Weights, head-lengths and class of tooth wear for koalas of various known ages.

Koala	Age (yrs.)	Weight (g)	H.L.(cm)	Class of wear on Pm 4, M 1.	
Blue 5 ♀	3 *	7,200	13.3	II-III, -	
Blue 5	5 *	7,250	13.4	-, III-IV	
Blue 5	$5\frac{1}{2}$ *	7,150	13.5	IV, IV	
Blue 5	8 *	8,050	13.7	V, IV-V	
Blue H ♀	2	5,850	12.9	II, II	
Blue H	3	7,500	13.1	- -	
Blue H	4	7,850	13.5	III, III	
Blue H	7	9,050	14.2	IV-V, IV	+
Yellow J ♀	1	1,750	9.0	I, I	
Yellow J	5	9,100	14.2	III, III-IV	
Red B ♀	4 *	9,700	14.5	III, II-III	
Red B	8 *	10,000	14.5	V, IV	+
Red C ♀	4 *	8,200	14.3	IV-V, III	
Red C	8 *	8,200	14.2	V, V	

H.L. = head-length

\+ = with pouch young

* = minimum ages

2.4 Sexual Maturity

Three females, BROWN P, RED J and RED 7, marked as dependent juveniles, were caught again at such times that something of their breeding history was known. BROWN P bred for the first time in the following breeding season at an age therefore of about two years. Eight other females which were caught when thought to be about two years old also had pouch young. RED J did not breed in the second season following the season of its birth since when caught early in the third season it still had the recessed nipples of the nulliparous female. However, from its size at capture, this female was probably born very late in the breeding season of its birth and so when it did carry a pouch young three breeding seasons later, it was probably nearer two and one half years of age than three. Another female which was caught was of this type since it had recessed nipples and an undeveloped pouch when, from its size and appearance, it was at least well into its third year of growth. RED 7 was caught at the end of a breeding season when about two and one half years of age. It did not have a pouch young but the pouch seemed to be developed and the nipples were not recessed, so this female may have been in oestrous but had failed to breed, or more likely, had lost a pouch young.

Sexual maturity is therefore reached by females at the end of the second or early in the third year of growth, but whether a female produces a young for the first time two or three breeding seasons after the season of its birth, may depend on whether it itself was born early or late.

In Table 22 I have given for periods encompassing the end of the breeding season, the percentages of females, excluding juveniles, with pouch young. The number caught is included in brackets.

TABLE 22 Females with Pouch Young (%), over periods encompassing the end of the breeding season. Total number caught in brackets.

Mar.-June 1966	May-Aug.1967	Mar.-July 1968	Mar.-June 1969
69(16)	71(7)	82(11)	63(19)

The values in the table include two females without pouch young which were known to have lost pouch young - but also include two females with pouch young caught twice at intervals during the periods to which the values refer. The figures suggest that at the end of a breeding season about 70% of all females more than one year old carry pouch young.

Not all of these young survive to independence but the increment from natality is prolific enough to suggest, in view of the constancy of the numbers of koalas in the manna gum areas and the absence therein of a marked mortality, that either many koalas must each year be dying during local movement to trees outside the river flats, or there is a significant dispersal of koalas from these areas, or both.

DISPERSAL

3.1 Localization

It became evident early in the study that many koalas were to be found within the manna gums only in certain circumscribed areas - perhaps in trees all within a few chains (40 m) of each other. In some cases this localization proved to be very enduring. Five females marked at the beginning of the study in April and May of 1966 were still to be found only in the same areas in June 1969.

Two other females, first caught and marked in January of 1967, were re-caught in the same places in February of 1972. This faithfulness to particular areas was also indicated in the return of four koalas which had been released at varying distances from their home areas (see Table 23). One animal was introduced to a small partially-isolated grove, from which the resident animals had been removed, at a straight-line distance of 1.9 km. It was not known how long this koala took to return, but its failure to remain in the unoccupied grove suggests that the tendency of koalas to leave an area to which they have been introduced involves more than their eviction by locally resident animals. Two animals released at greater distances (4 and 6.4 km) did not apparently return, and one was seen at the site of its release eight months later, so it is possible that the return of an animal to its home area requires that familiar ground is chanced upon in the course of a certain amount of extended local movement about the site of release.

TABLE 23 Results of translocating koalas from their home areas.

Animal	Distance translocated	Seen at site of release	Time for return
RED F	250 m	-	1 day
RED N	310 m	-	3 days
RED G	720 m	+ 4 days	4 - 69 days
YELLOW P	1,900 m	+ 18 days	19 days - 14 months
RED 9	4,000 m	-	-
YELLOW N	6,400 m	+ 8 months	-

The localization of koalas could, of course, take the form of faithfulness to an area - with a relatively indiscriminate use of trees therein. Alternatively, since koalas are arboreal, it could take the form of faithfulness to particular trees - with only occasional use of other trees in the immediate vicinity. Koala localization tends to the latter form. As such it is described by a number of discrete points (trees) within a relatively small area (which, however, is large enough for the trees favoured by the koalas to be interspersed between many others which are, at the most, only occasionally used). The term 'home range' clearly does not fit particularly well, but is convenient to use.

I have given an example of koala localization in Figure 23 with data for BROWN W, a young adult male koala found only in part of area B and adjacent scrub. The data represent 63 sightings of this animal over a period of thirty months. Area B is the part contained by the river (dark line) in which individual trees are represented by open circles. The size of these circles does not indicate the relative size of trees or the extent to which the crowns shield the ground. The wavy lines indicate the borders of scrub and forest without B. The filled-in circles represent trees in which sightings of BROWN W were made. They are of three sizes : the smallest represent a single sighting and the largest five or more sightings. These data illustrate:

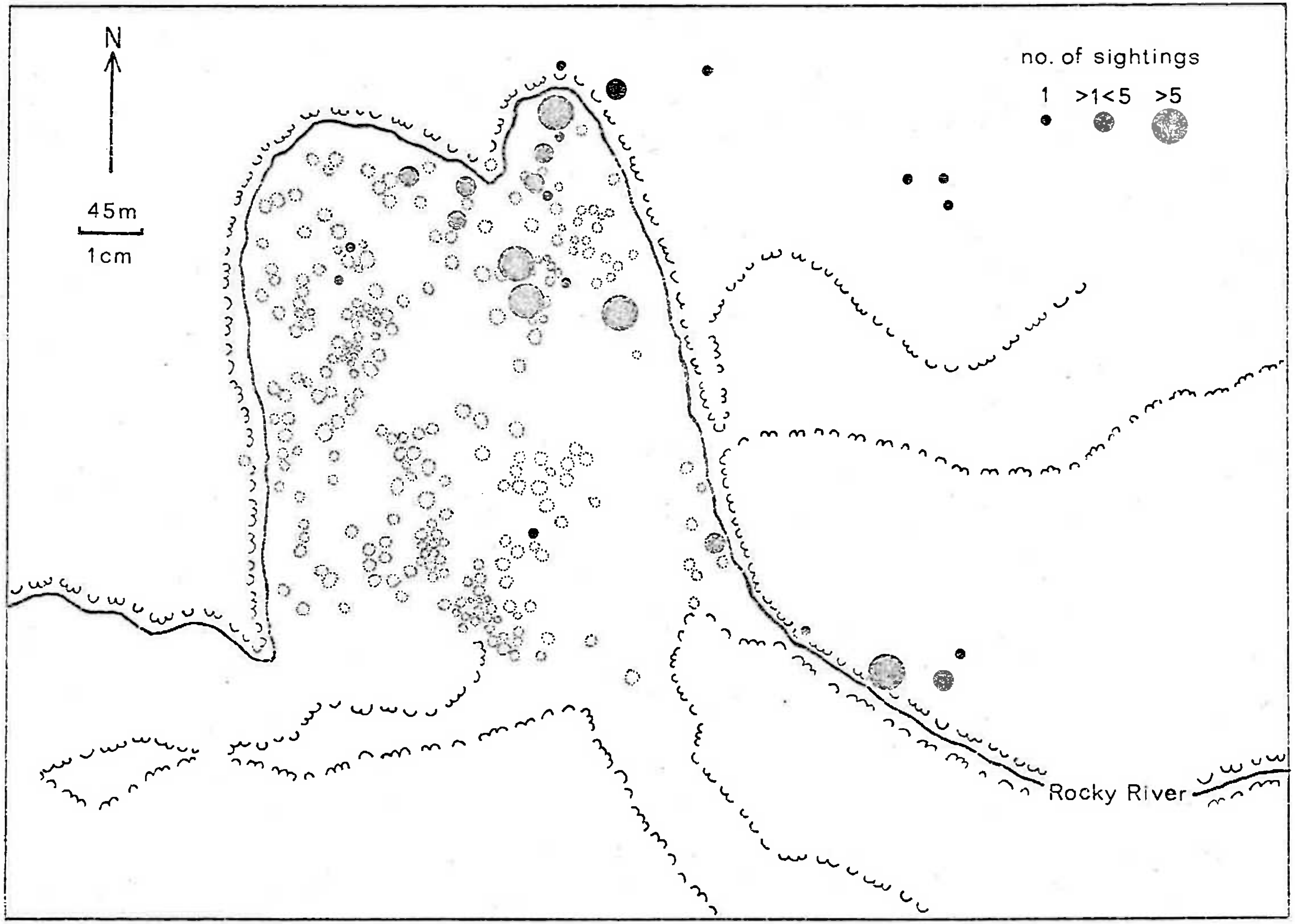


Figure 23 Area B. Localization of a male koala --- 63 sightings over a period of thirty months. WEST BAY TRACK

(1) the faithfulness of koalas to particular trees both inside and outside the manna gum areas,

(2) how the favoured trees, at least within the manna gum areas, tend to be concentrated in the one place, but may also be interspersed between trees not used.

Figure 23 does not illustrate the relative use made of the manna gum areas and other associations by BROWN W. This is shown, in the form of a proportion, in Table 24 which lists these data for all adult (two years and over) members of the populations using B and A_3, which remained members for at least six months. The proportion was calculated from the number of sightings made of these animals within the manna gum areas and the total number of complete searches made while the animals were known to be members of the population. The value of six months is not an arbitrary figure but this will be made apparent in part two of this section.

TABLE 24 The proportion of total time spent within A_3 and B by adult koalas which were members of the populations using these areas for a period of more than six months. The number of "searches" from which the proportion is derived is shown in brackets.

Males		Females	
Animal	Proportion	Animal	Proportion
BROWN N	0.98 (41)	BLUE J	0.92 (72)
BROWN S	0.86 (72)	BROWN R	0.86 (56)
BLUE O*	0.62 (180)	BROWN P	0.78 (49)
YELLOW D	0.56 (41)	RED 7*	0.74 (23)
BLUE 2*	0.50 (130)	YELLOW J*	0.63 (46)
BROWN W	0.40 (72)	RED 6*	0.52 (200)
YELLOW 3	0.29 (72)	RED J	0.50 (32)
YELLOW 5	0.28 (72)	RED Q	0.49 (72)
MEAN	0.56 (7)	YELLOW A	0.38 (32)
		YELLOW 4	0.30 (33)
		RED Y	0.17 (72)
		MEAN	0.57 (11)

* Area A_3

Burt (1943) discussed use of the term 'home-range' in mammalian ecological studies. He distinguished between a 'territory' - "a defended area" - and a 'home range' - "that area traversed by the individual in its normal activities of food gathering, making and caring for young". Jewell (1966) proposed a re-statement of this concept of home range as "the area in which an animal normally travels in pursuit of its routine activities". Jewell also cited subsidiary concepts such as "life-time range", "annual range", "core area", "foci of activity", "territory" and "monopolized zone". It is clear from the need for these latter terms that home range itself, as a simple area measurement, is a crude index of an animal's use of space. Notwithstanding, at a superficial level, it is extremely well founded and its chief problems lie in the need for objective criteria to distinguish "routine activities" and to assess changes observed with time.

Two measurements, at first sight, would seem to be appropriate for a koala home range. One is the number of trees involved and the second is the area which contains them. The two problems of measurement relevant to both are, of course, the separation of exploratory sallies and so forth from tree-occupancy with real home range significance, and the objective distinction of changes in home range with time. These problems can be overcome by considering the data for individual koalas in the form of an array of trees in which sightings were made against frequency of sightings. Data are given in Tables 25 and 26 for the animals listed in Table 24. In Table 25, for example, the koala RED 7 (R.7) was seen fifteen times in one particular tree; it was seen twice in each of three other trees and once in another. Values for 'total sightings' in Tables 25 and 26 do not necessarily correspond to those of Table 24. They exceed them in some cases since here I have used 'casual sightings' (i.e. sightings of koalas on days when the study area was not fully searched for all animals).

TABLE 25 A_3 and B: Frequency array of trees in which sightings were made against frequency of sightings - adult female koalas.

No. of sightings per tree	BL.J	BL.J	BR.R	BR.R	BR.P	R.7*	Y.J*	R.6*	R.J	R.Q	Y.A	Y.4	R.Y	Total
					Number of Trees									
82								1						
15						1								
14			1											
13	1								1					
12									1					
11										1				
10														
9										1				
8	1		1		1		1							
7				1	1		1				1			
6		2			1			2						
5		2		3	2					3	1			
4		2		1				1			1		1	
3		4		3	4			1		1	1	2	1	
2		5		4	2	3	2	1	4	3	2	1		
1		22		3	8	1		3	2	6	10	3	4	
Total sightings		95 ✓		68 ✓	55 ✓	22 ✓	19 ✓	106 ✓	35 ✓	50	33 ✓	11	11 ✓	505

* Area A_3

TABLE 26 A_3 and B: Frequency array of trees in which sightings were made against frequency of sightings - adult male koalas.

No. of sightings per tree	BR.N	BR.S	BL.O*	Y.D	BL.2*	BR.W	Y.3	Y.5	Total
	Number of Trees								
35					1				
30		1							
22	1								
21			2						
18			1						
16			1						
9						1			
8						1			
7		1	2					1	
6			2	1		1			
5			2		1	1			
4		2			2		1		
3	1	2			2	1	1	1	
2	1	6	3	9	3	5	2	2	
1	8	19	2	8	2	5	9	6	
Total sightings	35 ✓	82 ✓	120 ✓	32	62	46	20	20 ✓	417

* Area A_3

Addendum: TABLES 25 and 26

In the frequency arrays presented in TABLES 25 and 26, the "boxes" delimit the trees making up the home ranges of the animals concerned.

The total possible number of trees making up the home range of a particular animal are all those in which more than one sighting of the animal was made. In each case where there is a marked disjunction in the array, the home range is considered to be made up of those trees which fall above the disjunction, as discussed in the text. In the circumstance where there are several disjunctions in the array for a particular animal, the home range was determined by a subjective assessment which took into account the relative sizes of the several disjunctions.

As indicated in the text, the two home ranges given for each of the animals BL.J and BR.R refer to two successive periods in the study, the animals occupying quite separate areas during each period.

The existence of a 'home range' is indicated by multiple sightings in single trees (the alternatives are that animals are entirely nomadic or that there are insufficient observations). Disjunctions in the array among multiple sightings indicate intra 'home range' (trees in which multiple sightings were made) distinctions - core areas, for example - or changes in home range over time. These latter are apparent in the original data. Among the animals represented in Tables 25 and 26 two only (BL.J and BR.R) began to frequent a new set of trees during the period over which they were under study. They are each therefore represented twice in Table 25. In the cases where there are marked disjunctions in the arrays it is clear that the only part which, with very little doubt, fits the concepts of home range and which can be quite objectively distinguished, is that above the disjunction. I therefore reserve the term home range for this part. In Tables 25 and 26 home ranges are 'boxed'. Two home ranges, of course, are given for BLUE J (BL.J) and BROWN R (BR.R).

In Tables 27 and 28 I have given home range sizes (in terms of numbers of trees) for male and female adult koalas together with some supplementary information. Since the majority of koalas had a home range of only one or two trees I have not given any area measurements: I have instead given, for those with home ranges of more than one tree, the maximum distance between trees comprising the home range.

The values in Tables 27 and 28 suggest a difference in home range between male and female koalas. Five out of eight male koalas had a home range consisting of a single tree and this distribution differs significantly from the corresponding distribution of two in eleven for female koalas ($X_1^2 = 3.9$; $P < 0.05$).* On the other hand, the home ranges of female koalas accounted for 363 out of 492 sightings of these animals and this distribution differs significantly ($X_1^2 = 47.0$; $P < 0.001$) from the corresponding ratio of 215 in 415 for male koalas. It therefore seems

---

* X^2 is used throughout the text as the symbol for Pearson's chi-square.

TABLE 27 A_3 and B: Home ranges (within the manna gums) of adult female koalas.

Animals	No. of trees	Max.Distance between trees	% sightings accounted for	% time within manna gum areas
BLUE J	8.5 (av.)	149 m (av.)	73	0.92
BROWN R	7.0 (av.)	65 m (av.)	96	0.86
BROWN P	9	101 m	78	0.78
RED 7*	1	-	68	0.74
YELLOW J*	2	7 m	79	0.63
RED 6*	1	-	77	0.52
RED J	2	13 m	71	0.50
RED Q	2	13 m	40	0.49
YELLOW A	6	176 m	70	0.38
YELLOW 4	3	76 m	73	0.30
RED Y	2	85 m	64	0.17
Mean	4.0	76 m	72	0.57
Range	1-9**	7 - 176 m	40 - 96	0.17 - 0.92

* Area A_3

** or 1-15 if the two values for BLUE J are considered (see Table 25).

TABLE 28 A_3 and B: Home ranges (within the manna gums) of adult male koalas.

Animals	No. of trees	Max.Distance between trees	% sightings accounted for	% time within manna gum areas
BROWN N	1	-	63	98
BROWN S	1	-	37	86
BLUE O*	4	80 m	63	62
YELLOW D	1	-	19	56
BLUE 2*	1	-	58	50
BROWN W	4	100 m	61	40
YELLOW 3	4	234 m	55	29
YELLOW 5	1	-	35	28
Mean	2.1	138 m	49	56
Range	1-4	80 - 234 m	19 - 63	28 - 98

* Area A_3

that localization in male koalas tended to be expressed by faithfulness to particular trees, whereas localization in female koalas could, in some cases, be seen as faithfulness to particular areas; on the other hand males showed a greater tendency to make exploratory sallies and to generally occupy trees non-routinely.

In the case of four animals (BROWN N, BLUE J, BROWN R and BROWN S), these within-the-manna-gums home ranges were clearly very nearly complete home ranges. However, in other cases this was not so. In one case only (BROWN W) was it possible to accurately plot the positions of a koala away from the manna gums. Several animals were sighted a number of times away from the study areas for which the estimated distances were never more than three or four hundred metres. On the other hand several other marked koalas were found at distances of nearly 1 mile (1.6 km). It therefore seemed that the same sort of variability in home range behaviour within the river flats was characteristic outside the river flats. Since koalas leaving the manna gums have a virtually unlimited choice of trees and space it follows that home ranges here can be on a larger scale.

The data on home ranges so far discussed is referable to adult (two years and over) koalas which persisted in the populations using A_3 and B for at least six months (the choice of six months will become apparent in the next part of this section). Koalas less than two years old largely followed parental behaviour. Of the remaining animals, some persisted such a short time that it was clearly nonsense to talk of a home range while for others again there were too few observations to invite useful conclusions. However, the tendency of a koala to return to a tree it has formerly occupied was shown even in these animals by the ratio of total sightings to total number of trees in which sightings were made (sums of individual data). Of the 46 other koalas which were over two years old and which were members of the A_3 and B populations, 18 were seen only once; the remaining 28 were seen 149 times in 90 trees, i.e. there was an average of only 0.60 trees/observation showing a tendency to return to trees previously occupied.

The particular trees that were favoured strongly were usually large trees which rather naturally showed considerable or even extreme defoliation (a large tree though showing extreme defoliation may still carry many more kilos of foliage than a small one). In these cases the foliage that remained was mostly carried on epicormic shoots arising along the length of the main branches. However, there were trees of similar size and growth form, with foliage of a similar age-structure and distribution, that were not favoured, so there was no obvious physical basis to the preference shown for certain trees.

Some feeding trials were undertaken in order to test whether koalas would discriminate between the foliage taken from trees that were favoured and those that were not. Animals were caught and confined to a small Acacia or E. diversifolia mallee in which two or three containers with water were secured. During a trial a pair of branches were placed in each container, one of the pair coming from a favoured tree and one from a tree that was not favoured but was comparable in other respects. Each trial made use of only one pair of trees. Branches were taken from different parts of the upper crown where koalas usually feed and an abundance of foliage was supplied. Results were quantified by counting the number of freshly bitten-off ends - which for the most part represented single leaves. The trials were undertaken in January and March of 1968 so the results only refer to this time of the year, and the animals used were not ones resident in the vicinity of the trees.

The koalas did not take kindly to confinement and some escaped. All animals lost weight and one lost 16% of its initial body weight in five days and, like others, abraded the skin off its nose on the wire fence. However, fifteen trials were undertaken involving four animals and six different pairs of trees, of which five were manna and one water gum. Since animals sometimes fed sparely the average number of bitten-off ends was only 248, but 56% of these were taken from the unfavoured trees. I therefore have no evidence that koalas can discriminate between the foliage of such trees and while more adequate trials might reveal this faculty, I am inclined to think that chance, habit and other qualities of trees may be as important as differences in the palatibility of the foliage. Koalas certainly favour particular perches within trees.

3.2 Population Composition

In contrast to certain koalas which, having been caught and marked in A_3 and B at the beginning, remained members of the populations using these areas for the duration or greater part of these studies, were some that were not seen again. And there was a continuing small influx of animals new to these areas which were caught and marked and which were seen to remain members of the populations for a greater or lesser period. The source of these animals could only be other parts of the West Bay Track; indeed, six of the immigrants to B and five of those to A_3 had been caught and marked elsewhere. This immigration was most marked in the summer months and in Table 29 I have given, separately for the months of October to March and April to September, the numbers of known immigrants together with the numbers of days on which searches were made.

TABLE 29 A_3 and B: Number of immigrant koalas for the periods October - March and April - September. Number of days on which searches made in brackets.

	Oct. - March	April - Sept.	Total
A_3 (April 67 - June 69)	10 (99)	4 (89)	14 (188)
B (Oct. 67 - June 69)	27 (55)	5 (27)	32 (82)
Total	37 (154)	9 (116)	46 (270)

$$X_1^2 \text{ (Total)} = 10.27 \quad 0.01 > P > 0.001$$

Since the searches of A_3 and B were made at intervals I cannot say exactly how long immigrants remained, but in Tables 30 and 31 I have assumed that an animal seen during one search period was a member of the population for that month in which the search was made, while an animal seen on consecutive field trips was a member for those months and the intervening ones.

Addendum: TABLE 29

The Chi-square given in TABLE 29 is a "goodness-of-fit" Chi-square calculated for the frequencies of immigrant koalas given in the last row of TABLE 29. The expected frequencies were calculated from the total number of immigrant koalas and the frequencies of searches made during each of the two yearly periods.

TABLE 30 A_3: Duration of Residence of immigrants

Months	1	4
No. Koalas	13	1

TABLE 31 B: Duration of Residence of immigrants

Months	1	2 - 5	13	19
No. Koalas	21	8	1	2

It is apparent that most of the immigrants to A_3 and B remained a short time only. In view of the discontinuity between the twenty-nine koalas that remained in area B for from one to five months and the three that remained for from thirteen to nineteen months I have called all animals which persisted after they had been present for at least six months, 'residents'; I refer to the others as 'nomads'.

There was a considerable range in the frequency with which resident animals were seen during any particular field trip (see Table). Some residents were present on average only about once a week, while others were seen almost every day. Nomads too varied in this way but few of them were ever present for more than a few days in any search period. The mean proportion of time spent within the river flats by residents was 0.57; the corresponding value for nomads was only 0.32. Of further interest was a difference between male and female nomads in this proportion. This is illustrated in Table 32 where I have given, for males and females separately, the sum for all nomads of sightings and recorded absences of particular nomads while they persisted as members of the populations using A_3 and B.

TABLE 32 A_3 and B: Sightings and recorded absences of male and female nomads.

	Sightings	Absences	Total searches
Males	61	171	232
Females	99	168	267
Totals	160	339	499

$X_1^2 = 6.629$ P just > 0.01

This difference is a likely explanation in part for the large difference between the numbers of male and female koalas belonging to the '2 year' class caught in the total sample (see Table 6). There was no reliable evidence that:

(1) male nomad koalas persisted as members of a population for a lesser time than female nomad koalas

(2) male koalas in the 2 year class were more likely to become nomad than female koalas in the same class

but these factors may also have contributed to the difference in Table 6.

A possible explanation for the difference shown in Table 32 lies in a tolerance for nomad female, but not male, koalas by resident male koalas (see Section 4).

The five females and five males which were marked at the beginning of the studies of A_3 and B and of which nine remained resident for the duration of the studies and the other for the greater part, were all mature animals; the mean weight of the females was 8,450 grams, and that of the males 10,950 grams.

The forty-six immigrations to A_3 and B involved four animals which were immigrant to both areas and three others which were each immigrant to B on two widely separate occasions. The thirty-nine koalas therefore involved included nineteen females and one of unknown gender. This last was one of eight immigrants which were not caught and marked but which, because of their sex or some other characteristic were not confused with animals caught on succeeding trips; where such confusion was possible I have conservatively assumed that only one animal was involved. One other female immigrant which had been caught and marked elsewhere was not caught at the time of its appearance. Two only of the fifteen male immigrants which were caught were clearly fully mature and eleven were of young appearance. These eleven ranged in weight from 5,650 g to 8,800 g with head lengths from 12.8 cm to 14.7 cm. The values suggest that all these animals were in their third or fourth years of growth. One was of known age since it had been caught and marked elsewhere when its size and appearance marked it categorically as a young koala about one and one half years old. It was seen as an immigrant one year later. Of the sixteen female immigrants which were caught, three were fully mature but another was only about one year old. Eight others were of young appearance and of these seven ranged in weight from 5,150 g to 7,500 g with head lengths from 12.2 cm to 13.1 cm, suggesting that they too were all in their third or fourth years of growth. Three of the eight were of known age. Two were marked elsewhere as dependent juveniles and were between two and one half and three years of age while the other was marked when about one and one half years old and was three and one half years at the time of its appearance.

In Table 33 I have presented the composition of the population using B, in terms of residents, nomads and young, at various times from July 1967 through to June 1969. The data came only from field trips during which complete searches were made on seven or more days, and do not include other individuals seen in adjacent scrub or seen on other than search days during a field trip. Since catching and observations were begun in B in January of 1967, I have been able to categorize the animals seen from July of 1967.

The numbers of nomads seen were most variable but suggest that these numbers can be expected to fluctuate within a given range. The seasonal influence on the incidence of immigration is not particularly obvious but this is because nomads, having arrived, might stay for some months. In addition the number is likely to be more affected by sampling variation. The low value of January 1969 is probably not significant since in both December 1968 and March 1969 when a few casual searches were made, several nomads were immediately seen.

TABLE 33 B: Population Composition.

July 1967 - June 1969

	Resident	Nomad	1965 Pouch Young	1966 Pouch Young	1967 Pouch Young	1968 Pouch Young	Total
July 1967	8	2	0	4			14
Oct. 1967	8	5		4			17
Dec. 1967	8	7		2			17
Jan. 1968	7	8		4	3		22
Mar. 1968	8	7		4	3		22
May 1968	10	5		3	3		21
July 1968	11	4		4	3		22
Jan. 1969	10	1		2	1	5	19
June 1969	9	3		1	0	5	18

The number of residents was least variable. Four males and three females were resident throughout the study (though one female was not seen in January 1968 in the area during the search period, it was seen in adjacent scrub). The number of residents was increased by two females which came as immigrants in December 1967 and continued for the remainder of the study, and by one male which remained a member of the population for twelve months. One other female, resident at the start of this study, was lost from the area after nineteen months. This animal was later seen elsewhere in the West Bay Track, as a nomad.

The 1966 pouch young of this female continued in their common home range and, since it bred in 1968 and did not share the home range with other adults, probably had fully the same status as other resident females. This event was one reason why the 1966 pouch young persisted in the area longer than those from 1965 or 1967. Another 1966 pouch young remained until about March 1969, and in this case the parent female had shifted its home range somewhat but the young continued in the original range. It came to share this with a resident male but the absence of the female may have allowed it to continue as long as it did. It is evident that the loss of young from the area is the reason why, with an annual increment to the resident population of nearly fifty percent from breeding, the numbers remain relatively constant. The loss apparently occurs over a variable period of time but is itself a variable process as is indicated by the occasional absences of 1966 pouch young during 1967 and 1968. In fact, there were five 1966 pouch young marked in this area but they were never all present at the one time. The first 1966 pouch young lost permanently was late in its second year of growth. That these young form directly the bulk of the nomad population is indicated by the age at which they were lost from their home areas. Of the seven young lost from B, three were in the second year of growth, three were in their third and one was early in its fourth year. In addition, four of them were later seen elsewhere as immigrants.

Catching in A_3 was begun in April and May of 1966 and searches were made in May and August of 1966 and in January and April of 1967. From May - June of 1967 through to June of 1969, the area was regularly searched for longer periods. Data are given in Table 34. One adult female was resident throughout the entire study. An adult male was a member of the population in April, May and August of 1966 but was not seen thereafter, and another adult male took its place and was seen every search period from January 1967 through to June of 1969. A resident male and female were therefore characteristic of this population throughout the study. The number of nomads seen during any search period varied from 0 to 2, supporting the conclusion that this number can be expected to fluctuate within a given range. The resident female did not breed in 1968, so only three young grew to independence during the study. The 1965 pouch young was lost from the population midway through its third year of growth. The 1966 pouch young was temporarily absent in the latter half of its third year of growth but returned and was still a member of the population in June of 1969 at an age of about three and one half years. The 1967 pouch young was also still a member in June of 1969 at an age of about two and one half years. However, this area was also searched on four days in December of 1969. Both adult residents were seen and the female carried a dependent young. But neither the 1966 nor 1967 pouch young was seen which makes it possible that both were no longer members of the population. If this was so, then of the three young in this area, two were lost in their third year of growth and one in its fourth. The composition of the population using this area, and the changes observed, were therefore very similar to those in B, though all the young in A_3 persisted a long time. But it may have been significant that the resident female (RED 6) in this area was confined almost entirely, when present, to one tree (see Table 25), while all the young came to use other trees.

There was abundant additional evidence that the majority of the nomads were young animals and that they came directly from their parental home areas. Four females and one male which were marked in B in January of 1967 and which were not present in July of 1967 were therefore probably all nomads or 1965 pouch young from this area. The male weighed only 4,400 g and the four females were of young appearance and averaged only 6,200 g. One young male seen in A_3 in June and August of 1966 but not thereafter was probably a nomad or 1964 pouch young from this area. It weighed 8,100 g. Another female nomad seen in A_3 in January of 1967 was from its appearance only in its second year of growth and weighed 5,600 g.

TABLE 34 A_3: Population Composition, May 1966 - June 1969

	Resident	Nomad	Dependent/ Independent Young	Total
May 66	2	1	1	4
Aug. 66	2	1	1	4
Jan. 67	2	1	2	5
Apr. 67	2	0	2	4
May 67	2	0	2	4
Jul. 67	2	0	2	4
Oct. 67	2	1	1	4
Dec. 67	2	1	1	4
Jan. 68	2	2	2	6
Mar. 68	2	3	2	7
May 68	2	0	2	4
Jul. 68	2	1	2	5
Sep. 68	2	0	2	4
Oct. 68	2	0	1	3
Nov. 68	1	1	2	4
Dec. 68	2	2	2	6
Jan. 69	2	1	2	5
Feb. 69	2	1	2	5
Mar. 69	2	1	2	5
Apr. 69	2	1	2	5
May 69	2	0	2	4
June 69	2	2	2	6

Six other animals were marked in other parts of the West Bay Track which were later seen again in places widely removed from the site of their initial capture. One was a mature male but the other five, two females and three males were young animals. Indeed, the two females and one of the males were of known age since they were marked as dependent juveniles. It was not known how long these animals had been nomadic but when seen the male was only at the end of his second year of growth while the females were in their third and fourth years of growth. This, together with other data on the weights and ages of nomads, residents and independent young at the time of their loss from parental home ranges, is summarized in Tables 35 - 38.

TABLE 35 A_3 and B: Persistence of young in parental home ranges.

	Males			Females	
Animal	Age when lost	Age still remaining	Animal	Age when lost	Age still remaining
BR.N.	3-3½ yrs.	-	BR.P.	-	3-3½ yrs. **
BR.V. *	1½ yrs.	-	Y.4 *	2½ yrs.	-
BL.2	3½-4 yrs.	-	Y.2	2½ yrs.	-
Y.K. *	2-2½ yrs.	-	R.7	2½ yrs.	-
Y.M. *	1½-2 yrs.	-	Y.J.	2½-3 yrs.	-
W.H.	-	1½ yrs.	Y.H.	1½-2 yrs.	-
W.J.	-	1½ yrs.	W.F.	-	1½ yrs.
W.K.	-	1½ yrs.			

* Seen elsewhere as nomads.

** Breeding. Apparent full resident status.

TABLE 36 Male and female nomad koalas of known ages.

Males		Females	
Animal	Age	Animal	Age
BL.A	2 yrs.	R.9	3½ yrs.
BR.V. *	1½ yrs.	BR.J.	2½ yrs.
Y.K. *	2-2½ yrs.	Y.4 *	2½ yrs.
Y.M.*	1½-2 yrs.	R.N.	3½ yrs.
BL.N.	2½ yrs.	R.J.	2½ yrs.

* Also in Table 35.

TABLE 37 Female resident and nomad (apart from those listed in Table 36) koalas, by weight and age classes.

Age class	Criteria	Weight classes within age class	Nomad n	Resident n
4 years +	8600 g (p.52)	-	4	8
2 - 4 years	by difference	7600-8600	1	7
		6600-7600	7	4
1 - 2 years	p.51	-	6	0
0 - 1 year	p.51	-	1	0
Totals			19	19

TABLE 38 Male resident* and nomad (apart from those listed in Table 36) koalas, by weight and age classes.

Age class	Criteria	Weight classes within age class	Nomad n	Resident n
4 years +	9500 g (p.52,f.19)	10500-12500	2	6
		9500-10500	2	1
2 - 4 years	by difference	-	15	0
1 - 2 years	p.51	-	1	0
Totals			20	7

All this evidence shows very clearly that the numbers of koalas to be seen within the West Bay Track manna gums remain relatively constant due to the dispersal of young from their parental home ranges. These young become members of a floating section of the population composed chiefly of animals of this category. Since the nomadic part of the population is a reservoir for the annual natural increase, and yet remains apparently no more in numbers than the mature resident population (Tables 33 and 34), it follows that either there is a considerable mortality within this group or the dispersal carries much wider than the limits and immediate surrounds of the manna gums i.e. beyond the limits from which the koalas might return.

---

* There are fewer resident male than female koalas listed here (and elsewhere) because males were more likely to fight and lose their identifying tags.

3.3 Survival of nomads

Five carcasses were found during the study. One was that of a dependent young but the other four were of unmarked animals and were found in the vicinity of the study areas, so all were nomad animals. Several of these carcasses were moderately fresh when found but there was nothing in the appearance of the body or the internal organs to suggest the cause of death. The guts in all cases were full of food though the carcasses were lean and devoid of organ fat.

Some nomads were seen a number of times in widely different parts of the West Bay Track. And there was an exchange of animals between the West Bay Track and the Rocky River Station some two miles away. This suggested that despite wide movements nomads were inclined to remain faithful to either the manna gums or to areas where other animals were to be found. Seven young nomads were seen eventually to become resident members of a part of the West Bay Track population, so not all perish! This adherence to the river flats by some nomads was most likely a response to the presence of manna gums, since at Yakka Flat, an area some distance from the Rocky River Station, some koala droppings were found underneath a few of the half-dozen small manna gums (each only four or five feet in height) that struggle to survive on the edge of thick mallee scrub and abundant sugar gum stands. No other droppings were found in this locality. It is remarkable that the animal or animals that wandered here found these miserable dwarfs and I am inclined to think that by means of their olfactory sense, koalas may be able to detect some species of eucalypts from a distance. This may seem fanciful but during the growing season I have indubitably detected at some distance the odour of the essential oils of the high-yielding species, <u>E. globulus</u>.

Yakka Flat is distant from the Rocky River Station some four to five miles (6 - 8 km). The presence of droppings here was clear evidence of a very much wider dispersal of koalas. There was other direct evidence of such a dispersal. During the period covered by this study the sightings of two koalas, one on the West End Highway and one on the Cape Borda Road, were reported to me. The relation of these places to the Rocky River manna gums can be seen in Figure 3. Philpott (1965) also reported the sighting of a koala on the Borda Road and the Rangers informed me that over the years there had been very infrequent but more or less regular reports of koalas seen outside the boundaries of Flinders Chase. Some of these animals have been seen at the top of iron telegraph poles. This testifies to perhaps both the koala's climbing ability and its single-mindedness. Such behaviour when seen is usually regarded as very mysterious but my own experience suggests that homeless, wandering koalas are sometimes caught on the ground by dawn and, half-blind, make shift to climb anything. The presence of a koala at the top of a telegraph pole is a clear indication that it is an animal wandering far from familiar ground. These infrequent reports of lone koalas, seen transiently in places miles from the known occurrences of other koalas, indicate that while some nomads may remain faithful for a time to the general area of their origin, others are wandering more widely. It seems likely that a nomad that does lose contact with the river flats is likely to travel a considerable distance.

Nomad koalas were rare or absent during the winter (Table 29). This was partly because young animals of the age appropriate for dispersal had already been incorporated into the nomad part of the population during the summer breeding season, and with a continuing loss of nomads through wider movement away from the river flats, the numbers of nomads remained low until the susceptibility of another generation and the initiation of the stresses of another breeding season reconstituted the nomad population. This high rate of turnover in the nomad chapter raises a point hitherto unremarked. Nomadic females were apparently as likely as residents to breed and carry small pouch young (Table 39) but since most were lost from the population through mortality or wide dispersal they did not, as a rule, contribute to the annual natural increase.

TABLE 39 Females of known status and reproductive age captured during the breeding season.

	With Pouch Young	Without Pouch Young	Totals
Resident	15	11	26
Nomad	4	5	9
Totals	19	16	35

Adj. $X_1^2 = 0.09$ $0.80 > P > 0.70$

The wide dispersal of nomad koalas indicates that koalas can survive for a time away from the manna gums. But the failure of koalas to establish persistent populations elsewhere, and the continuing rarity and transient nature of their presence in places far removed from the manna gums, is indirect but nonetheless convincing evidence that the nomads that wander widely from the manna gums have a much lower probability of survival.

The dispersal of young koalas from the home ranges of their birth and their incorporation into a nomad chapter of the population is the mechanism whereby the density of koalas in the manna gums remains more or less constant. It is difficult to invent plausible reasons for this dispersal and its characteristics other than social interaction between animals. And there is evidence that social behaviour is very important.

SOCIAL BEHAVIOUR

4.1 Adult-Young Relationships

Young koalas, after they have completed pouch life, cling as they will to the back or belly of the parent female. The females are clearly very tolerant of their young though they show little apparent interest in them. However, until the young are about one year old they are rarely separated from the female by a distance greater than the length of one or two branches, so there is probably much more to the maternal behaviour of koalas than a simple tolerance of the presence of the young and its suckling demands. On one occasion I caught a female the dependent young of which was in another part of the tree. This young seemed agitated at the disappearance of its parent (which I had lowered to the ground in a bag) and began to climb down (backwards, as is customary). I seized it and as I did so the young began to give a series of short, high-pitched squeals. These cries elicited a response from <u>another</u> female some distance away, which came on the ground to the tree in a series of short rushes following each cry. By observing this female on the ground and by encouraging or discouraging the cries, I was able to assure myself that she was responding to the young. Eventually, she climbed a short way up the tree but it had become imperative to secure the young some other way, and on my doing so, the female removed herself some distance, but how far I could not tell since it was then quite dark. I suspected that the female concerned was one which was separated from her own young since I had earlier in the day seen a dependent young by itself (for the first and only time) near this place.

Since there were other animals present in the vicinity that did not respond, it would seem that sensibility to such cries may be confined to females deprived of young. However, I have noted adults in captivity, particularly males, respond in a similar if less marked manner to the variety of squeals and grunts uttered by other animals, both young and adult, which were being handled. In captivity it is apparent too that adults are generally very tolerant of dependent or newly independent young, which supports the common opinion that females will very readily foster-mother young. In the wild, newly independent (i.e. fully weaned and no longer carried on the back or belly of the female) young continue to use many of the trees frequented by the parent female, and female and young are often seen together in the one tree.

This relationship, however, changes considerably during the second year of growth. The independent young continue to share trees with the parent female but come less and less to occupy them at the same time. This can be seen by inspecting Table 40 in which I have presented, separately for ten young, the number of sightings made of these young in trees together with the parent female, and in trees alone, for both the periods of January -- March and May - June. These periods correspond to the times at which the young are newly independent and about half-way through the second year of growth. I have also given the chi-square values, adjusted by Yates' correction for continuity, together with the associated probability of a larger value, for the six young which were observed seven or more times in each period.

It is clear that in either of these periods during the year there may be considerable differences between young in the likelihoods of seeing them alone or together with the parent female. It is also clear that in individual cases there may be a significant difference between these likelihoods in January - March and May - June.

TABLE 40 Observations of Independent Young

Young	Time	No. obs'v'ns. young in tree together with parent	No. obs'v'ns. young alone	Total obs'v'ns.	Adj. X_1^2
Y.J.	Jan.-Mar.	7	2	9	20.7
	May-June	0	26	26	$P < 0.01$
Y.K.	Jan.-Mar.	8	5	13	3.9
	May-June	3	13	16	$P < 0.05$
Y.H.	Jan.-Mar.	5	10	15	4.4
	May-June	0	17	17	$P < 0.05$
Y.M.	Jan.-Mar.	3	5	8	0.16
	May-June	7	12	19	$P < 0.70$
W.H.	Jan.-Mar.	7	1	8	2.4
	May-June	3	5	8	$P < 0.20$
W.J.	Jan.-Mar.	8	1	9	9.1
	May-June	0	7	7	$P < 0.01$
W.F.	Jan.-Mar.	5	1	6	
	May-June	0	4	4	
Bl.2.	Jan.-Mar.	2	3	5	
	May-June	8	5	13	
Br.P.	Jan.-Mar.	3	0	3	
	May-June	1	11	12	
Br.N.	Jan.-Mar.	2	0	2	
	May-June	2	8	10	

It is possible to carry this analysis a step further by subdividing the number of observations of young alone into those made of the young alone in trees which were also used (at some other time) by the parent female and those which were not. If this is done in individual cases the numbers of observations falling into some of the categories become small; Yates' adjustment for continuity cannot be used following the addition of an extra degree of freedom and the probabilities associated with chi-square values may be misleading. I have therefore given this further analysis, in Table 41, on the pooled data for the ten young represented in Table 40.

TABLE 41 Pooled Observations of Ten Independent Young

Time	Treatment 1: No. obs'v'ns. young in trees together with parent females	Treatment 2: No. obs'v'ns. young alone in trees also used by parent females	Treatment 3: No. obs'v'ns. young alone in trees not used by parent females	Totals
Jan.-Mar.	50	11	17	78
May-June	24	37	71	132
Totals	74	48	88	210

X_2^2 = 49 $P << 0.01$

X_1^2 (Tr.2v. Tr.3) = 0.2460 $0.70 > P > 0.50$

X_1^2 (Tr.1v. Tr.2; Tr.3) = 48.8 $P << 0.01$

The evident differences between young in Table 40 require that the chi-square value for Table 41 be assessed conservatively. However, its very large value of 49 confirms the conclusion that there may be a very significant difference in the behaviour of young at these two periods during the second year of growth. It also seems evident on this pooled data that this difference is brought about by a greatly reduced likelihood of observing young together with the parent female in May - June, rather than in a change in the likelihood that young seen alone will be in trees also used or not used by the parent female.

A number of explanations may be advanced for this change in the behaviour of young during the first half of the second year of growth. It might be argued that the change was a response by the young to a growing shortage of browse in trees also used by the female; however, in this case, it would be expected that young would come to use trees which were not used by females. Again, it might be argued that the change is an expression of the growing behavioural independence of the young (which no longer actively seek out or follow the parent female). Alternatively, it may be thought that the female becomes intolerant of the close proximity of the young and drives it away. These last two hypotheses seem to me the most plausible. They might be separated by comparing the probabilities of movement to another tree when the young are alone and when they are, in fact, together with the female. However, since those young which showed a clear change were seen rather rarely with the parent female, I am unable to evaluate these alternative hypotheses.

In any event, this change is over-shadowed by the complete loss of many independent young from the parental home range during the latter half of the second year of growth (text 3.2). Few persist through the third year of growth. The loss may be quite sudden or may be preceded by occasional temporary absences in the case of those that remain the longest.

The variability in the age at which the young are lost coupled with the manifest tendency of some koalas independent of age to remain within a home range does not support the view that this dispersal of young results from an innate tendency at a particular stage of development.

The rapid growth of the young (text 2.3), the abundance of browse in at least some home ranges, and the enduring localization of most adult females (text 3.2), does not suggest that the dispersal comes from a shortage of food. The lack of support for these hypotheses suggests that the tolerance of females for their dependent young yields to an increasing hostility, and this hostility eventually drives the young away from the parental home range. The one really critical observation pertaining to this hypothesis - and model for an experimental test - was the fate of the young of the one female which itself departed the home range during the second year of growth of the young. The young remained in the home range, bred, and seemed in its fourth year to have fully the status of a resident adult. This evidence is strong support for the hypothesis of parental hostility. Direct physical conflict between females and their young was not observed. However, such encounters are certain to be nocturnal, few in number and of brief duration. Thereafter the constant threat mediated by the sight, sound or smell of the female, perhaps coupled with the dissatisfaction arising from the consequent restriction of its movements, is probably sufficient pressure to eventually drive the young away.

4.2 Vocalizations and Scents

Among mammals the dispersion of individuals is often largely governed by the responses they make to their fellows and this is epitomized in the maternal and mating relationships. It is also common for interaction to take place at a distance due to the development of various long-range signalling systems involving principally the auditory and olfactory senses.

Some marsupials seem to be extraordinarily well endowed with respect to olfactory communication. Petaurus breviceps has five different types of scent glands and in addition has marking behaviour associated with micturition and salivation (Schultze-Westrum, 1965). Koalas possess only one obvious scent gland but this, the sternal gland developed in males, produces a very pungent odour. I have not seen koalas exhibit any specific marking behaviour (but see Burnet, 1938) but the usual method of climbing is such that it obviously results in the incidental transfer of secretion to the tree.

I reported in Section 1 that koalas on being released often sniff at the bark of the tree, particularly when they are released away from the site of their capture and on these occasions they also do not seem very eager to climb. When they do climb and settle down, they may 'wind' the air with such vigour that they seem to be literally tasting it.

Koalas are also quite vocal and two distinctive calls are of especial interest. Mature males can give a loud call which in still air may be heard for half a mile or more. The sound is uncouth and is best described as a series of rasping indrawn breaths followed each time by a growling expiration. When given in full the first part is dominated by the inspirations and the latter by the longer, bubbling expirations. The snout is pointed skywards during the call which is most commonly heard during the breeding season, when it may be given during the day. It is often uttered when they first wake and become active, and this immediately, which suggests that it is a non-specific response, but it is also associated with pairing and aggression. Commonly, a call which has broken the silence of an hour or more is rapidly followed by calls from other males but the call may be heard in isolation and other males close by do not necessarily respond.

Another distinctive vocalization is an interrupted murmuring sound made with the mouth very slightly open, of low frequency and intensity which can easily be mistaken for the droning of an insect in flight. It may be given by both males and females and very young animals. I have heard it uttered in a variety of situations but it seems to be most reliably associated with the presence of two animals in one tree. When given in a non-specific manner it may produce a like response in other animals but I have also observed it to fail to elicit a manifest response in nearby animals.

4.3 Adult Relationships

Koalas are solitary rather than gregarious mammals and it is uncommon to observe more than one animal in a tree, apart from the special case of females and their young. This is documented in Tables 42 and 43. In Table 42 I have analysed all sightings of koalas in B in terms of group size. In Table 43 I have classified the pairs and triads of koalas seen according to the classes of animals involved. For this purpose I have taken each triad as three pairs; the total number of groups is therefore inflated over that in Table 42.

TABLE 42 B: May 66-June 69. Sightings of single koalas, and groups of three. % of total number of groups accounted for in brackets.

Single Koalas	Pairs	Triads	Total no. of 'groups'	Total Sightings
828 (88)	108 (11)	7 (1)	943 (100)	1065

TABLE 43 B: May 66-June 69. Composition of koala groups-of-two according to class of animals.

Class	% Total (No.)
Young in second year of growth, with parental female	53 (68)
At least one nomad	24 (31)
Mature resident and resident young persisting in parental home range	16 (20)
Mature residents	5 (7)
Other	2 (3)
Total	100 (129)

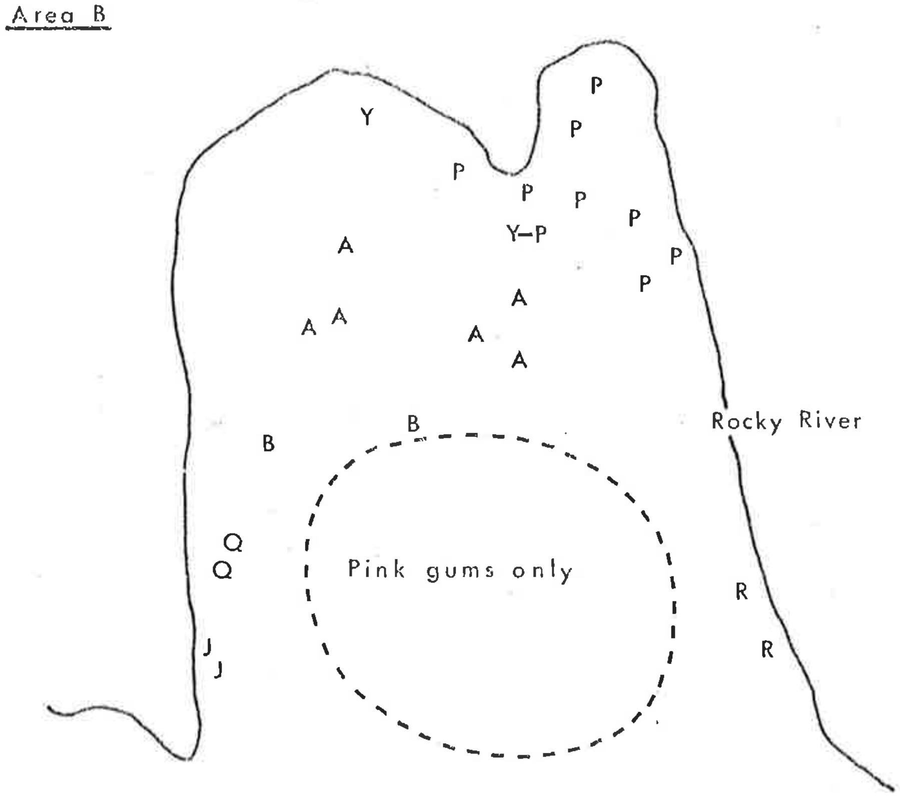


Figure 24 Area B. Distribution of 'home-range trees' of resident adult female koalas. Sharing indicated by hyphen.

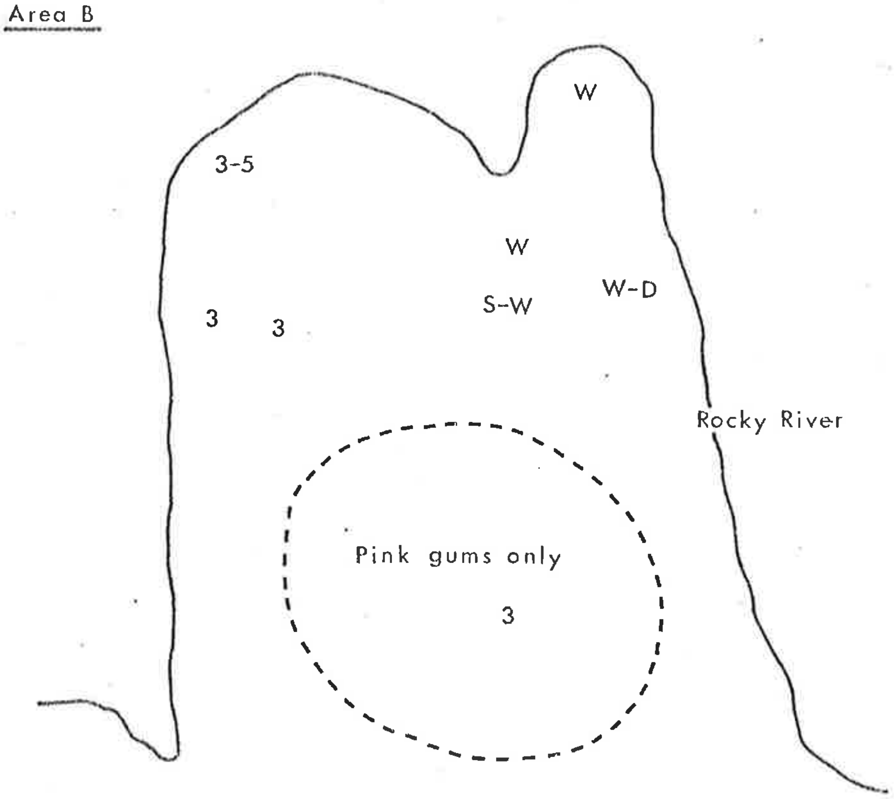


Figure 25 Area B. Distribution of 'home-range trees' of resident adult male koalas. Sharing indicated by hyphen.

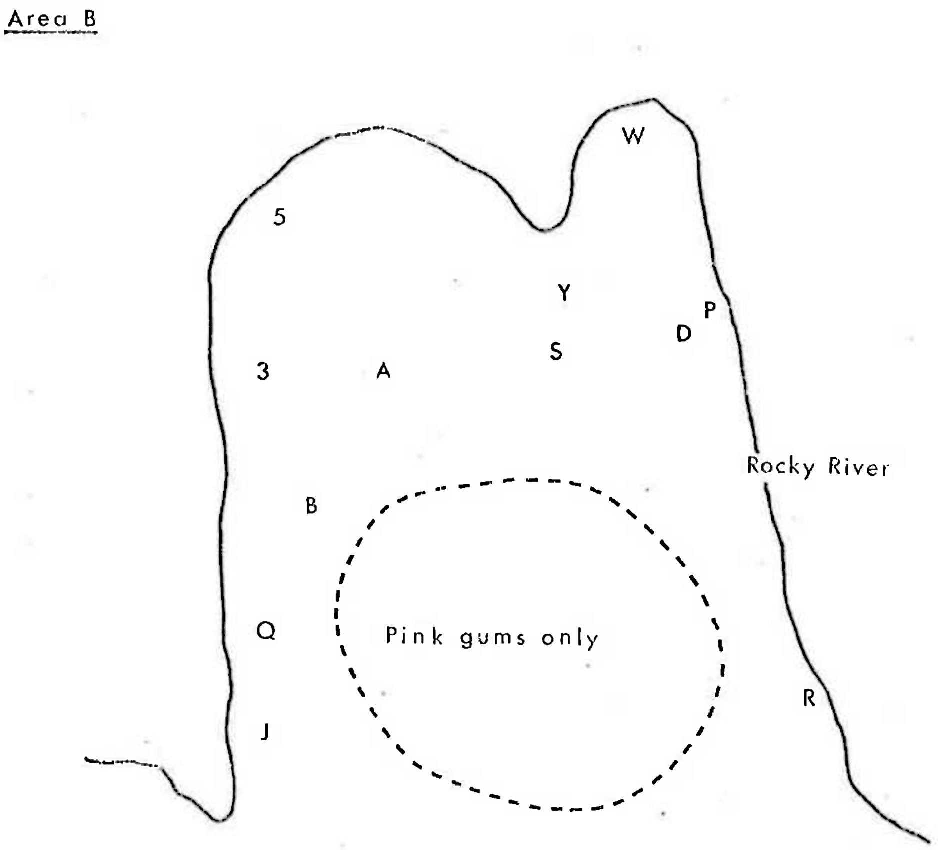


Figure 26 Area B. Distribution of most commonly used 'home-range trees'----resident adult koalas.

The most significant values in Table 43 are those for the 'mature residents' class. These animals were responsible for only 5% of the total pairs seen, but 44% of the total sightings. It is evident that the home ranges of mature residents were largely, if not entirely, separate. This is illustrated in Figures 24, 25 and 26. In Figures 24 and 25 I have shown the distribution of home range trees (see Tables 24 - 28 and text) for the seven female and five male koalas which were resident in B during the study (see Table 33 and text). In Figure 26 I have shown the distribution of the most commonly used home range tree for these animals.

Koalas, of course, were not entirely confined to their own home ranges and 'trespass' was observed. This could be of two kinds: trespass into an unoccupied tree and trespass into an occupied one. In Table 44 I have summarized the data on the relationship between adult, resident koalas with respect to home ranges. For this purpose, I have, in the case of those animals which shared a home range tree, allotted the tree to the animal which used it most frequently, and counted the presence of the other as a trespass. The data show trespass to be uncommon.

TABLE 44 B: July 67-June 69. Sightings of adult, resident koalas and trespass on home ranges.

Classes of Trespass	Trespass into Occupied Trees	Trespass into Unoccupied Trees	No Trespass	Total Sightings
Male-Female, Male-Male, Female-Female	6	56	363	425
Male-Male, Female-Female	3	30	392	425

Burt (1943) thought that Noble's definition of 'territory' as 'any defended area', was comprehensive and to the point. Pitelka, on the other hand, emphasized that 'territory' was primarily an ecological (rather than behavioural) phenomenon and defined it as 'an exclusive area, not merely a 'defended' one' (Jewell, 1966). Kaufmann (1971) gave several examples of an exclusive use of space by mammals which did not involve any 'defence' (interpreted quite broadly) but which had the same effects on the exploitation of resources as allocation of space involving overt aggression. Leyhausen (1971) emphasized:

(1) in mammals (c.f. birds) territories are often made up of a number of places which are used routinely, together with a network of paths between them. This probably follows simply from the economy of effort practiced by a ground-living animal where ease-of-passage varies with terrain.

(2) the relative nature of territoriality, i.e., the dependence on specific locality and time-of-day of ranking among individuals which arises as a result of territoriality.

(3) the essential identity of territoriality, social hierarchy and the struggles of even the most primitive organisms to gain from their fellows literal breathing space.

It is clear that the home ranges of koalas may quite properly be called territories since they have the property of being used rather exclusively by one particular animal. Since these territories allocated a limited resource (manna gums) it may be thought that the exclusiveness of home ranges depended on more than just some mutual, passive avoidance of their fellows by koalas. And evidence for this came from attempts to obtain more direct evidence on the relationships between adult koalas through observation.

Koalas may be more difficult than many animals to study in this way, since they are arboreal, nocturnal and, when active, alert and secretive. Furthermore, they betray little by their expressions or the attitudes they assume and immobility which is always ambiguous is very characteristic. Experiments on the introduction of koalas to trees already occupied have the same problems of data gathering and interpretation as observation of potentially informative natural situations, as well as additional ones. Koalas are usually reluctant to climb strange trees to which they are introduced and often leave at the first opportunity in any case, and the distress calling not infrequently given can communicate to others and render any subsequent observation of doubtful value. Most of my attempts at observation and experiment gave, by themselves, ambiguous results. But it did seem that the presence of two adults of the same sex in one tree was quite reliably associated with:

(1) a murmuring vocalization

(2) a failure to browse for any sustained period of time <u>or</u> the close approach of one animal to another <u>or</u> the failure of either to alter position for a long period of time.

(3) the withdrawal of at least one of the animals from the tree.

Some experiments on the introduction of animals to occupied trees and one fortuitous observation did give less equivocal results. One young male forced into a tree occupied by a resident male and a nomad female was promptly attacked very fiercely by the resident male. The introduced male made no defence but emitted single loud cries of one note, with a brassy quality like that produced by blowing through a folded leaf. He eventually escaped to the extremity of a branch where the resident could not successfully attack him. He remained there for many hours. The resident attempted to renew the attack on at least one other occasion and after both this attempt and the initial attack he returned to a fork low down on the main trunk, giving as he did so the loud call characteristic of males and then almost immediately assuming a sleeping position. A fortuitous observation made six months later in the non-breeding season, of a nomad male climbing into a tree favoured by a resident male, presented an almost identical picture with the same cries, ferocious attack, pursuit and resumption of sleep. In view of the ferocity displayed, it was very intriguing in this case that only twenty minutes after the initial attack the nomad was unconcernedly browsing while the resident slept, while three hours later, when the tree was briefly revisited both were fairly close together, though on different branches, and the nomad was (apparently) asleep while the resident browsed. Both of the animals were gone from the tree the following day. Some other experiments suggested that intolerance can also occur between females and between males and females.

In the latter case a female and then a male were introduced to a tree entirely new to both. The male approached the female, giving as he did so the male call. The female responded with a series of stiff-legged jumps and sharp squeals. The animals sniffed at each other and then the female struck repeatedly at the male, who retreated and was pursued. Both settled down shortly after and apparently went to sleep, though the male was known to have not long after left the tree. The female remained.

Aggression between koalas may be generally unsanguine since few animals I have caught have shown any signs of conflict, but I have attributed to it the loss of some ear tags as well as the peculiar condition of others. Koalas may also readily habituate to the presence of other animals since, although Fleay (1937) reports sustained aggression between males kept in captivity, it is common for numbers of females to be closely confined without apparent threat to their survival or condition.

These observations of aggression or atypical behaviour (failure to browse, unusual vocalizations, etc.) in koalas either seen or brought together in the one tree invite the conclusions that koalas are quite generally intolerant of each other in a high degree and that territories are maintained by aggressive responses to any trespass. The absence of frequent conflicts may be explained by the role of vocalizations and scents in facilitating avoidance of confrontations.

This conclusion about the relationship between adult koalas is consistent with the idea that the young disperse from their parental home ranges in response to the intolerance shown them by the females. Both these ideas are of course open to further test. In the case of the dispersal of young, the experimental removal of females from home ranges suggests itself. In the case of adults it should be possible to contrive situations where two adults have the same 'claim' to the one home range, through the removal of koalas, the introduction of others and then the reintroduction of the former. Such an experiment is elaborate but it avoids the difficulty that when animals separate themselves they may do so because they prefer a certain solitude in a way that does not imply an intolerance that would limit density when a shared resource was in short supply (and it is precisely this which requires testing). Both these experiments would be refined by some control or measure of the food available to animals. They would, of course, be considerable undertakings. It might be more practicable to pursue direct observations of free-living animals in the wild, aided, perhaps, by image-intensifying or infra-red sensitive devices.

The summer breeding season is very likely a time of greatly increased rivalry among males. The frequency of male-calling certainly reaches a peak during this season. I have not witnessed koalas mating but from hearsay reports it seems that it usually takes place in the trees, the male approaching the female. It can involve preliminary aggression by the female and is associated with some striking vocalizations. Coupling is apparently of brief duration.

4.4 Intolerance and Density

If, as I have suggested, the intolerance shown by koalas to their fellows brings about the dispersal of young and to a large extent governs the dispersion of adults within the river flats, it tends to limit the density of koalas in these areas. Intolerance, of course, seems a natural adjunct of localization since its absence may jeopardize a continuing sufficiency of easily accessible and good quality browse. Even so, the intolerance shown by the koalas in the West Bay Track would not seem to be nearly adequate, at least with respect to the number of trees controlled by each animal, since in many parts most of the manna gums are severely defoliated. The area is without doubt steadily degenerating as a habitat for koalas and the survival of many animals now living there must soon be threatened. This makes interesting comparison with the situation in Scotch Thistle Flat, where in an area of comparable size, a similar number of animals browse in trees which for the most part maintain well-developed crowns. One reason for this is that Scotch Thistle Flat is an almost pure stand of manna; within a given area there are, on average, rather more than twice as many manna gums and intolerance is here far more efficient in conserving the resource. This statement of course implies that the 'territory' of a koala is an area; whereas elsewhere I have emphasized that the 'home-range' of a koala is a number of discrete points (trees) which are sometimes quite scattered. This is appropriate for considering the movements of an individual koala, but it may be presumed that the sight, sound and smell of a koala give him a 'sphere of influence', so while the 'home range' is a number of discrete points, the 'territory' is an area or number of areas. Of course, numerous other factors which may affect the vigour and suitability of the trees, the quality of the browse and its importance to the animals are likely to contribute to the differences between the West Bay Track and Scotch Thistle Flat. And it may be beyond the physical capabilities of koalas to pre-empt a more extensive home range. But none of this is subversive to the conclusion that the limit set to the density by intolerance is not necessarily nicely adjusted to the abundance and condition of the resource.

This is not a singular instance. Koalas have apparently multiplied in a number of island sanctuaries to which they have been introduced to the extent where they have destroyed most of their trees and then undergone a catatrophic decline in numbers (McNally, 1957). Indeed it seems that the intolerance, which though not successful in preventing the degradation of the habitat must have arrested its rate of decline, breaks down under extreme conditions for McNally has published a photograph of four koalas in what appears to be the extremely defoliated branches of a single small tree, with another koala close by.

It is not known to what degree the numbers and distributions of truly natural populations living in continental areas may fluctuate. Nor is it known in what ways conditions of life commonly differ from those in island sanctuaries. However, it may be argued that since koalas were once very abundant in many parts of a very wide range in Eastern Australia, it is likely that in these places a limit set to their density by intolerance was commonly reached. In the near-absence of reports of koalas defoliating their habitats it would seem that in these places conditions were often such that localization and intolerance did suffice to preserve the habitat (for a report of a natural population of koalas on mainland Australia defoliating trees and declining in numbers, see Kershaw, 1934). The qualities of such places may have simply resided in the size and vigour of the trees. Under favourable conditions some eucalypts can completely replace the crown within three months (Jacobs, 1936) and a large, vigorous tree in a good habitat should be able to withstand almost continuous browsing from a single koala. This argument is reasonable, if somewhat ethereal. However, it can only be applied to certain places within the geographical range of koalas. So it remains possible that it was also common for intolerance to fail to preserve the habitat in places perfectly suited for colonization. In these places colonies may have prospered for a time but eventually become extinct, or so reduced the resource that the density of the koalas was limited by other risks. Extinction of the koalas through starvation or forest fire; or the occurrence of exceptionally favourable seasons, may have allowed the trees to recover which might permit recolonization and another cycle of excessive multiplication culminating in extinction of the koalas from the locality.

It is possible to conceive of a very complicated balance of selective forces that may have shaped localization and intolerance in koalas. But the only statement that can presently be maintained with any confidence is that localization and intolerance are behaviour that under a wide range of conditions probably further the chance of survival of individuals possessing them. These behaviours *may* limit the density of a population at a level which ensures the preservation of the habitat but, in such cases, they do so only by virtue of certain qualities of the habitat. Therefore they cannot be regarded as factors which *by themselves* are generally capable of limiting density in the long term.

The summer breeding season is one of increased activity. But there are factors other than new dimensions to social inter-action that determine seasonal differences in the behaviour of koalas; these are discussed in the next section.

SEASONAL VARIATION IN BEHAVIOUR

5.1 Feeding Behaviour

Koalas can show wonderful dexterity in reaching leaves carried on shoots at the extremities of branches and in most trees there are very few places, if any, that are inaccessible to them. Feeding usually begins within a half hour after night fall and though animals may be active at any time, they are mostly so in the late evening and early morning. Koalas typically begin to browse by grasping a shoot and pulling it towards them. They run their snout along the length of a leaf and, seizing the leaf by the petiole, detach it with a quick jerk. This action is probably the most effective method of ingestion but it can give the appearance of deliberation and is, I think, responsible for the common belief that koalas are selective in their feeding to the point of smelling each leaf individually. Whilst at times koalas do smell foliage carefully and are very selective, hungry animals browse with nothing like the discrimination often attributed to them. Koalas consume a fair amount of stem material and eat buds and flowers. They are said to occasionally ingest a little earth and Bolliger (1962) has reported on the finding of gravel in the caecum of a koala, its presence presumably the result of this habit. I have seen evidence of bark-stripping and I have also seen one animal eat a tough, woody fruit, but the bulk and principal item of diet is leaf.

The quality of the browse carried by the various eucalypt species seemed the only possible explanation for the discrimination between species that was manifest. This was most obvious within the river flats where, in the West Bay Track, pink gum shared the same physical environment and grew side by side with manna gum. Of a total of 1,024 sightings of koalas made in B, where pink gum was slightly more abundant than manna gum, 872 sightings were of koalas in manna gum, and the small differences between the species in size and growth form were totally inadequate to explain this strong preference.

This inference (together with other assumptions about koala behaviour) was, of course, based on sightings of koalas during the day, when these animals feed at night; so it was thought to be of some importance to learn the extent of inter-tree movement at night.

Searches were therefore made in A_3 and B at night when these areas were also being examined by day. On two occasions three searches at intervals were made but on other occasions a single search at around midnight was made. In these latter cases it was assumed that animals had remained in their trees or had moved only once during each half of the night. The data are therefore rather crude and may err on the side of underestimating the chance that an animal will move more than once during the night. On the other hand, some of the tenancies recorded when animals changed trees twice or more were very transient and these animals had not fed largely from trees other than those in which they were seen on successive days. The searches were as thorough as those undertaken during the day. This was only possible after I had become very familiar with the trees in these areas, for the narrow beam of a powerful torch illuminates only a very small part of a tree and in these conditions it is difficult to know whether a tree has been properly examined. On nights when there was a full moon and a thinly overcast sky, the light was superfluous since the crowns of the trees silhouetted very nicely against the cloud. In Table 45 I have summarized the information gained. The data include six sets of observations which came from searches made of part of A_1, and three other sets which came from tracking animals carrying radio transmitters.

TABLE 45 Inter-Tree Movement at Night

Movements	Zero or One	Two	More than Two
Observations	47	15	3

These data show that for the most part, animals found in the one tree on consecutive days have remained there throughout the intervening night, and that those that have been seen to change trees have most probably made the one change. Since these likelihoods did not apparently differ when various species were involved, it seemed that the trees in which an animal was seen during the day tolerably indicated the source of its diet.

5.2 Koalas and Manna Gum 1

The koalas' preference for manna gum was very striking but it was by no means clear that all the other eucalypt species growing in Flinders Chase were equivalent. Koalas moving from the manna gums of A_3 into adjacent mallee scrub had the choice of three species: E. rugosa, E. diversifolia and E. fasciculosa. E. rugosa is the dominant species in the part of this association nearest A_3, but it was nonetheless noteworthy that of fifteen sightings of koalas in this association, thirteen were of animals in E. rugosa. In a similar way, the distribution and abundance of faecal pellets in the area surrounding B, reported in Part 3 of Section 1, suggested that the E. baxteri - E. cosmophylla association was more attractive to the koalas than stands and associations of other species outside B. The grading of species in order of apparent acceptability did not yield any obvious relationship with the physical characteristics of the foliage. Both E. baxteri and, particularly, E. cosmophylla for example, have leaves thicker, more fibrous and with a viler taste than those from E. fasciculosa, a species which seemed to be less attractive to koalas but which yet more closely resembles E. viminalis in the obvious physical characteristics of its leaves. It did not prove possible to collect rigorous data on the relative utilization of these other species but, with one possible exception, all were alike in that koalas had failed to establish resident populations in them despite a continuing dispersal from the over-populated river flats. The one possible exception to this rule was the water or swamp gum E. ovata. Trees of this species were common in the vicinity of the

Rocky River Post Office where there were also four mature manna gums and two small plantations of manna gums at sapling and pole stages. Searches were regularly made in this area and koalas were often seen in the water gums, indicating that this species was to some degree an acceptable source of browse. One female, easily recognised from pelage characteristics, during a period of five months was consistently seen in a particular grove of E. ovata but nowhere else. She was occasionally absent from the grove and since the searches did not, at one time, include both all the manna gums and the water gums as well, it was possible that she was then in manna gum. However, this animal was never seen in the manna gums when searches were made of them, so it seemed very likely that one koala at least lived principally on water gum for a period of five months without recourse to nearby manna gum. These observations were in accord with the reports of the original introduction of koalas to Flinders Chase, when animals were confined for some time to water gums in this area, though they eventually escaped and deserted the water gums for the manna gums of the Rocky River. On the other hand, there are numerous trees of E. ovata in the region of the up-river end of the West Bay Track manna gums, but a number of searches here did not yield a single koala. Furthermore, the trees in this area carried abundant foliage and faecal pellets were scarce on the ground, despite the close proximity of the trees to the manna gums of the West Bay Track. The water gums here differ from those at the Rocky River Post Office in that they are mostly large, over-mature specimens, but such considerations were not important in considering the use of manna gums. From the point of view of an assessment of water gum it was unfortunate that there were no known groves remote from manna gums (see Figure 10), where sightings of koalas would have had more significance. It was also unfortunate that the damp habitat that water gum usually prefers encourages great thickets of Hakea and Acacia, which make searching difficult. The status of E. ovata therefore remains obscure.

The conclusion that eucalypt species on Flinders Chase, apart from manna and (possibly) swamp gum, were not ones favourable to the survival of koalas, centred attention on the relative physical well-being of resident and nomad sections of the population. In Figures 19-22, I presented in graphical form some gains in weight and increases in head length with age for a number of young koalas. Not all these animals had resident status throughout the interval covered by the graphs, but an assessment of nomad resident status as a variable affecting growth and weight gain is complicated since periods of non-residency were known with varying precision. In Figures 27 and 28 I have therefore re-introduced the data for only four females. In these graphs periods of non-residency are indicated by broken lines. There are a number of features to the graphs but it is noteworthy that the two females which were nomadic for a period had a reduced weight gain during the intervals including non-residency. This difference, however, was less obviously indicated in their growth, so it seemed possible that while non-residency might not affect growth as measured by head length, it could be reflected in poorer physical condition.

The thick pelt and robust build of a koala usually gives the impression of an animal carrying a lot of condition, but this is superficial for all the animals I have examined have proved to be lean; the ribs, vertebral column and pelvic girdle are always easily felt and seem to be covered only by the hide. This leanness may be generally characteristic of koalas since Bolliger and Shorland (1963) were unable to collect more than a few grams of fat from the abdominal cavities of several koalas which were animals of normal appearance killed in the wild. This invites the inference that koalas maintain a very critical digestive economy. Be that as it may, the leanness of koalas made it difficult to distinguish grades of condition and only one or two animals, when handled, were judged with any confidence to be 'wasted'. However, body weights and head length measures were available for a number of animals which were quite strictly known to be nomads or residents and these data gave a basis for comparing the physical condition of these two categories. A rigorous comparison was not straight-forward though, principally because these two divisions of the population had very different age-structures, and

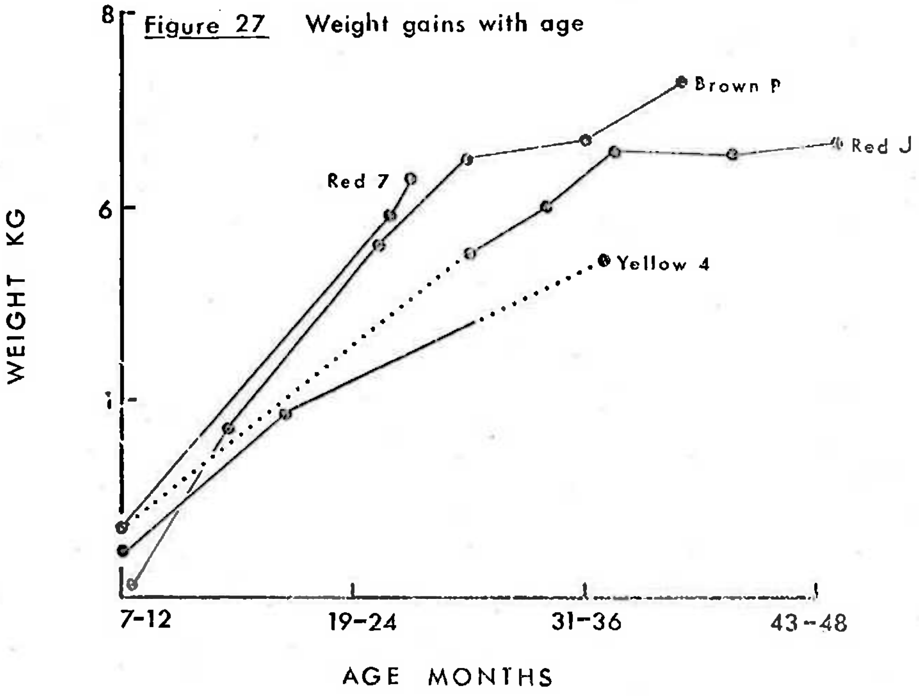


Figure 27 Weight gains with age

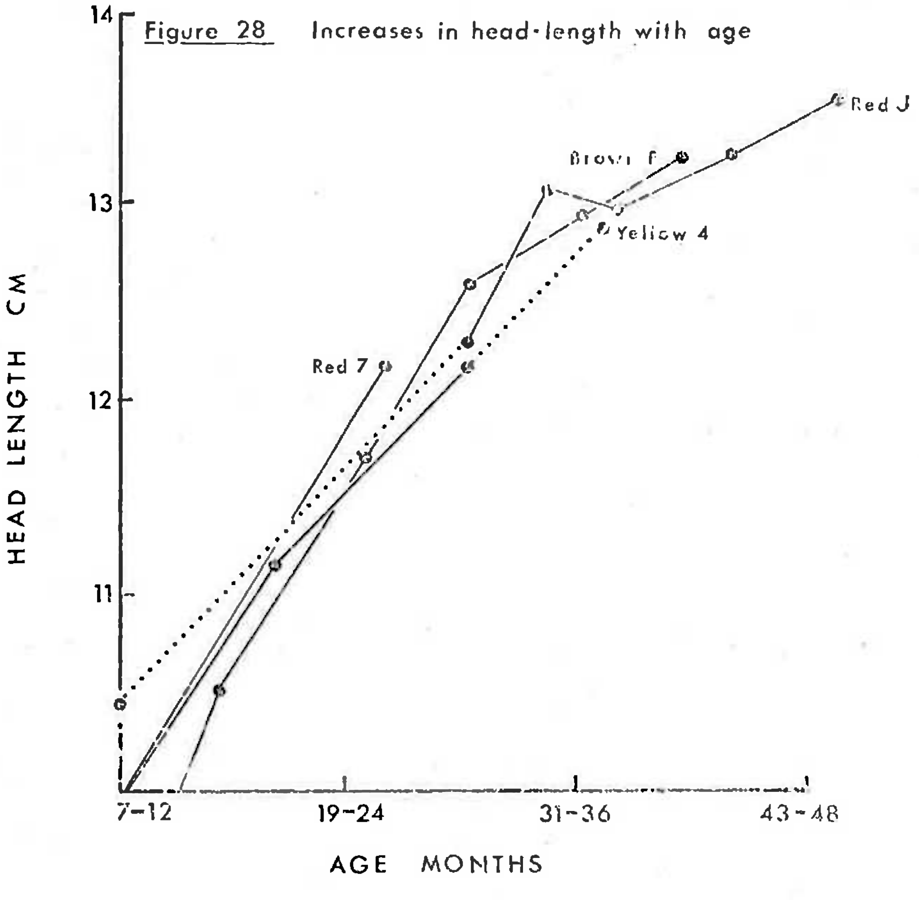


Figure 28 Increases in head-length with age

though the body-weight of an animal could be divided by its head-length to give a condition factor (C.F.) hopefully independent of body size, this factor was obviously still dependent on age. A matching procedure was therefore adopted in which, on the basis of sex, head-length, season when caught and physical appearance indicating age, nomads were matched with residents and the difference between the condition factors examined. Since many nomads, but few residents, were young animals in their third or fourth years of growth, six young female and twelve young male nomads could be matched against only one female and two male residents respectively, and in some cases extrapolations from the curves for gain in weight and increase in head-length, available for these residents, were necessary. In these cases the means of the values for the nomads and resident(s) were treated as single paired comparisons. In several other instances means were used when two nomads could be fitted to only one resident. Three mature animals caught both as nomads and residents were matched with themselves but several animals could not be accommodated. In this way data on 35 nomads was reduced to fourteen paired comparisons. These are given in Table 46, where n refers to the number of animals from which the condition factor (C.F.) was derived.

TABLE 46 'Condition Factors' - Nomads and Residents

RESIDENTS n	RESIDENTS C.F. (g/cm)	NOMADS n	NOMADS C.F. (g/cm)	Difference (D) (resident-nomad)
1	711.5	2	617.2	+ 094.3
1	487.7	1	422.1	+ 065.6
1	757.4	1	707.1	+ 050.3
1	636.0	1	587.6	+ 048.4
1	501.6	6	457.0	+ 044.6
1	706.8	1	666.7	+ 040.1
1	547.4	2	516.4	+ 031.0
1	705.7	1	690.8	+ 014.9
1	669.1	1	658.3	+ 010.8
1	546.4	2	537.9	+ 008.5
1	631.4	1	636.0	- 004.6
2	530.6	12	538.5	- 007.9
1	477.2	1	568.2	- 091.0
1	691.8	1	793.0	- 101.2

$$\bar{d} = + 14.6 \text{ g/cm}; \quad s_{\bar{d}}^2 = 212.5$$

It will be noted that although most of the differences in this table are positive, there are two very large negative values. These values are probably more extreme examples of the error embodied in this data arising from the difficulties of accurately measuring head lengths in a consistent manner, the hazards of using head length as an index of body size and the problem of matching animals for age. Notwithstanding, the distribution of differences is not sufficiently skewed to prohibit the use of normal theory ($g_1 = -1.0940$; $0.10 > P > 0.05$). The value of t was calculated to be unity. With 13 degrees of freedom, the one-tail probability of $t = 1.0$ lies between 10 and 20%. There is, therefore, no reliable evidence that the nomad section of the population differs from the resident section in physical well-being. Even so, a negative result need occasion no surprise. Firstly, though all nomads used in these comparisons were known quite strictly to be nomad when caught, in only a few cases was it known how long they had been so. Second and more importantly, many nomads were as frequent in manna gums as some residents and there was no evidence that residents differed in condition according to the varying degrees to which they used manna gums. This is illustrated in Table 47 where I have given the summer condition factors (C.F.) together with head-lengths (H.L.) and the proportion of time spent in the study area (P) for adult resident koalas from B. Indeed, the values for P and C.F. in Table 47 suggest, if anything, that higher condition-factors were associated with animals present in the manna gums least! (The association is however spurious: it is explained rather by the fact that the larger and older residents were present in the area least, see the values for head-length, than by better nutrition being associated with greater use of species other than manna gum).

TABLE 47 B: Condition Factors - Residents

MALES			FEMALES		
P	H.L. (cm)	C.F.(g/cm)	P	H.L. (cm)	C.F. (g/cm)
0.86	15.5	603.2	0.94	13.0	515.4
0.40	16.1	667.7	0.92	13.5	592.5
0.30	15.9	691.8	0.87	12.8	597.7
0.28	16.2	706.8	0.50	13.3	492.5
			0.49	14.3	629.4
			0.38	13.6	636.0
			0.17	14.4	597.2

P.	Proportion of time spent in the study area by adult resident koalas.
H.L.	Head-length.
C.F.	Condition Factor.

The koala's need for manna gum was apparent from the static distribution which was maintained despite a continuing dispersal. The absence of reliable evidence that this need was reflected in the physical well-being of animals using the manna gums to varying degrees is not subversive to the hypothesis suggesting a nutritional origin for the relationship between koalas and manna gum. But it does imply that what the manna gums provide is needed only at intervals, or that the spring, summer and early autumn seasons, when many animals are nomad, are not times when this need is acute.

5.3 Seasonal variation in behaviour

In places where weather patterns are seasonal, it is usual among many species of animals to show parallel changes in behaviour. These changes arise from either the direct influence of the weather itself or its indirect influence through the quality of food available to grazing animals. Kangaroo Island weather is markedly seasonal, but temperatures, regardless of season, are usually equable, with extremes of 0^{o}C and 38^{o}C being reached very rarely. The foliage of *Eucalyptus* spp. remains green throughout the year. Growth can occur at any season but is unusual during the winter. It is 'discontinuous' (and hence prolonged) in that only parts of the crowns of individual trees may show growth at any one time and, as an extension, in that particular trees may be showing vigorous growth while others close-by do not (c.f. pasture). There was, therefore, no *a priori* reason for expecting seasonal changes in the behaviour of koalas. However, the impression was gained early in the study that there were changes during the year in the behaviour of koalas which seemed to involve their preference for manna gum. The searches made of the study areas B, A_3 and $A_{1.19}$, in which all trees (of several species) within these areas were examined, and those made of A_1, in which, though all trees were not examined, a particular route was always followed, have provided unbiased data on the likelihoods at different times of the year of animals within the river-flats choosing to browse on manna gum, and of animals making over-night, inter-tree movements from manna gums (to another tree of any species). I have tabulated these data in Tables 48 - 52.

TABLE 48 B: Sightings of koalas in manna gum (as percent of total sightings) by year and month. Total sightings in brackets.

	1967	1968	1969	TOTAL
Jan.	67 (21)	87 (87)	79 (89)	81 (197)
Feb.				
Mar.		73 (104)		73 (104)
Apr.				
May	90 (29)	92 (91)		92 (120)
June			81 (77)	81 (77)
July	85 (55)	84 (148)		85 (203)
Aug.				
Sep.				
Oct.	80 (93)			90 92 ~~83~~ ~~(80)~~
Nov.				
Dec.	86 (88)			86 (88)
TOTAL	83 (276) 286	84 (430)	80 (166)	83 (872)

TABLE 49 A_3: Sightings of koalas in manna gum (as percent of total sightings) by year and month. Total sightings in brackets.

	1967	1968	1969	TOTAL
Jan.	70 (10)	69 (35)	73 (22)	70 (67)
Feb.			88 (17)	88 (17)
Mar.		90 (30)	88 (17)	89 (47)
Apr.			65 (17)	65 (17)
May	91 (45)	76 (29)	94 (17)	87 (91)
June			88 (41)	88 (41)
July	82 (34)	85 (52)		84 (86)
Aug.				
Sep.		86 (14)		86 (14)
Oct.	77 (30)	42 (12)		67 (42)
Nov.		67 (12)		67 (12)
Dec.	85 (26)	90 (21)		87 (47)
TOTAL	83 (145)	79 (205)	83 (131)	81 (481)

TABLE 50 A_1* and $A_{1.19}$: Sightings of koalas in manna gum (as a percent of total sightings) by year and month. Total sightings in brackets. Small numbers of total recordings given alone, sightings in manna gums added to column and row totals.

	1966	1967	1968	1969	TOTAL
Jan.		51 (55)*	57 (7)*	50 (22)*	51 (84)
Feb.					50 (4)
Mar.			29 (7)		45 (11)
Apr.		66 (38)*			69 (42)
May	77 (181)*	88 (8)*	86 (7)	85 (34)*	79 (230)
June					100 (5)
July			69 (29)*		69 (29)
Aug.	68 (25)*				68 (25)
Sep.			77 (22)*		77 (22)
Oct.					100 (2)
Nov.					80 (5)
Dec.		61 (36)*	57 (14)*		62 (53)
TOTAL	76 (206)	60 (137)	68 (94)	75 (75)	70 (512)
Mean	73	67	68	68	68

TABLE 51 B: Recorded over-night, inter-tree movements from manna gum, as a % of the total possible movements from manna gum, by year and month. 'Total possible movements' in brackets.

	1967	1968	1969	TOTALS
Jan.	88 (8)	65 (43)	82 (60)	76 (111)
Feb.				
March		81 (62)		81 (62)
Apr.				
May	67 (15)	70 (74)		70 (89)
June			74 (57)	74 (57)
July	69 (32)	68 (96)		68 (128)
Aug.				
Sep.				
Oct.	68 (44)			68 (44)
Nov.				
Dec.	73 (51)			73 (51)
TOTALS	71 (150)	71 (275)	78 (117)	72 (542)
Mean				73

TABLE 52 A_3: Recorded over-night, inter-tree movements from manna gum, as a % of the total possible movements from manna gum, by year and month. 'Total possible movements' in brackets.

	1967	1968	1969	TOTALS
Jan.	100 (3)	94 (17)	86 (14)	91 (34)
Feb.			86 (14)	86 (14)
Mar.		77 (26)	75 (12)	76 (38)
Apr.			91 (11)	91 (11)
May	30 (37)	65 (20)	50 (14)	44 (71)
June			65 (31)	65 (31)
July	56 (25)	60 (42)		58 (67)
Aug.				
Sep.		55 (11)		55 (11)
Oct.	72 (18)	80 (5)		74 (23)
Nov.		100 (6)		100 (6)
Dec.	63 (16)	81 (16)		72 (32)
TOTALS	52 (99)	72 (143)	73 (96)	66 (338)
Mean	64	77	76	74

TABLE 53 A_1* and $A_{1.19}$: Recorded over-night, inter-tree movements from manna gum, as a % of the total possible movements from manna gum, by year and month. 'Total possible movements' in brackets. Small numbers of total movements given alone, movements added to column and row totals.

	1966	1967	1968	1969	TOTALS
Jan.		94 (18)*	3	1	95 (22)
Feb.				2	100 (2)
Mar.			2	2	100 (4)
Apr.				3	67 (3)
May	67 (51)*		4		67 (55)
Jun.				3	67 (3)
Jul.			1		100 (1)
Aug.	47 (19)*				47 (19)
Sep.					
Oct.			1		100 (1)
Nov.			3		67 (3)
Dec.				2	50 (2)
Totals	61 (70)	94 (18)	86 (14)	77 (13)	71 (115)
Mean					78

Inspection of these tables suggests a difference between the months of January (mid-summer) and May (early winter). It seems that during May there is a slightly increased probability of sighting koalas in manna gums (as opposed to other species within the river flats) and a decreased probability of observing over-night, inter-tree movements from manna gum i.e., koalas (in manna gums) are more likely to remain for several days in the one tree. Other months of the year are not so well represented, but the figures indicate a sudden change in May followed by a slow recovery to January levels, which are maintained through to March at least. The data also show -

(1) little or no differences 'between years' apart from that explained by seasonal differences in koala behaviour and the relative contribution of observations from different seasons.

(2) the considerable use made at times of trees of other species (of which the great majority are pink gum). The lowest value, for a substantial number of sightings (55), is only 51% in manna gum. It was made in A_1 during January of 1967. Nonetheless, since the ratio of manna gums to trees of other species in this area is 1 : 1.8, this value still, in all probability, represents a strong preference for manna gum ($X_1^2 = 5.0$; $0.05 > P > 0.02$).

(3) little or no differences between the three areas with respect to the mean over-all probability of over-night, inter-tree movement from manna gums (0.73, 0.78, 0.74).

(4) an evident difference between A_3 and B, on the one hand, and A_1 on the other, in the over-all probability of sighting a koala in a manna gum rather than a tree of some other species. This difference may be attributed to:

   (4a) a smaller proportion (1 : 1.8) of manna gums in A_1 than in B (1 : 1.5) or A_3 (1 : 1).

   (4b) a greater incidence and severity of defoliation of manna gums in A_1.

In Tables 54, 55 and 56 I have tested for heterogeneity in the over-all monthly totals by means of chi-square. Because of the difference between A_1 and the other areas in the probability of sighting a koala in a manna gum, I have tested these data separately, but I have pooled all other data.

TABLE 54 A_3 and B: Sightings of koalas in manna gum (%) by months. Total sightings in brackets. Small values of total sightings in separate column.

Jan.		78 (264)
Feb.	88 (17)	
Mar.		78 (151)
Apr.	65 (17)	
May		90 (211)
June		83 (118)
July		84 (289)
Aug.		
Sep.	86 (14)	
Oct.		75 (125)
Nov.	67 (12)	
Dec.		87 (135)
TOTAL	82 (1,353)	

$X^2_{10} = 25.2 \quad P < 0.01$

TABLE 55 A_1 and $A_{1.19}$: Sightings of koalas in manna gum (%) by months. Total sightings in brackets. Small values of total sightings in separate column.

Jan.		51 (84)
Feb.	50 (4)	
Mar.	45 (11)	
Apr.		69 (42)
May		79 (230)
June	100 (5)	
July		69 (29)
Aug.		68 (25)
Sep.		77 (22)
Oct.	100 (2)	
Nov.	80 (5)	
Dec.		62 (53)
TOTAL	70 (512)	

$X^2_{9} = 33.7 \quad P < 0.001$

Addendum: TABLES 54 and 55

The Chi-squares given in TABLES 54 and 55 are Heterogeneity Chi-squares (see Snedecor and Cochran, 1967) which in these cases have the same numerical values, but one degree of freedom less, as the sums of the individual Chi-squares calculated for each row (class) of data. The individual Chi-squares were calculated for the absolute frequencies in each class. The expected frequencies of these Chi-squares were calculated from the total number of sightings in each class and the absolute frequencies of the table totals. Classes were pooled, prior to the calculation of the Chi-squares, only when expected values were less than unity.

TABLE 56 A_1 and $A_{1.19}$, B and A_3: Recorded over-night, inter-tree movements (%), from manna gum, by months. Total recordings in brackets. Small values for total recordings given in separate column.

Jan.		81 (167)
Feb.	88 (16)	
Mar.		80 (104)
Apr.	86 (14)	
May		60 (215)
June		70 (91)
July		65 (196)
Aug.	47 (19)	
Sep.	55 (11)	
Oct.		71 (68)
Nov.	89 (9)	
Dec.		72 (85)
TOTAL	72 (995)	

$$X^2_{11} = 38.8 \qquad P < 0.001$$

I have followed Snedecor and Cochran (1967) p. 235 in pooling classes within each table only when the 'expected value' was less than one. The values of chi-square can all be regarded as highly significant. Inspection of the tables suggests the distinctiveness of the 'winter' months (May, June and July) and May in particular. This is borne out by the data in Tables 57, 58 and 59 where I have compared values derived from summing 'sightings' and 'recordings' made during the principal 'summer' (December, January and March) and 'winter' (May, June and July) field trips. The values of chi-square are again all significant, so it can be concluded that the early winter, and most especially the month of May, is a time when there is an increased probability

TABLE 57 B and A_3: Sightings of koalas in manna gum (%), summer and winter. Total sightings in brackets.

Summer	(Dec., Jan. and March)	80 (550)
Winter	(May, June and July)	86 (618)

$X_1^2 = 6.4 \quad 0.02 > P > 0.01$

TABLE 58 A_1 and $A_{1.19}$: Sightings of koalas in manna gum (%), summer and winter. Total sightings in brackets.

Summer	(Dec. and Jan.)	55 (137)
Winter	(May and July)	78 (252)

$X_1^2 = 21.6 \quad P \ll 0.001$

TABLE 59 A_1 and $A_{1.19}$, B and A_3: Recorded over-night, inter-tree movements (%), from manna gum, summer and winter. Total recordings in brackets.

Summer	(Dec., Jan. and March)	79 (356)
Winter	(May, June and July)	64 (502)

$X_1^2 = 22.0 \quad P \ll 0.001$

of observing koalas within the river-flats in manna gums, rather than other species, and a decreased probability of observing over-night, inter-tree movements from manna gums. This 'winter behaviour', however, has at least three other, so far unremarked features. They are:

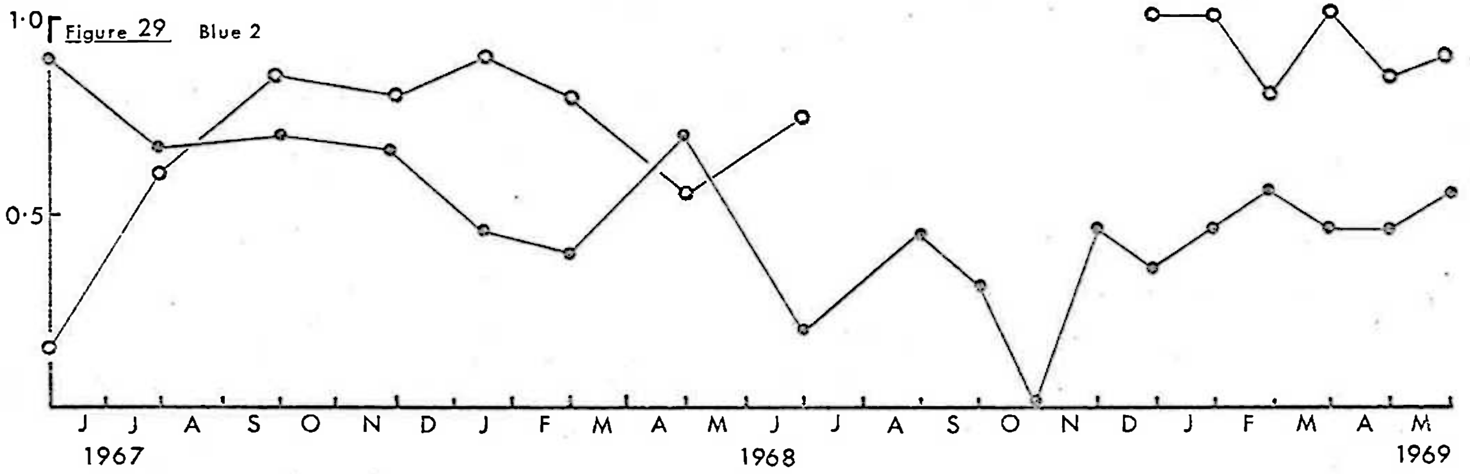
(1) Resident koalas showing 'winter behaviour' were not only making greater relative use of manna gums within the river flats, but they were also present within the river flats more frequently. However, there was no corresponding seasonal change in the numbers of koalas to be seen. This was because nomad koalas were rare or absent during this part of the year (Table 29).

(2) There was a great deal of variation between koalas in the timing and degree of change from normal to 'winter behaviour'. Thus some animals might show 'winter behaviour' while others didn't. Because of this variability the phenomenon was far more obvious when following the behaviour of individuals in the field than from contemplating the pooled data in which differences between individuals tended to cancel out.

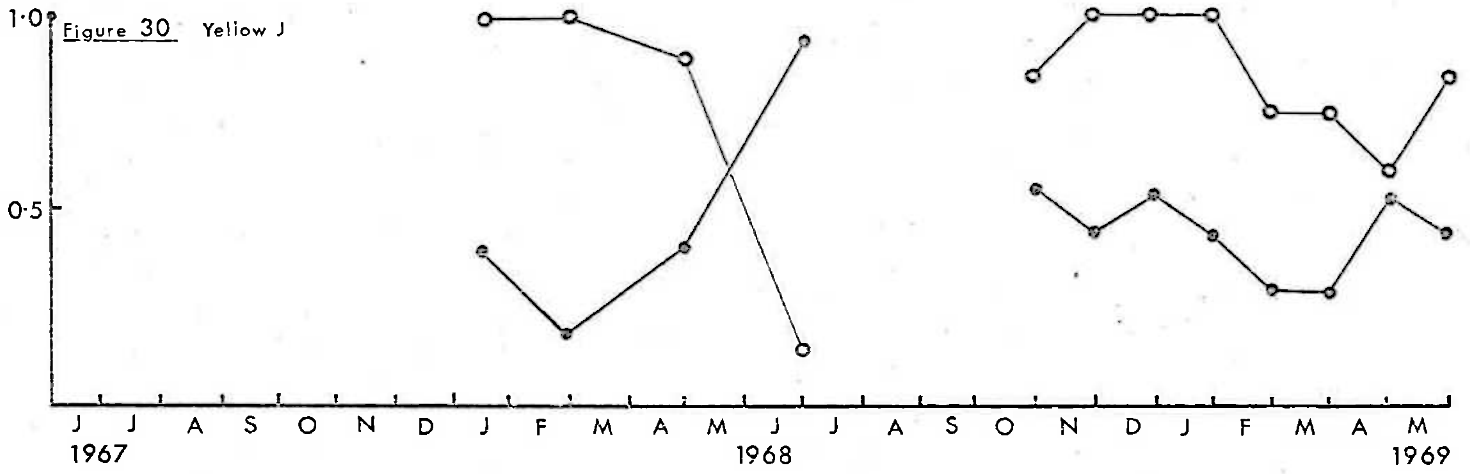
(3) The individual variation in the degree of change was in part due to the significance of age: The 'winter behaviour' pattern was shown by animals of all ages, but the very large changes characteristic of animals in their second year of growth were much less common among older animals.

These last two features are illustrated in Figures 29, 30 and 31. In Figures 29 and 30 I have presented in graphical form for BLUE 2 and YELLOW J (young born in A_3 in 1966 and 1967) estimates of the proportion of time these animals were in manna gum ('manna gum'), and estimates of the frequency with which they were changing trees, ('movement'). The several gaps in these records were occasioned in Figure 29 by the failure of BLUE 2 to remain within the study area sufficient days at a time during field trips of relatively short duration for tolerable estimates of 'movement' to be made, and in Figure 30 by the temporary removal of YELLOW J from the area for another purpose.

The graphs clearly illustrate marked individual differences in the timing and degree of change. Thus in 1968 BLUE 2 showed 'winter behaviour' most strongly in May, whereas this was delayed in YELLOW J until July. In the progressive reductions in the degree of change, the graphs also suggest a moderation with age. In Figure 31 I have given the mean values of the probability of sighting a koala in manna gum, and the probability of observing over-night, inter-tree movement from manna gum, separately for four 1967 pouch young, six 1966 pouch young and twelve 'adults', over the period January to July, 1968. These animals are those of the populations using B and A_3 which were observed on each of the field trips covering this period. These graphs (in Figure 31) show:



Figures 29 & 30 Seasonal variation in behaviour – Blue 2 & Yellow J



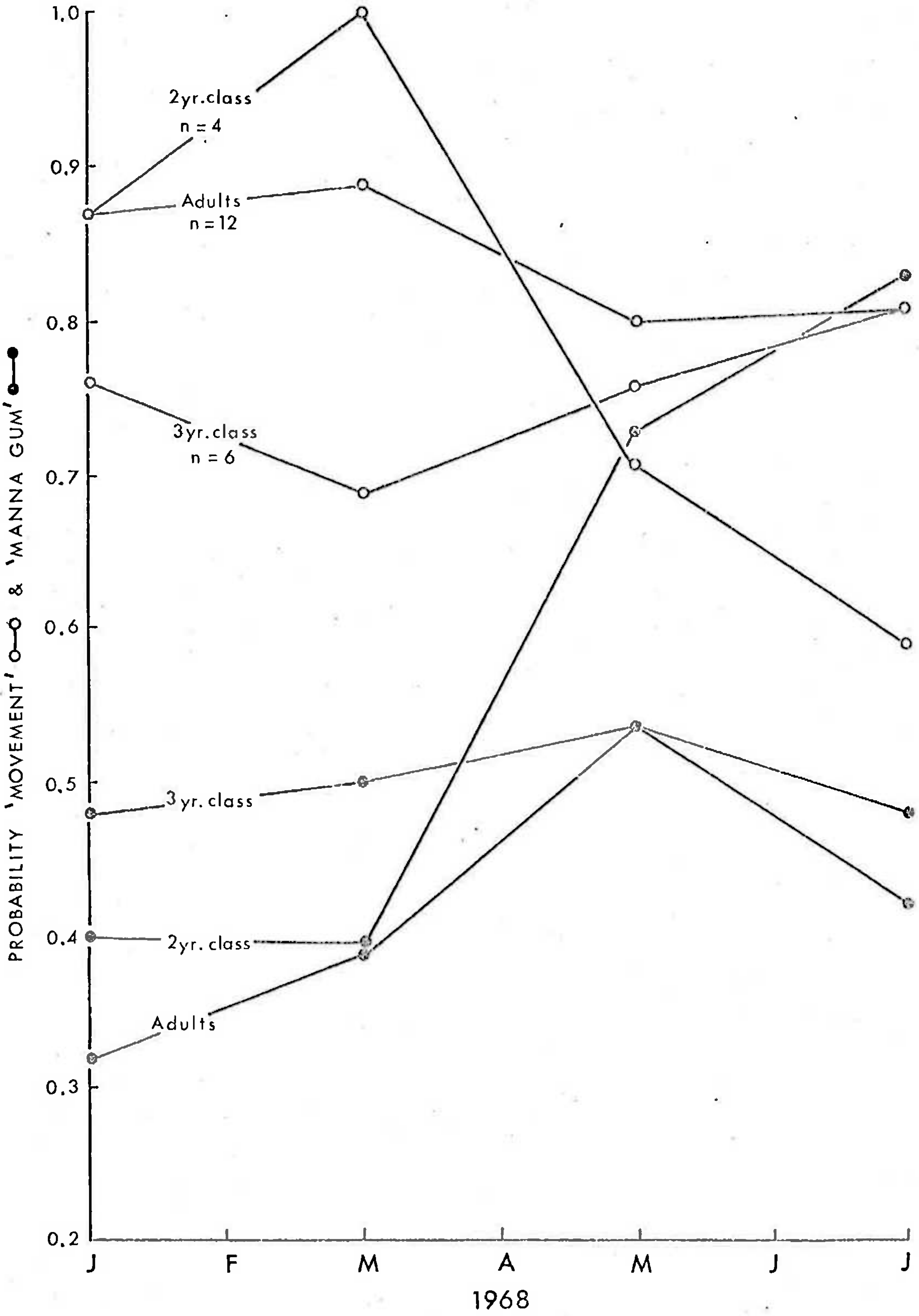


Figure 31 Seasonal variation in behaviour ---- adults and young, areas A_3 and B.

(1) Very considerable changes in the average behaviour of those animals in their second year of growth.

(2) The same pattern of change (albeit a peak in May rather than July) in the average behaviour of adults, but developed to a much smaller degree.

(3) A near absence of any indication of change in the average behaviour of koalas in their third year of growth. Of course, animals in this class are subjected to considerable and changing social pressures, so it is hard to assess the significance of this result.

(4) The considerable use that is made of other species of eucalypts even during 'winter behaviour' (the plotted values for use of manna gums take into account absence from the river-flats when the animals are feeding on other species).

There seemed to be two possible explanations for 'winter behaviour'. The first was that the attraction of manna gums for koalas was increased - and hence koalas were more likely to remain within one for several days at a time and more likely, if they did choose to leave, to seek out another of the same sort. The alternative was that the increased usage of the relatively few manna gums which constitute a koala's 'home range', followed, in a passive way, a reduced mobility brought about by something unrelated to the relative attractiveness of Eucalyptus sp. This second alternative was very simply tested by considering the probability of over-night, inter-tree movements within the river-flats from trees belonging to species other than manna gum. Data is given in Table 60 (c.f. Table 56). The value of chi-square is non-significant, so there is no evidence that the likelihood of a koala moving out of a pink gum, for instance, changes with the seasons. This cannot be plausibly squared with an hypothesis attributing reduced mobility about manna gums to a general cause. And in view of the fact that some animals were observed to increase their use of manna gums during early

TABLE 60 A_1 and $A_{1.19}$, B and A_3: Recorded over-night, inter-tree movements (%), from pink gums, sugar gums and *E. rugosa*, by months. Total recordings in brackets. Small values for total recordings given in separate column.

Jan.			94	(69)
Feb.			100	(24)
Mar.	90	(10)		
Apr.	80	(5)		
May			92	(39)
June			83	(18)
July			97	(33)
Aug.	100	(1)		
Sep.	100	(2)		
Oct.			86	(21)
Nov.	67	(3)		
Dec.			94	(16)

TOTAL 93 (241)

$X^2_7 = 5.3 \qquad 0.70 > P > 0.50$

winter without reducing their mobility at all, there is little doubt that the explanation of 'winter behaviour' lay in an increased attraction of manna gums for koalas.

A number of hypotheses can be advanced to explain this increase in manna gum's attraction for koalas. It is tenable, for example, that a gradual change in the quality of all browse species as a result of the ageing of the annual shoot might bring about a nutritional stress which would make existing differences between species more critical; or such a nutritional stress might be precipitated by the rigours of winter weather. However, since 'winter behaviour' was common or typical only during May or early June it is unlikely to have been simply related to the operation of any such enduring seasonal factors. Instead it seems necessary to postulate a change in the quality of browse peculiar to this time of the year, with manna gum becoming more favourable or other species less so. The variability between individual koalas in the timing and degree of the change in their behaviour and, particularly, the importance of the age of animals, argue involvement of the koala's 'physiological state'.

Seasonal changes of the kind described here in the behaviour of koalas, have been observed elsewhere. The curator (J. McNamara) of 'Koala Park', Sydney, says that koalas maintained on a staple diet of E. punctata, but offered a variety of other species, attack such species least readily during the winter months. Fleay (1937) reported that the appetite of koalas in the Melbourne Zoo was 'more than usually fastidious' ... 'over 6-7 weeks in early to mid-winter'. Remarkably, however, this fastidiousness sometimes showed itself in a rejection of the staple food species, E. viminalis. However, Fleay contrasts this with the behaviour of koalas in the wild at the same season, which 'do not refuse manna gum', although they become 'lethargic and dormant in the cold winter days of June' (this presumably implies that koalas in the wild were observed to remain for days at a time in particular trees and, see above, in manna gums at that).

5.4 Seasonal variation in condition

The re-capture of marked koalas revealed some changes in the physical condition of some koalas, as measured by body weight. Some of these differences are illustrated in Figure 32 where the weights of six adult koalas which were caught a number of times during consecutive years are presented graphically. It is apparent from this Figure that the two females BLUE J and BROWN R underwent a cyclic variation in weight with maximums occurring in the winter and minimums in the summer. The weights of the other two females, RED Q and RED Y, are consistent with this cycle if the gains were made quite sharply in the early winter. The values for the two males, YELLOW 5 and BROWN W, are also consistent with this cycle but indicate that gains may continue till spring. This is not anomalous since the graph for BROWN W, in which the winter-summer downward movement of the cycle is represented in 1967-68 by a drop in

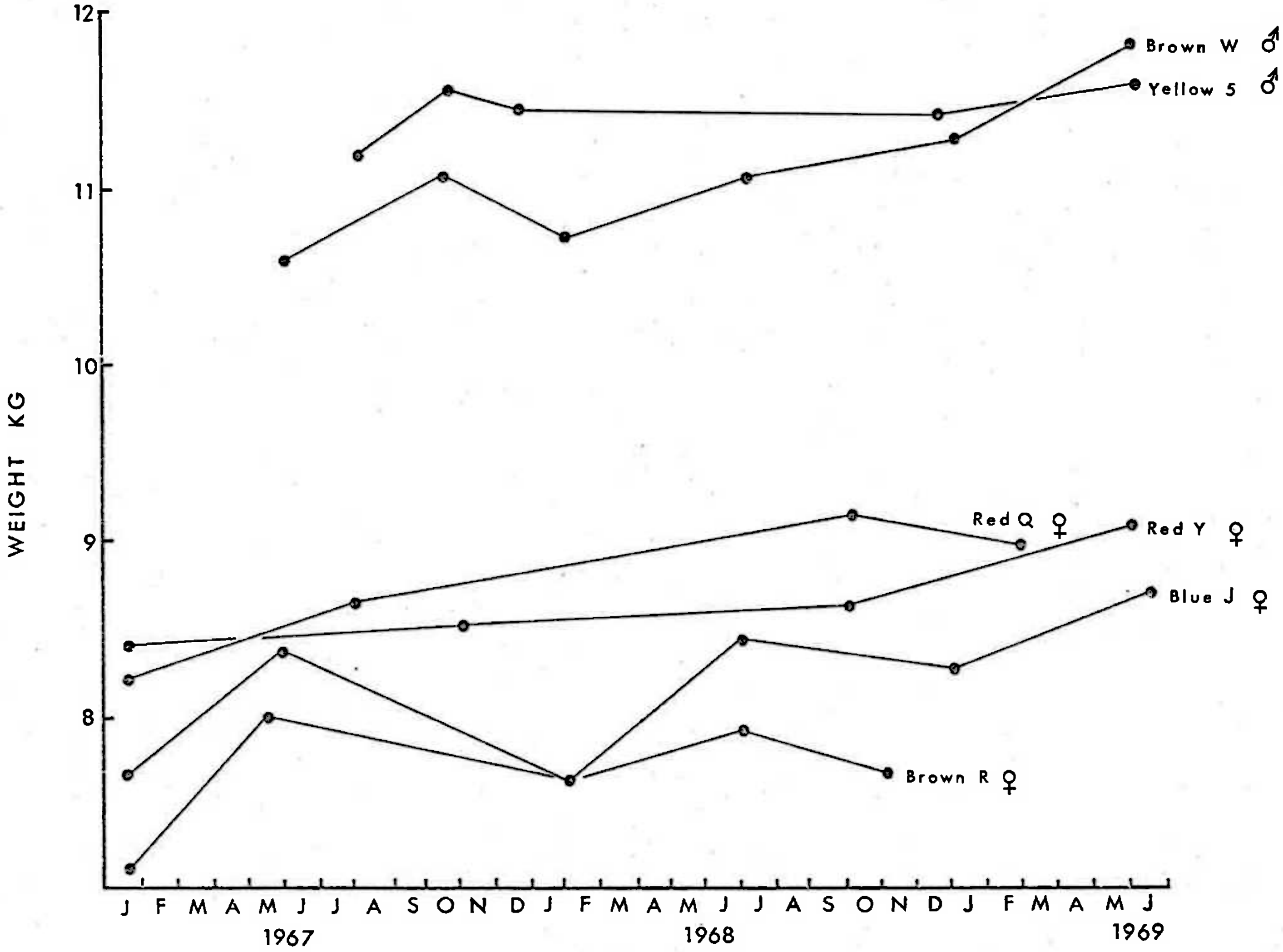


Figure 32 Seasonal variation in weight of adult koalas

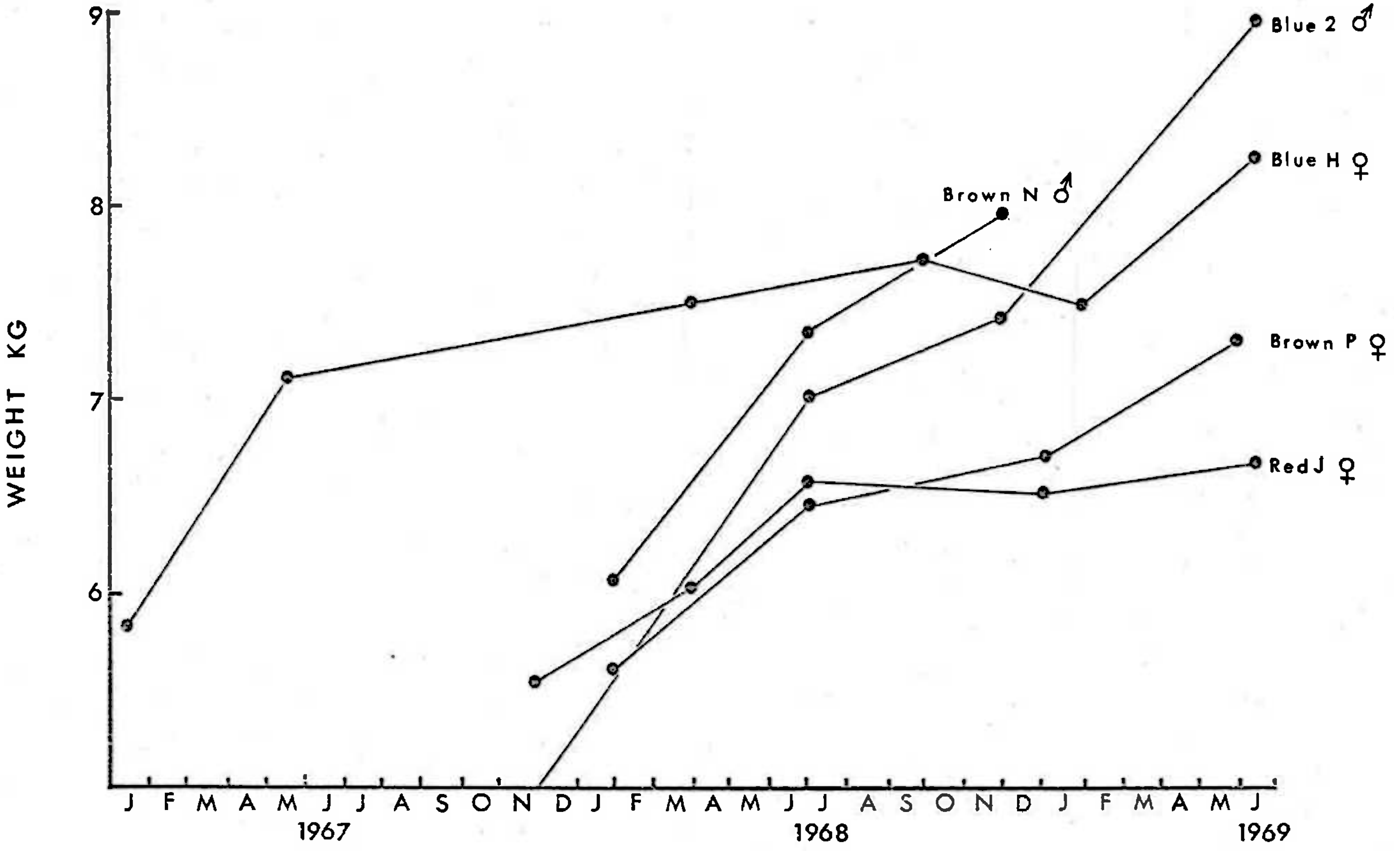


Figure 33 Seasonal variation in weight gains of young koalas

weight, but in 1968-69 is represented by a reduced rate of weight gain, shows that more than one variable is involved. The data therefore suggests a rather variable seasonal cycle in condition which, in some animals, may be the result of quite sudden gains in the early winter. This cycle was also indicated in those animals caught a number of times during their third and subsequent years of growth, but since it is here necessarily a question of rate of weight gain, this data is given separately in Figure 33.

The cycle was not obvious in the growth of animals during their second year (Figures 16 and 18). Koalas at this stage seemed to gain weight quite steadily, though this implies that they gained proportionately more weight from summer to winter (the first half of the second year) than from winter to summer.

Since this cycle was apparent in males as well as females, it may be presumed to be to some extent independent of breeding; though this is likely to be an important variable affecting condition which would stress females most severely in the late spring, when the absolute growth of young is greatest while the young are still suckling to an important extent. The young are usually fully weaned by the middle to late summer.

There was some additional evidence for this cycle. Although weight changes shown by animals caught only twice during the one year were ambiguous, since the cycle may have been affecting a rate of weight gain or loss, three of five young animals in their third or fourth years showed such excellent weight gains between summer and winter that it seemed unlikely that they would have been maintained for long. Further, the heaviest animals recorded were caught during the winter.

I have therefore concluded that while there may be a number of variables important in relation to condition and which may act independently there is good evidence that a seasonal cycle is involved. There are a number of explanations that can be advanced for such a cycle. It may relate to the increased consumption of manna gum characteristic of the winter season, or it may be referred to a more favourable energy balance associated with the reduced activity also typical of the winter season. The cycle could be involved with ageing foliage and a consequent greater dry matter intake or it might reflect the influence of weather on appetite. It would also be consistent with a seasonal change in the nutritive value of the browse.

5.5 Growth of eucalypts

The conclusion that the quality of the browse carried by the eucalypts was the cause of the preferences displayed by koalas, admitted the possibility that the koalas' responses were governed by differences in the palatability or nutritive value of leaves at different ages, associated with contrasting growth patterns in the various species.

Jacobs (1936, 1955) has described the growth habits of eucalypts. Buds do not require a resting stage and shoots are capable of growing almost indefinitely but drought, frost, desiccating winds and insect attack bring about interruptions to growth. In South Australia the spring, summer and autumn are the seasons in which the annual growth occurs. Usually two or three successive annual shoots are represented in the crown and the growth history of shoots can often be reliably traced by detecting points of die-back marked by axillary rings and from consideration of the appearance of the leaves.

In January and April of 1967 attempts were made to quantitatively assess and compare the age structues of the foliage carried by trees of five species - E. viminalis, E. cladocalyx, E. fasciculosa, E. rugosa and E. diversifolia. In addition it was thought that the defoliated manna gums relying on the development of epicormic shoots might be presenting a different pattern of growth to those in which the primary crown (of terminal shoots) was relatively intact. So the manna gums were divided into two groups: the 'epicormic' manna gums (Me) and the 'terminal' manna gums (Mt). For convenience, these two classes of manna gum are called 'species' in the following discussion. In January four trees were selected from each of two species and two trees were selected from each of the remaining four species. This difference in the number of trees was forced by labour considerations. In April two trees from each species were selected, as before, by a random method from all trees of the species growing within a large part of the West Bay Track river flats and margins. The populations sampled were restricted to trees at later than the pole stage of growth. Four foliage samples were taken from each tree. In January each sample was made about double in size. Samples were selected by progressive random selection of one half of the foliage based on the division of the foliage into equal parts by visual estimation. The growth history of each shoot was studied and the leaves it carried then assigned to three categories termed young, mature and old. 'Young' leaves were carried on growing tips and had the characteristic colour, texture and appearance of the newly unfolded leaf: 'mature' leaves were still near perfect in appearance but had lost the characteristics of the young leaf, while 'old' leaves had a rough texture, dark colour and other blemishes. This categorization was adopted in preference to one based on the growth history of the shoots since this latter was at times difficult to interpret and seemed of less relevance. However, since mostly only three growing seasons were represented, in January the categories of young, mature and old corresponded to the current and two preceding growing seasons.

The data were converted to proportions and then transformed by the arcsine proportion of radians, when the error distribution was found normal and the variances homogenous. Interaction between 'trees' and 'leaf category' in several species precluded a two-way classification, so a nested single classification Analysis of Variance was carried out. The results are given in Tables 61 - 66 and are summarized in Tables 67 and 68.

TABLE 61 Comparisons of growth among Eucalyptus spp. - proportion of young leaves:

Jan. 1967

	D.F.	S.S.	M.S.	F Value	P
Species	5	2.9387	0.5877	2.07	> 0.10
Trees	10	2.8371	0.2837	3.43	< 0.005
Samples	48	3.9634	0.0826		

TABLE 62 Comparisons of growth among Eucalyptus spp. - proportion of mature leaves:

Jan. 1967

	D.F.	S.S.	M.S.	F Value	P
Species	5	3.3968	0.6794	3.98	0.05 > P > 0.025
Trees	10	1.7073	0.1707	2.11	< 0.05
Samples	48	3.8812	0.0809		

TABLE 63 Comparisons of Growth among Eucalyptus spp. - proportion of old leaves:

Jan. 1967

	D.F.	S.S.	M.S.	F Value	P
Species	5	1.8285	0.3657	4.36	0.025 > P > 0.01
Trees	10	0.8384	0.0838	2.21	< 0.05
Samples	48	1.8243	0.0380		

TABLE 64 Comparisons of Growth among Eucalyptus spp. - proportion of young leaves:

April 1967

	D.F.	S.S.	M.S.	F Value	P
Species	5	0.7866	0.1573	1.21	> 0.25
Trees	6	0.7777	0.1296	6.86	< 0.005
Samples	36	0.6801	0.0189		

TABLE 65 Comparisons of Growth among Eucalyptus spp. - proportion of mature leaves:

April 1967

	D.F.	S.S.	M.S.	F Value	P
Species	5	2.3927	0.4785	3.65	0.10 > P > 0.05
Trees	6	0.7863	0.1310	2.17	> 0.05
Samples	36	2.1796	0.0605		

TABLE 66 Comparisons of Growth among Eucalyptus spp. - proportion of old leaves:

April 1967

	D.F.	S.S.	M.S.	F Value	P
Species	5	2.2850	0.4570	2.65	0.25 > P > 0.10
Trees	6	1.0331	0.1722	2.60	< 0.05
Samples	36	2.3852	0.0663		

TABLE 67 Comparisons of Growth among Eucalyptus spp. - summary of Tables 61, 62 and 63 (Jan. 1967)

	Young	Mature	Old
Species	$P > 0.10$	$0.05 > P > 0.025$	$0.025 > P > 0.01$
Trees	$P < 0.005$	$P < 0.05$	$P < 0.05$

TABLE 68 Comparisons of Growth among Eucalyptus spp. - summary of Tables 64, 65 and 66 (April 67)

	Young	Mature	Old
Species	$P > 0.25$	$0.10 > P > 0.05$	$0.25 > P > 0.10$
Trees	$P < 0.005$	$P > 0.05$	$P < 0.05$

The difference between species in January in the proportions of mature and old leaves had two sources. In the case of the two mallees, *E. rugosa* and *E. diversifolia*, included in the examination, it was noted that many buds on leaf bearing twigs developed and instead of the production of a further single dominant shoot, a number of competing shoots developed. Most of these shoots did not survive but this meant that during the growing season these trees might produce relatively as many new leaves as others even if there was a much smaller real turnover of leaves in the crown. The other source was related to the association between growth and leaf-fall. In this case those trees that had begun growth most recently carried more foliage and that with a greater proportion of old leaves since the main leaf-fall had yet to occur. The young leaves carried by such trees were still mostly very small and it would have been useful to weigh the different categories.

Apart from these differences, this analysis on samples collected in about the middle and end of the annual growing season did not suggest that there were any marked differences in growth responses or ageing processes of the leaves between the six 'species', *E. cladocalyx*, *E. fasciculosa*, *E. rugosa*, *E. diversifolia*, *E. viminalis* (Mt) and *E. viminalis* (Me).

Following this analysis, regular qualitative observations were made of the growth of all the species on Flinders Chase. These observations did not reveal any considerable differences between species. They did however confirm that there are commonly large differences between individual trees of one species in the timing and intensity of new growth. These intra-species differences are presumably brought about by accidents of light, shelter, soil moisture etc. As such, growth differences can sometimes be observed in trees growing side by side. It was very striking that such differences did not apparently bear any relation to the relative use made of trees by koalas.

These conclusions were supported by observations on koalas feeding in captivity. Because of their manner of feeding (Part 1 of this section) koalas, when given vigorously extending shoots, fed largely on young leaf material. But, if by chance they began to feed on a part of the shoot bearing only old leaves, they were as likely to persist as they were when young leaves were involved. Animals diffident about feeding were more likely to accept young leaf than old, but hungry animals did not seem to make any selection. This was confirmed in a single feeding trial in which four koalas were each offered, in a container separate from other foliage provided, two shoots taken from the one manna gum. The shoots were of similar size and carried about the same number of leaves. But one of the pair offered carried only leaves from the current growing season. The other carried only leaves from a previous growing season which, in comparison, were large, coarse, leathery and scarred. Three of the animals ate from both shoots; their scores were 75,143 and 171 leaves. The proportions of young leaves in these totals were 0.20, 0.58 and 0.50.

5.6 Koalas and Manna Gum 2

In Part 2 of this section it was argued that the static distribution of koalas which was maintained despite a continuing dispersal implied that the koalas not only preferred manna gum but also needed it. However, it was also noted that the absence of reliable evidence that animals using the manna gums to varying degrees differed in physical well-being during the spring, summer and early autumn, admitted the possibility that the need was absent during these times of the year or indicated that it was one which could be satisfied at intervals, in which case it might be termed 'chronic' rather than 'acute'. The observations on dispersal given in Section 3, in which it was made clear that during the summer a few koalas may occasionally be seen at very considerable distances from the manna gums, were in accord with these conclusions.

In Part 3 of this section, a capricious but well marked increase in the manna gum's attraction for koalas during the late autumn and early winter was described. A satisfying conclusion would be that during this season koalas experience a need for manna gum or, if that need is always present, a need to a more acute degree. The evidence for this conclusion is indirect but the results of an experiment relating to colonization of manna gums were consistent with this hypothesis.

The area termed $A_{1.19}$ is indicated in Figure 4. It is an isolated group of 11 manna gums, 7 pink gums and 3 sugar gums, about half way between A_1 and B. Searches made of this area in June and August of 1966, January, April and December of 1967 showed it to be part of the home ranges of an adult male and female resident, and these animals were commonly seen in the area. In January of 1969 the resident female was seen. This female was caught and released at Scotch Thistle Flat. Thereafter, the area was regularly searched for a number of days at a time. In Table 69 I have summarized the results of the searches made subsequent to January 1968. The first column gives the number of days on which searches were made; the second gives the number of different koalas seen and the third and fourth give, respectively, the average and range for the number of days on which individuals were seen.

TABLE 69 Colonization of Manna Gums, $A_{1.19}$

	No. Days	No. Koalas	Av. No. Days Individual Koalas seen.	Range No. Days Individual Koalas seen.
Mar. 1968	7	4	1.3	1 - 2
May 1968	7	3	3.7	1 - 5
July 1968	6	1	1	1
Sept. 1968	5	1	1	1
Oct. 1968	5	2	1	1
Nov. 1968	6	4	1.3	1 - 2
Dec. 1968	5	0	0	0
Jan. 1969	6	1	2.0	2
Feb. 1969	7	1	4.0	4.0
Mar. 1969	6	3	1.3	1 - 2
Apr. 1969	5	3	1.3	1 - 2
May 1969	5	0	0	0
June 1969	6	1	4.0	4.0

As can be seen in the last two columns of this table, there were only three occasions when koalas may have been judged to have assumed occupancy. The first of these was in May of 1968. The two individuals concerned were young male nomads which had not previously been seen in the area. They were caught and released elsewhere. The second was in February of 1969 and involved an aged male which was caught and then released back in the area. This animal was not seen here again but was subsequently seen a number of times in the nearest part of A_1. The last occasion was in June of 1969. The koala seen was again a young, truly nomad male. Therefore, of the four possible 'colonizations' of this area, three took place in the early winter and the fourth was in some question since the animal concerned was thought to already maintain a home range.

This is in accord with the finding that the early winter is a time when manna gum is likely to have an increased attraction for koalas.

It is, however, stronger evidence than the quantitative changes in behaviour described in Part 3 of this section, since it concerns a qualitative change in behaviour. As such it favours the view that the koalas which 'colonized' the manna gums of $A_{1.19}$ did so because of a definite seasonal need. There are several other observations that are relevant to this point. The first is that while a very few koalas were occasionally seen far from the manna gums, all these sightings were made during the summer. The absence of further sightings of such animals during the winter could be most simply explained by their being dead. The second arises from the importance of age in seasonal variation in behaviour. The larger response of the young suggests an increased attraction for manna gum critically related to nutrition.

The relationship between koalas and manna gum on Flinders Chase indicated by this study may be summarized as follows. Manna gum is the most preferred browse species and the failure of koalas to establish persistent populations elsewhere, despite a continuing dispersal from the over-populated manna gum stands, establishes that it is necessary for survival. Notwithstanding, there is no reliable evidence that it is indispensable during the spring, summer or early autumn, though the need for it may be chronic. It is always very attractive to koalas, as is indicated by the way nomads seek it out. However, during the late autumn and early winter, manna gum is likely to be even more eagerly sought and numerous observations are consistent with the idea that there is a more acute need for the manna gum during this season.

It is not known whether the manna gum's attraction for koalas and the seasonal variation in its attractiveness, the chronic or acute need for this species, the bias shown for particular trees of one species and the non-equivalence of other species, are all responses to a single variable quality; or whether a more complex explanation must be sought.

6. THE ECOLOGY OF KOALAS

In studying the ecology of the koala on Flinders Chase, my first aim was to give an explanation for their distribution and abundance (density). Andrewartha and Birch (1954) pp. 5-10 point out that 'distribution' and 'abundance' are concepts which commonly may be usefully separated only as a methodological device. I give two distinct explanations for (a) the distribution and (b) the abundance of koalas on Flinders Chase. The uncommonness in this case arises from the signal importance of one component of the environment, which therefore stands in relation to the distribution in a determinate rather than a stochastic way, such as comes about when a number of independently varying components of the environment are important. The heart of the evidence is as follows:

(a) The koalas are found in and around groves of manna gum. They have colonized all the available stands and, relative to the number of trees, are numerous. The koalas browse on other species, as well as manna gum. But those animals which do not include manna gum in their diet, do not survive. The distribution of koalas within Flinders Chase is limited by their need for manna gum.

(b) Adult koalas living within the manna groves remain faithful to particular trees within limited areas. They are intolerant of the close proximity of other koalas and trees are not used in common. The koalas are fecund, and within the manna groves recruitment through natality exceeds loss through death. Their numbers, however, do not change. Females drive their young away from the parental home range. These young wander widely and, severing their connection with the manna gums, perish in the alien bush. Within the distribution the abundance of koalas is limited by intolerant social behaviour.

(c) In places where the manna gums are vigorous and, free from competition with other species, grow thickly, the abundance of koalas does not reach a level which endangers the survival of the trees. In other places the koalas may eventually kill the trees on which they feed and so bring about their own extinction.

This account raises a number of points of some general interest.

(1) the social behaviour of koalas limits population density

The study of animal populations has led to two kinds of comprehensive theory. On the one hand there are theories, such as those of Nicholson, (1933); Lack, (1954) and Wynne-Edwards, (1962), which deduce from the persistence (sic) of populations an analogy to physiological homeostasis i.e., a population must be part of a system in which there is feed-back from density to environmental factors which affect density (stated explicitly by Nicholson, 1933 p. 135; Lack, 1966 p.292; Wynne-Edwards, 1962 p.11, and others, e.g. Williamson, 1957 p.423). These are the theories of the 'regulation' of populations by 'density-dependent mortality'. They differ among themselves in the generalizations they offer within this framework. Thus Lack (1954; 1966) concluded that populations were mostly regulated by the density-dependent operation of the 'extrinsic' factors of food-shortage, disease and predation. Wynne-Edwards (1962), however, argued that the (proximate) regulating factor was mostly the 'intrinsic' one of social behaviour.

On the other hand there is the theory of Andrewartha and Birch, 1954 (see also Andrewartha and Browning, 1961; Andrewartha, 1970). This theory explains the 'persistence' of populations in terms of the low probability of the environment becoming either so unfavourable (in degree and duration) that the population is brought directly to extinction, or so favourable that the population is brought indirectly to extinction through excessive multiplication and habitat destruction i.e. populations are stochastic systems and densities are determined by 'density-independent mortality'.

In theories of population regulation by density-dependent mortality, fluctuations in numbers are seen as departures from some 'equilibrium density' (Nicholson) or 'optimum number' (Wynne-Edwards) which reflects basic attributes of the species in relation to its niche. It follows that the causes of these departures are usually irrelevant to the central problem of identifying the regulating factor (s) i.e. that (those) factor (s) of the environment which acts (act) to return the density to equilibrium or optimum (e.g. Solomon, 1964 p. 10). In the theory of populations as stochastic systems, on the other hand, the determinants of fluctuations are expected to be qualitatively identical with the determinants of any particular value of density (i.e. the problems of levels of density and variation in density are identical).

The two classes of theory differ in logical status. Thus it is claimed for Andrewartha and Birch's theory that it is an induction from case-histories, whereas the other theories are built on a deduction, which gives them the status of 'conceptual models' rather than 'theories' (Andrewartha, 1957; 1959). Be this as it may, from a practical point of view the two classes of theory amount to assessments of the relative importance to generalizations about populations of density-dependent and density-independent mortality (implicit in Andrewartha and Birch, 1954 pp. 20-26; Milne, 1957 pp. 264-265; explicitly stated by Andrewartha, 1970 p. 158).

Lack (1966) p. 291 thought that no instance of density-dependent mortality had been demonstrated for a natural population (though he attributed this to inadequate evidence). Watson and Moss (1970) p. 171 thought this was probably still true for vertebrates at the time at which they wrote. These authors reviewed in particular the role of dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. They took a rigorous approach to the evidence which they found inadequate for the drawing of any firm conclusions. The conditions under which Watson and Moss were prepared to accept that 'behaviour, via socially-induced mortality (or socially-induced depression of recruitment), limits a breeding population,' are set out in Table 70. This is a slight re-phrasing of Table 1 in Watson and Moss (1970) p. 170. The table requires two comments. The idea of 'limiting factors' first arose in the study of chemical reactions.

A limiting factor in a chemical reaction is detected by augmenting in separate reactions the supply of each factor, while keeping the supply of the other constant, and recording which addition results in an increased reaction. Watson and Moss point out that complicated phenomena like populations may be simultaneously limited by a number of factors. Secondly, the table is aimed at populations remaining more or less constant in numbers. It applies equally well to steadily increasing or decreasing populations, but here the conditions refer to the limitation of a rate of increase or decrease.

TABLE 70 "Conditions which will show that behaviour, via socially-induced depression of recruitment, limits a breeding population." (after Watson and Moss, 1970).

(1) A substantial part of the population does not breed, either because animals die; or because they attempt to breed but they and/or their young all die; or because they are inhibited from breeding even though they survive, and may breed in later years.

(2) Such non-breeders are physiologically capable of breeding if the more dominant or territorial (i.e. breeding) animals are removed.

(3) The breeding animals are not completely using up some resource, such as food, space or nest sites. If they are, the resource itself is limiting.

(4) The mortality or depressed recruitment attributed to behaviour changes in an opposite sense to, and at the same rate as, other causes of mortality or depressed recruitment. If it does not, then behaviour is only one of the limiting factors (assuming (1), (2) and (3) are fulfilled.)

Conditions (1), (2) and (3) of Table 70 were true of koalas on Flinders Chase. So the conclusion that social behaviour was a limiting factor is unequivocal. The other component of environment which might also have been limiting on density was that of food resources. A point here is that two areas, the West Bay Track and Scotch Thistle Flat, had very similar area-densities of koalas, although they differed considerably in abundance of food (through both the density of manna gums and their crown development). This suggests that food resources as such were not a limiting factor additional to social behaviour. Of course, the certainty of this is lessened by the speculation that the relative palatability of the associations surrounding the two areas might have influenced density. However, since mortality was virtually absent from the manna gums and followed induced dispersal, social behaviour was certainly the limiting factor in the proximate sense at least. It therefore seems, although manipulations of density were not undertaken, that this study might be reasonably cited as an example of population regulation by density-dependent mortality. It is important to remember, however, that -

(a) the koala population is exotic to Flinders Chase, so the significance of this example for the theory of natural populations is accordingly lessened.

(b) the description is not apt. Mortality is density-dependent by virtue of the interaction between dispersal from the manna gum habitat and density (number of koalas in the manna gum habitat) - in the same way that a glass under a trickling tap remains full by virtue of the interaction between overflow from the glass and 'density' (number of water molecules in the glass).

(c) the limit set to density ...... but see text 4.4 and below.

(2) the limit set to density by social behaviour is not necessarily nicely adjusted to the carrying capacity of the area.

Although social behaviour may limit the density of a population, it does not follow that it has evolved as a mechanism for preventing over-exploitation of a food resource, as is implied by Wynne-Edwards (1962) pp. 11-12 and elsewhere. Indeed, it is difficult to see how this could come about through the available agency (natural selection), since the apostate in such a system ought to be at an immediate advantage. Wynne-Edwards, of course, explained the evolution of the altruism implied in this view by means of a process he termed 'group selection'. Group selection is 'species selection' at the cultural level. Both, however, are abstractions and add irrelevant dualising to the mechanism of natural selection when they are invoked in dialectic concerning characteristics which pertain to individual organisms. Thus while, in abstract terms, one culture or one species may replace another, in real terms individuals of one class replace individuals of another - and this is in no ways different from the evolution of a particular culture or a particular species. And while many examples of altruism or selflessness are explicable in terms of the natural selection of a particular behaviour pattern (see Hamilton, 1964), or of the sort of pre-disposition to cooperative living which sometimes give rise to selfless behaviour, these processes are very strained to account for Wynne-Edwards' hypothesis.

It therefore seems that the adaptive value (function) of territoriality cannot be the prevention of over-exploitation of a resource. It could, of course, quite logically be the pre-empting of access to a resource which was in short supply. Indeed, although it is possible to think of numerous advantages which territoriality (as distinct from localization) might confer on a solitary or colonial animal (see Hinde, 1956; Catchpole, 1972) this is perhaps the most plausible. Even so, selection for the basis of territorial behaviour may occur under the pressure of a number of factors, not all of which are associated with high density. The best provisional conclusion is that territoriality is a useful strategy for many animals at any density, and regardless of whether the carrying capacity of the habitat is being exceeded. It may limit the area-density of animals but area-density is an abstract notion and this effect is incidental to the function of territoriality.

(3) crowding, emigration and the stress syndrome.

A conclusion drawn during this study was that many animals were forced by social pressures into a nomadic way of life, which sooner or later brought about their deaths from malnutrition. It is worth noting that there was no evidence of significantly impaired breeding, or of a general morbidity, in either resident or nomad sections (while the latter persisted in the manna gums) of the population, such as to suggest the occurrence of the stress syndrome (Christian, 1950). This is not particularly surprising since although it is well documented in confined populations at artificially high densities (e.g. Myers et al., 1971) field evidence is lacking or equivocal (Munday, 1961; Watson and Moss, 1970; but see Christian and Davis, 1964).

(4) The ecologies of Phascolarctos cinereus, Schoinobates volans (greater glider) and Pseudocheirus peregrinus (ring-tail possum).

Schoinobates and Pseudocheirus are medium-sized (adult body weights c. 1 k) arboreal marsupials, smaller and more cat-like (they have long tails) than Phascolarctos (adult body weight c. 10 k). However , the three species share a number of physical characteristics. These were formerly considered to indicate a relatively close taxonomic relationship, but now seem more likely to be examples of convergent evolution. Like Phascolarctos, Schoinobates browses exclusively on the foliage of Eucalyptus and is reputed to be very selective. Fleay (1947) lists a number of species which are acceptable to the greater glider, amongst which is E. viminalis. Pseudocheirus is more catholic in its tastes, but Eucalyptus foliage is certainly an important component of its diet in many places. Wakefield (1970) describes Schoinobates as a sedentary, slow-moving, silent animal of minor gliding ability, and thinks that confusion with the gifted Petaurus australis has given it an undeserved reputation (e.g. Troughton, 1941). Schoinobates rests during the day in a hollow branch or trunk. Pseudocheirus, on the other hand, builds a number of nests or 'dreys'. It is a more active and vocal animal. The geographic ranges of Schoinobates and Phascolarctos are broadly coincident. Pseudocheirus is much more widespread. Reported densities for populations of Phascolarctos, Schoinobates and Pseudocheirus include, respectively, 1 adult/0.5 ha, 1 adult/1.2 ha (low-density population) and 1 adult/0.3 ha (very dense population).

Schoinobates has been studied by Tyndale-Biscoe and Smith (1969a, 1969b; Smith, 1969) over a period of six years during the successive annual clear-felling of blocks of a native forest in the Tumut area of New South Wales. The species is monovular and polyoestrous during a rather short annual breeding season (March to May). Young become fully independent at about nine months; sexual maturity is attained by both sexes in the second year; longevity is estimated to be about 15 years.

Schoinobates is apparently very sedentary; most gliders deprived of their homes but uninjured by felling operations did not attempt to emigrate but remained and died in situ. Individuals are generally observed alone, except during the breeding season, when pairs may be very common. The overall distribution of animals was significantly more uniform than random in two out of three years, but male and female portions of the population treated separately showed a consistent trend to uniform distribution in all three years, and it was concluded that animals tend to space themselves out in the forest. Animals were relatively rare; the over-all density was one adult to 3 ac. (1.2 ha) and this density, in successive blocks of forest, did not differ much over six years.

An imbalance in the sex ratio of adults was evident (38% male), apparently brought about by a sex-specific mortality of unknown origin of male weanings. A close relationship also existed between the numbers of adult males and the numbers of breeding females. It was concluded that the glider population was affected by factors affecting the birth-rate as well as by age-specific mortality. It was suggested that if the species is monogamous and the mortality of juvenile males density-dependent, then a mechanism exists whereby the population size may be regulated.

There is no evidence that koalas are monogamous and there are reasons for believing them to be promiscuous. Thus, during the breeding season, males may be seen with a number of different females; occasionally a grouping of males around one female will be observed. Further, males do not remain with individual females for any length of time (in Schoinobates, the proportion of animals seen as pairs may be as high as 0.80, which suggests the formation of a 'pair-bond' during the breeding season). It therefore seems that although Schoinobates and Phascolarctos exploit the same niche and have rather comparable life-histories, there may be a considerable difference in their ecologies, depending, in part at least, on a considerable difference in social behaviour. Perhaps one essential difference between these two species is the apparently less extreme sedentary nature of koalas, permitting the dispersal of individuals as a response to density. This, in turn, could follow from the larger size and generally more robust build of koalas, leaving such dispersing individuals less sensitive to predation.

This comparison is admittedly speculative because of our very imperfect knowledge of these two species. In any event, such a difference between two species would not be unique. Thus Heinsohn (1966) studied the two bandicoots, Perameles gunni and Isoodon obesulus which are sympatric in the Smithton area of north-western Tasmania. He found these two species to have very similar

- breeding biologies
- life histories
- habits
- food requirements

However, he found the density of Perameles to be much greater and more variable than that of Isoodon, which differed in showing strong, intra-specific aggressive behaviour with little overlap in home ranges.

The comparative study of social structure in relation to ecology has been termed socio-ecology. And some progress has been made in evaluating the relationship between habitat and gross social structure in primates and ungulates (see Crook, 1970). But it seems clear from this discussion that generalizations about the adaptive significance of mammalian social behaviour are only likely to come about with better concepts of behaviour and better measurements than are presently available for most species.

Thomson and Owen (1964; 1965) reported a field study of Pseudocheirus populations in Victoria. This species is polyovular and polyoestrous during a breeding season extending from May to August (though breeding may occur as late as November or even December). The modal litter size is two, and young are weaned approximately 6-7 months after birth. Sexual maturity is reached during the first twelve months and longevity, in captivity, may exceed eight years.

In *Eucalyptus* forest where the dominant species do not show an abundance of hollow limb sprouts or trunk sections, nests of *Pseudocheirus* are almost exclusively located in mistletoe (*Loranthus* spp.) clumps which parasitize *Eucalyptus* and *Acacia*. In such habitats there may be a close relationship between population density and the incidence of mistletoe parasitization. However, high population densities of *Pseudocheirus* seem to be associated with the distribution (usually riparian) of the shrub genera *Melaleuca*, *Leptospermum*, *Kunzea* and others, which provide both good nesting sites and important food items.

One dense (1 adult/0.3 ha) population in a *Leptospermum-Kunzea* scrub association, studied by Thomson and Owen over a period of 20 months, was characterized by a stable density but rapid population turn-over. This was due, in part at least, to a high mortality among juveniles. However, there was no indication that social behaviour was limiting the numbers of ringtails. Thus nests were sometimes placed contiguously and individual nests were commonly shared by pairs of adults. Indeed, as many as eight *Pseudocheirus* were flushed from one such nest complex. On the other hand it was not apparent that nest sites were limiting either, since, at any one time, some 5-10% of nests were uninhabited. Food, however, may have been limiting. *Pseudocheirus* apparently prefers the young growth of the shrub genera (although it favours mature over either young or old *Eucalyptus* growth) and such preferences may indicate nutritional requirements. Furthermore, there was evidence of -

(1) seasonal and annual changes in body weight associated with periods of maximum growth.

(2) higher population densities associated with stands of young shrub genera than with senescent stands.

It is therefore possible that the abundance of palatable and nutritious food fluctuates from super-abundance to a seasonal scarcity which limits population density. Presumably juvenile animals are more susceptible to predation and less thrifty on poorer browse than adults.

There is insufficient evidence to regard this as more than a very provisional model. Even so, it does not seem likely that the ecology of Pseudocheirus will prove to resemble that of Phascolarctos.

(5) the ecology of natural populations of koalas elsewhere in Australia.

The ecology of the koalas on Flinders Chase may be not uncharacteristic of koala populations, since throughout their geographic range hearsay reports indicate that koalas are remarkably dependent on relatively few of the locally occurring eucalypt species (see Introduction, Part II). It therefore seems reasonable to suggest that koala populations in continental Australia might be classifiable as some inter-gradation of the following:

TYPE A:

In these dense populations the important food species forms a thickly growing mono-culture. The size of the population is limited by the distribution of the food species and by social behaviour.

Associated with such populations are non-breeding 'populations' made up of dispersing koalas, which survive for a time on surrounding nutritionally-inadequate species.

TYPE B:

These are low-density breeding populations. Trees of the important food species form a sparse population i.e. are subordinate species in a tree association or form a savannah-woodland. The size of the population is limited by the distribution and density of the food species. Social behaviour does not limit density since (a) animals wander too widely to maintain territories or (b) so heavily browse trees that foliage itself is limiting.

In a TYPE A ecology, over-browsing, crown-destruction and a phase of population decline would follow loss of vigour in trees due to disease, senescence or unfavourable changes in climate or edaphic factors. The phase of decline might end in extinction or the development of a persistent TYPE B ecology, in which the probability of a koala finding and consuming more than the annual growth was less than the probability of the standing crop being maintained by growth of new trees.

TYPE B ecologies, of course, are more susceptible to over-browsing. However, the likelihood of over-browsing within TYPE B ecologies might be strongly influenced by the relative palatability of other species in the tree association. It should also be noted that, since in a TYPE B ecology there is no part of the population relatively secure from starvation/malnutrition, fluctuations in climate (or outbreaks of phytophagous insects) are more likely to bring about temporary phases of decline and recovery.

The role of seasonally or climatically-induced changes in the nutritive value of eucalyptus foliage is too speculative to include in this tentative model. It is, however, important to note that:

(1) the selective values associated with 'aggressiveness' may differ in the various circumstances permitted by this model (see Chitty, 1967; Watson and Miller, 1971). Some characteristics of certain populations might be explicable only in terms of the past history of the population.

(2) there is no documented evidence of significant non-human predation on koalas, but animals such as the wedge-tailed eagle Aquila audax, the powerful owl Ninox strenua, and the dingo Canis familiaris dingo, may be viewed as potential predators.

(3) there have been a number of reports of disease in koalas. Troughton (1941) reported that very severe epidemics involving some form of ophthalmic disease and periostitis of the skull occurred in natural populations of koalas

in 1887 - 9 and 1900 - 3. Pratt (1937) and Bolliger *et al.*, (1960a, 1960b, 1961, 1962 and 1963) have listed a number of morbid conditions to which koalas admitted to sanctuaries have been found prone. Remarkable amongst these are relatively high incidences of cryptococcosis and cystic ovarian lesions.

(4) weather may be an important component of the environment in places where high temperatures are common. Although koalas can thermoregulate efficiently (Robinson 1954), this may impose stresses on their water economy which they could not withstand (Section 7).

(5) fire is a periodic phenomenon in southern Australia. Philpott (1965) thought that fire might be important in keeping koala densities below the maximum, long-term carrying capacity of the habitat.

(6) Finnemore, Reichard and Large (1935) reported that one of two samples of *E. viminalis* foliage tested for hydrocyanic acid gave a positive result. Pratt (1937) thought that the presence of a cyanogenetic (sic) glucoside in *Eucalyptus* foliage constituted a hazard for koalas.

PART 2

CONFINED ANIMAL STUDIES

INTRODUCTION

Many herbivorous mammals are known to be very selective feeders. But the koala's unusual habit of remaining unconcealed during the day in the trees on which it feeds, has meant that its discrimination in choosing species of eucalypts is apparent to even the casual observer. This, together with the common failure of koalas to thrive in captivity and the apparent impossibility of weaning them to more conventional diets, has made the koala's specialization in respect of its food an article of folk-lore.

A number of naturalists, Sutton (1934), Lewis (1934), Pratt (1937), Fleay (1937), have reported their observations on the species of eucalypts preferred by koalas. But these observations have been necessarily couched in vague terms and are often inconsistent, one with another. Thus Lewis lists four species as the staple food trees of koalas in Victoria. Sutton adds two others but does not mention two in Lewis' list. Pratt includes those mentioned by Lewis, with the addition of two others, which were not mentioned by Sutton. Fleay reports the results of offering Victorian koalas twenty different species. Only three of them were completely rejected but four were found to be generally preferred (of which one was a species not mentioned in the other reports). There is as little agreement with respect to the species which are rejected. Thus Pratt reports that koalas have been known to thrive on E. botryoides - while Fleay records for this species that it is 'not liked, though growing points (are) occasionally eaten'. Some of these inconsistencies may be due to regional differences. Fleay reports that koalas are 'keen' on E. globulus 'as a variation' while, according to Pratt, E. globulus is 'relished' by koalas in New South Wales but eaten 'very rarely and sparingly' by koalas in Queensland. Again, Fleay records for E. leucoxylon that it is 'disliked', while in South Australia this species is apparently a very acceptable source of browse (this study - Table 85). Perhaps the only reliable conclusions that can be drawn from these reports are that:

(1) in the field koalas are observed to strongly favour one or two of the locally occurring species, but there is a striking lack of documentation.

(2) in Victoria, E. viminalis is the only species which unequivocally is able to satisfy the koalas' nutritional requirements. In Queensland and northern New South Wales only E. tereticornis and E. punctata have an equivalent status (E. viminalis does not occur north of the extreme south of Queensland and does not occur in the uncleared coastal forest areas of central and northern New South Wales).

(3) koalas do not thrive in captivity and this is usually considered a dietary problem. Periodic, heavy mortality is a common experience. In captivity koalas show striking preferences but nonetheless attempt a wide range of species. However, since it is practice to always provide such proven staples as E. viminalis, E. tereticornis or E. punctata, and to feed other species as additions to the staple, there is again a plentiful lack of data on the ability of koalas to survive on other species.

In any event, speculation about the basis of such discrimination as koalas may show is made hazardous by a lack of information about the digestive physiology of koalas and the nutritive qualities of eucalyptus foliage. The koala's alimentary tract is characterized by a simple stomach (with a marked concentration of glands along the lesser curvature) and a very large caecum (Mackenzie, 1918). The caecum is therefore the principal site of digestion, which must depend on the activity of a vigorous flora. However, Bolliger and Shorland (1963) in a study of fats found koalas unlike both ruminant and other non-ruminant herbivores; they differed from the former in the absence from depot fat of trans unsaturated acids, and differed from the latter in that the composition of the depot fat was not markedly affected by dietary fat. Koalas may also be expected to differ from eutherian herbivores in their requirements for dietary energy and nitrogen following the lower basal energy expenditure (by 30 - 40%) which seems to be characteristic of marsupials (Brown, 1968; MacMillen and Nelson, 1969; Dawson and Hulbert, 1970). Brown reports that the nitrogen requirements of the euro and some other species of ruminant-like macropod marsupials are equal to, or less than, the requirements of eutherian monogastric species, and considerably lower than values given in the literature for sheep. The relatively low requirements of the macropods may reflect in part a lower basal energy expenditure, but also reflects the ability of these animals to recycle urea when on low nitrogen intakes. Notwithstanding such abilities, nitrogen has been shown to be a limiting factor for the physical condition of macropods in some feral populations, though the relationship may be subtle (Main, 1968).

The alimentary system and digestion of macropod marsupials is ruminant-like (Moir, Somers and Waring; 1956). A number of studies have been reported in which comparisons are made between digestion in kangaroos and sheep. Some data on mean excretion times (M.E.T.), dry matter intake (D.M.I.) and apparent dry matter digestibility (D.M.D.) are also available for the wombat, *Lasiorhinus latifrons*, an herbivorous marsupial which resembles the koala in that it depends on post-gastric bacterial fermentation. Data are given in Table 71 for the purpose of comparison with some calculations of D.M.I. and D.M.D. in koalas. These data were collected incidentally during three separate feeding trials held for other purposes. In the first the daily consumption by weight of *E. bridgesiana* foliage was measured over a period of eleven days for a single male koala weighing 6.315 kg and confined in a small pen (2m x 2m). The average moisture content of the foliage was assumed to be 50%. Faecal pellets were collected each day and weighed; samples were dried to constant weight and the apparent dry matter digestibility calculated. The koala had been largely fed on this species for some weeks and maintained weight. Mean dry matter intakes and apparent dry matter digestibilities were similarly determined for four koalas fed on one occasion for ten days on *E. viminalis* and *E. obliqua* and on another occasion for nine days on *E. viminalis* and *E. fasciculosa*. Here the D.M.D. values calculated

TABLE 71 Intakes, Excretion Rates and Digestibilities in various marsupials and sheep

Authority	Species	Diet	M.E.T. (hrs) 5%	M.E.T. (hrs) 90/95%	D.M.I. g/kg/24 hrs.	D.M.D. %
Calaby (1958)	Quokka	Oaten/Lucerne Chaff	14.0	60.0	21.5	57.0
	Quokka	Lucerne Chaff	13.8	37.5	47.1	59.1
Foot and Romberg (1965)	Kangaroo	Oaten Chaff	?	54	40.4	36.0
	Sheep	Oaten Chaff	?	104*	28.9*	38.8
McIntosh (1966)	Kangaroo	Oaten Chaff	31.3	61.3	24.2	48.1
	Sheep	Oaten Chaff	29.1	85.3	43.4*	51.5
Forbes and Tribe (1970)	Kangaroo	Oaten Chaff	?	56.2	28.7	32.1
	Sheep	Oaten Chaff	?	106.2*	36.0	46.9*
Wells (unpub. data)	Wombat	Oaten Chaff	69	118	26.7	57.5
This study	Koala	*E. bridgesiana*			44.7	42.5
	Koala	*E. viminalis* and *E. obliqua*			45.2	60.0
	Koala	*E. viminalis* and *E. fasciculosa*			29.4	45

M.E.T.	mean excretion times
D.M.I.	dry matter intake (body weight to the 0.73 or 0.75 power)
D.M.D.	apparent dry matter digestibility
Quokka =	*Setonix brachyurus* (Quoy and Gaimard)

* differences significant at the 5% level of probability

are minimal; the faecal pellets collected were left for several months in the laboratory to air-dry before weighing. They probably still retained some moisture. These two experiments are reported later (text 8.2) and the differences between them in D.M.I. and D.M.D. discussed.

The inconsistencies between the three studies tabulated here in their comparisons of sheep and kangaroos (*Megaleia*, and, in Forbes and Tribe's study, *Megaleia* and *Macropus*) have been attributed to differences in the age of experimental animals and the proximate compositions of the oaten chaff diets. It is apparent that such measurements are very specific to particular circumstances. In view of this it is not at all clear what these few statistics for koalas signify. The long retention times for the wombat may, however, be thought noteworthy. They considerably exceed the value of 48 hours given by Alexander (1946) cit. Calaby (1958) for complete elimination in the horse (a eutherian monogastric herbivore). Gilmore (1970) reported excretion times of 12-120+ hours in the Phalangerid marsupial *Trichosurus vulpecula*. Gilmore thought that 'digestive efficiency' in *Trichosurus* might compare with efficiencies in macropod marsupials such as *Setonix brachyurus*, and be intermediate between the efficiencies characteristic of true ruminant and non-ruminant (eutherian) herbivores. *Trichosurus* has a large and specialised caecum, but since *Phascolarctos* shows the greatest instance of caecal development in the Mammalia (Mackenzie, 1918) it is unlikely that 'digestive efficiency' is less in *Phascolarctos* than in *Trichosurus*.

Cleland (unpublished data) measured the concentrations of urea, uric acid and other nitrogenous compounds in the urine of koalas and compared them with ones derived for a sheep fed a synthetic diet with a comparable (sic) level of protein (6 - 9%). There were no marked differences.

Bolliger and Backhouse (1960b) have reported absolute and relative abundances of cellular constituents of koala blood. They also measured haemoglobin levels and give a mean value of 12.90 g/100 ml ± 1.23 g/100 ml. The haemoglobin was determined as oxyhaemoglobin in an ammoniacal solution and was measured in a photoelectric colorimeter.

The mean was derived from 29 determinations on 24 apparently healthy koalas maintained in captivity. Ealey and Main (1967) measured haemoglobin levels in small samples of euros, Macropus robustus, collected seasonally from two feral populations. They reported mean values ranging from 12.3 g/100 ml to 21.0 g/100 ml. Bolliger and Backhouse remark that the levels of haemoglobin they encountered in koalas were low compared with those characteristic of either man or echidna (range, for the latter, 16.5 - 19.4 g/100 ml).

The following measurements of haemoglobin, plasma protein and packed cell volume in koala blood were made in the course of an experiment on water turn-over rates in koalas, reported in Section 7. Blood samples were taken from six koalas about 24 hours after their capture in the wild from French Island, Victoria, and just prior to their release in a 15 acre (6.1 ha) enclosure of natural bushland in the Tidbinbilla Nature Reserve, Australian Capital Territory. Five of these animals were recaptured after about one fortnight and further samples were taken. Two samples of blood were similarly taken from each of two animals already present in this enclosure. A further two samples of blood were drawn at the release and recapture of another koala in an adjacent 9½ acre (3.8 ha) enclosure. This animal had been captured locally in the wild and had been maintained in a small pen for some weeks. All these animals appeared vigorous and thrifty when released and though all, with the exception of the two resident animals, lost weight during the fortnight, they did not seem dangerously wasted when re-caught. Haemoglobin (HbO) was measured with a Farstab Resistance Haemometer. Packed Cell Volume (P.C.V.) was measured with micro haematocrit tubes, centrifuge and reader. Plasma protein (P.P.) levels were measured with an Atago Serum Protein Refractometer.

Means of duplicate determinations are reported for all samples in the case of P.P. and for three and six samples in the cases of HbO and P.C.V. the largest errors between successive, independent determinations were of the order 29% (HbO), 7% (P.C.V.) and 6% (P.P.). Data are given in Table 72.

TABLE 72 Values for koala Haemoglobin (HbO), Packed Cell Volume (P.C.V.) and Plasma Protein (P.P.)

Animal	Wt. (kg)	HbO (g/100 ml)	P.C.V.(%)	P.P. (g/dl)
E1	11.5	8.9	40	6.8
E2	7.25	9.6	37	6.5
	6.25	6.4	29	5.2
E3	8.5	12.0	41	6.9
	8.0	8.5	35	5.9
E4	6.75	7.6	33	6.6
	6.25	8.3	35	6.6
E5	5.25	9.5	39.5	6.8
	4.75	8.8	33	6.0
E6	8.25	8.8	34	6.0
	6.75	7.7	41	5.5
C1	5.5	8.9	41.5	5.5
	5.75	9.4	37	6.0
C2	9.5	9.3	36	5.3
	9.75	9.2	39	6.5
E2.1	6.65	10.0	41	6.0
	6.0	9.4	41	6.3

The mean ± S.E. values for the initial determinations are:

9.4 ± 0.4 g/100 ml (HbO); 38 ± 1% (P.C.V.); and 6.3 ± 0.2 g/dl (P.P.)

It is clear from this table that these characteristics of blood tended to reflect the weight changes to similar degrees. They very likely might be used with profit in field studies to assess the 'nutritional status' of koalas since they ought to be less dependent than weight on age and general body conformation (c.f. Table 46). The low values for haemoglobin are notable. It seems unlikely that the low values can be attributed to the stress of capture and confinement in those animals from which initial blood samples were taken only after a delay of about 24 hours because haemoglobin levels for the three animals (C1, C2 and E2.1) from which blood samples were taken immediately after capture were comparable.

MacKenzie and Owen (1919) reported that the adrenal glands of koalas were rudimentary. They associated this with diminished activity and speculated (in effect) that some substance in eucalyptus leaves has adrenal cortical hormone activity. Bolliger (1953) confirmed a lower adrenal gland/body weight ratio in koalas but doubted that it could be interpreted as evidence of a constitutional insufficiency, particularly since the histology of the adrenals of the koala was of the usual mammalian pattern. Weiss and Richards (1970) reported that, 'the biosynthetic capacity of the koala adrenal cortex as derived from cortisol secretion is comparable with that of larger eutherians'. Bolliger (1953) said that no evidence existed of adrenal hormone-like substances in eucalyptus leaves.

Eucalyptus browse seems an unpromising food. Except for the very young leaves the foliage is tough and fibrous. Pratt (1937) p.88 reported the following proximate composition for eucalyptus leaves generally, but gave no further details.

Water	34 - 40%
Ash	2.5 - 4%
Fibre	6 - 9%
Fat	3 - 7%
Protein	6 - 9%
Carbohydrates	37 - 42%

This analysis was apparently accepted by Cleland (1946). I have been unable to find much corroboration for it. Philpott (1965) reported average water contents for leaves of six species ranging from 47 to 53%. McKern, Spies and Willis (1951) mention average moisture contents for young leaves of E. dives of 60% and 53% for mature leaves. However, Bolliger and Shorland (1963) found that the amount of lipid in four species ranged from 6.7 to 12.8% of the dry matter, which is more consistent with the composition quoted by Pratt.

On the other hand there is a deal of information about the essential oils characteristic of many species of eucalypts. Perhaps partly because of the availability of this information, but also because the various components of the oils are generally toxic substances, the possible significance of these oils for the koalas has frequently attracted comment.

Pratt advanced a two-fold theory which explained the various preferences and dietary requirements of koalas on the basis of the lethal toxicity of large doses of oil and thermoregulatory needs coupled with the physiological effects of sub-lethal doses. The evidence given for this theory is as unconvincing as the latter part of it is implausible. Thus one item of evidence for this theory is that all the species allegedly preferred by koalas in Queensland have an oil with a relatively high cineole content. But this is derived, in part, from the amazing non-sequitur that a number of Queensland species from which koalas eat 'very rarely and sparingly' have cineole-rich oils!, (Pratt, 1937) p. 85 - and the argument anyway completely overlooks the incidence of such oils among Queensland species generally. Furthermore, it must be observed that the advantage on a hot Queensland day of a hypothermia induced by cineole-intoxication is more than likely to be offset by the accompanying disposition to cardiac and respiratory failure (text 8.3).

The experiments described in the following sections relate to rates of water turn-over in koalas, the koalas' selection of particular species of Eucalyptus when offered a choice of several, and their ability to maintain weight when fed particular species of Eucalyptus. All these experiments were done on animals in captivity. Koalas may be generally unthrifty in captivity (see text 8.1) but they also become very docile.

7. WATER TURN-OVER

One requirement of the food taken by koalas is that it must fully satisfy their needs for water, since these animals do not drink in the wild (p.168). This peculiarity is an item of folk-lore (Troughton, 1941) p.135 and is celebrated in aboriginal legend (Roberts and Mountford, 1965). Of course, Eucalyptus browse remains green throughout the year. However, the water content of the young leaves ('tips' or 'flush' with a mean age of one month or less) measured by McKern et. al. (1951) was only 60% and, in relative terms, only 7% greater than that characteristic of mature leaves. Koalas may be expected to prove thrifty in their water economy. Faecal pellets excreted by koalas are remarkably dry. The moisture contents of two samples of pellets collected as evacuated were 44% and 48%. These values are about the limit possible for dehydrated sheep (MacFarlane, 1968) and are close to those characteristic of camels and kangaroo rats, Dipodomys sp., maintained without water (43% and 45% respectively; Schmidt-Nielsen, 1964). Cleland (unpublished data) found that koalas maintained in captivity voided an average of 58.3 ml of urine per day. This average was derived from 55 determinations made on 12 koalas. The average weight of five of these animals was 6.28 kg, so it may be estimated that the 58.3 mls represents about 0.01 ml/g/24 hours. Two determinations by Cleland on a sheep fed a synthetic diet of a similar (sic) protein level (6 - 9%) suggest a value of about 0.02 ml/g/24hours.

Elsewhere in this thesis it is suggested that the range of koalas in the more inland areas of Australia is possibly restricted by stress imposed on their water economy by thermoregulatory needs. These interests in the water economy of koalas prompted an investigation into water turn-over rates. Water turn-over was measured by the dilution of injected tritiated water (TOH).

Water turn-over was measured in seven animals. Five of these were koalas which had been captured in the wild on French Island, Victoria, and brought to the Australian Capital Territory for release into a 15 acre (6.1 ha) enclosure of natural bushland in the Tidbinbilla Nature Reserve. The remaining two animals were Victorian koalas which had been resident in the enclosure for over a year. All the newly introduced animals appeared vigorous and thrifty when released and though all lost weight in the course of the investigation, none appeared dangerously wasted when re-caught. These koalas had lived largely on E. viminalis which was the dominant species in the enclosure.

Animals were weighed to the nearest 250 g and given an intraperitoneal injection of 1 ml of tritiated water (250μCi/ml). Five hours were allowed for equilibration after which a sample of blood was drawn from a vein in the fore-limb. The koalas were re-caught 12-16 days later when a further blood sample was drawn and the animals re-weighed. Two of the koalas were then re-injected with a further 1 ml of tritiated water and blood samples taken after equilibration. The purpose of this second injection was to test for changes in the total body water (T.B.W.). The appropriate correction was made for the tritium remaining in these animals from the first injection. Care was exercised during injections to avoid leakage of the charge.

The time allowed for equilibration was chosen with regard to the literature. Some justification for it was obtained when the activities of blood samples taken from another animal three and five hours post-injection were nearly identical (4,453 and 4,586 counts/minute; background 60 c/m). The actual levels of these activities suggested an unrealistically small T.B.W. Clearly an error was involved and data from this animal is not reported, but the error is unlikely to have affected the test of equilibration time.

All samples were distilled to apparent dryness, care being taken to avoid combustion of the residues. 100μl samples of the distillates were each added to 10 ml of scintillation fluid (333 ml Triton X 100, 667 ml Toluene, 4 g PPO (2,5 - diphenyloxazole) and counted in a Beckman CPM 100 liquid scintillation spectrometer with a 2% error setting. Background activity was measured with distilled water and a standard (250 mμCi/ml) counted. Replicate counts of several samples suggested a high degree of reliability. In one case faecal pellets were collected and the activity of moisture distilled from them agreed very closely with the activity of moisture distilled from the blood.

The enclosure was regularly searched during the course of the experiment and the trees in which animals were found were marked. This was done in order to detect gross differences in the behaviour of animals. No such differences were apparent. The introduced animals dispersed to different parts of the enclosure and though animals moved about within greater or lesser areas, all were changing trees every night.

The experiment was undertaken during the summer months of December and January. The trees within the enclosure were all growing vigorously and the free-water content of the browse must have been at a maximum. The weather remained equable with cool nights and mild to warm days. During the final seven days, temperatures and humidities were continuously recorded with a thermohygrograph secured in a Stevenson screen suspended some 10m above the ground. Daily maximum and minimum temperatures and humidities are given in Table 73.

TABLE 73 Temperature and humidity - Tidbinbilla enclosure

Day	9	10	11	12	13	14	15
Max. T°C	26	16	22	26	25	21	22
Min. T°C	10	10	11	14	12	4	4
Max. R.H.%	96	88	94	89	93	98	95
Min. R.H.%	62	44	37	47	38	39	38

Weather statistics for the whole period were obtained from the Canberra Meteorology Bureau. These were recorded at R.A.A.F. Base Fairbairn, some 20 miles (32 km) from Tidbinbilla. The weather in Canberra clearly differed from that at Tidbinbilla, but these statistics show the absence of extreme conditions. Thus the greatest daily maximum recorded for the period of the investigation was 30°C, and the least daily maximum 19°C. Canberra also recorded seven 24-hour periods registering rain of 2, 2, 3, 4, 26, 58 and 77 points.

The high nocturnal humidities at Tidbinbilla suggest considerable exchange of TOH for HOH at the respiratory surfaces. Failure to consider this variable would tend to maximize calculated estimates of the food intake necessary to account for the measured dilution of the tritium. Possible sources of error with this technique arising from its assumptions are detailed by Roberts, Fisher and Allen (1958) and Lifson and McClintock (1966).

Total body water (T.B.W.) was calculated from the relationship,

$$\frac{Y_{\text{standard}}}{Y_{\text{sample after equil.}}} = \text{T.B.W.} \quad (1),$$

where Y is the activity (counts/minute), the standard was 250 mμCi/ml and 1 ml 250μ Ci/ml was injected. Estimates of total body water, expressed in litres and as a percentage of body weight, are given in Table 74, together with initial and final weights, and the time between release and re-capture.

TABLE 74 Water Turn-over - Weight Changes and T.B.W.

Animal	Wt.$_I$(kg)	Wt.$_F$(kg)	% Loss	Days	T.B.W.$_I$ (1)	T.B.W.$_I$ % wt.	T.B.W.$_F$ (1)	T.B.W.$_F$ % wt.
E2	7.25	6.25	13.8	15.71	5.686	78.4	4.807	76.9
E3	8.5	8.0	5.9	13.96	6.198	72.9		
E4	6.75	6.25	7.4	13.96	5.245	77.7		
E5	5.25	4.75	9.5	15.71	4.010	76.4		
E6	8.25	6.75	18.2	15.71	6.386	77.4	5.517	81.7
C1	5.5	5.75		12.79	4.586	83.4		
C2	9.5	9.75		13.67	6.905	72.7		
Mean						77.0		
S.E.						1.4		

Subscript 'I' = initial, 'F' = final

The mean value of 77.0% by weight for T.B.W. in these koalas is high compared with measures made of other mammals. Thus corresponding values reported include 67 - 70% for mule deer, Odocoileus hemionus, (Knox, Nagy and Brown; 1969), 56 - 67% for domestic dogs (Gaebler and Choitz; 1964), 69% for camels (MacFarlane, Morris and Howard; 1963) and 55 - 72% for a vole, Microtus californicus, (Church; 1966). Values for domestic poultry are 56 - 67% (Chapman and Black; 1967) and for the reptiles, Varanus gouldii, (Green; 1969), Amphibolurus ornatus (Bradshaw and Shoemaker; 1967), Dipsosaurus dorsalis (Minnich; 1970) are 77%, 73 - 74% and 71 - 78% respectively. All these values, apart from those for the vole and the last two reptiles, were determined from the dilution of injected tracers. This technique gives values slightly greater (by 1 - 3% in ruminants) than those obtained by desiccating carcasses (MacFarlane, 1968). Change in T.B.W. as a fraction of weight reflects changes in the fat content of the body and, largely through this variable, age. Merino sheep in the hottest areas of Australia may have an average T.B.W. of 74% wt., and cattle in the wet tropics reach 85% (MacFarlane, 1968). These high values reflect, in part at least, the capacious guts of these animals which may hold significant amounts of very moist material and lean carcasses resulting from the grazing of poor pastures. A lean carcass is characteristic of koalas.

The koalas that lost weight during the investigation must have had a correspondingly reduced T.B.W. Final T.B.W.'s were calculated for two animals following their re-injection with TOH. Since in these two cases the final T.B.W. (% wt.) was much the same as the initial value, Table 74, the T.B.W. for all animals at the end of the investigation was calculated from the initial T.B.W. (% wt.) and the final weight (Wt.F).

The dilution of the tritium per unit time is the rate constant for intake of water (K_{TOH}). It may be calculated from the relationship,

$$K_{TOH} = \frac{\ln (TOH)i \; - \; \ln (TOH)f}{time}$$

The time required for dilution of the tritium to half its original concentration is given by -

$$T\tfrac{1}{2} = \frac{\ln 2}{K_{TOH}}$$

In the case where the T.B.W. does not change, the actual rate of water intake (r H_2O) can be calculated from -

$$r\,H_2O = K_{TOH} .\ T.B.W.$$

Roberts, Fisher and Allen (1958) and Lifson and McClintock (1966) discuss the case for the exact calculation of r H_2O where T.B.W. is a function of time. In the absence of knowledge of this function, r H_2O was calculated from K_{TOH} and the average of the initial and final T.B.W. These rates of intake may be converted to outputs by adding to them the fractional changes in the total body water. These data are presented in Table 75.

TABLE 75 Water Turn-over in Koalas

Animal	$\overline{\text{T.B.W.}}$ (1)	K_{TOH}	$T\frac{1}{2}$ (days)	rH_2O (Intake) mls/24 hrs.	rH_2O (Output) mls/24 hrs.	Intake mls/$\overline{\text{Kg}}$/24 hrs.	Intake mls/$\overline{\text{Kg}}^{0.82}$/24 hrs.
E2	5.247	0.052	13.3	273	329	40	57
E3	6.015	0.049	14.2	295	321	36	52
E4	5.051	0.058	11.9	293	321	45	63
E5	3.820	0.057	12.0	222	246	44	58
E6	5.952	0.045	15.4	268	323	36	51
C1	4.691	0.071	9.8	333	317	59	81
C2	6.997	0.065	10.7	455	442	47	71
Mean		0.057	12.5			43.9	62.1
S.E.		0.003	0.7			3.0	4.1

It is difficult to assess these statistics comparatively. Water turn-over for a number of inter-specific comparisons varies as the 0.82 power of body weight (MacFarlane; 1968), but there are some considerable exceptions. Thus cattle may have $T\frac{1}{2}$'s of the same order as rodents. Further, water turn-over rates must be intimately related to all aspects of an animal's metabolism, so their dependence on particular circumstances is to be expected.

Most studies have been made on animals confined within laboratories. These results may have little relevance for the field. Thus Mullen (1970) showed that $T\frac{1}{2}$'s for the heteromyid rodent Perognathus formosus are 2.4 - 4.0 times greater in typical laboratory circumstances than in the field (15.6 ± 4.4 days cf. 3.8 - 6.5 days). Mean $T\frac{1}{2}$'s for the vole, Microtus californicus, are 1.6 - 3.7 days, according to the water ration (Church; 1966). Knox, et. al. (1969) found, alternatively, much shorter $T\frac{1}{2}$'s for mule deer, Odocoileus hemionus, confined to metabolismcages than deer given greater freedom of movement (2.3. days cf. 6.5 days). This was attributed either to the confined animals fretting against their restraint or to differences in age, or both. Some remarkable results have been reported. Chapman and Black (1967) found a very significant difference in water turn-over between domestic hens and cocks ($T\frac{1}{2} = 3.61 \pm 0.33$, 7.3 ± 0.32 respectively). This was not attributed to egg production and no explanation was offered.

Lactation is an important variable affecting water turn-over. MacFarlane et. al. (1963) reported that lactating camels exposed to very severe summer conditions in central Australia had an average water flux of 93 ml/kg/24 hrs., which was considerably greater than that measured in non-lactating camels (61 ml/kg/24 hours). These fluxes were smaller than those characterizing merino sheep, shorthorn cattle and red kangaroos in the same or very similar circumstances (fluxes of 110, 148 and 88 mls/kg/24 hours respectively). In some studies, individual differences are very marked. Gaebler and Choitz (1964) measured water turn-over in five dogs maintained in metabolism cages. Their values of $T\frac{1}{2}$ ranged from 7.8 to 17.0 days.

Notwithstanding these sources of variability in water turn-over, I have compared, in Table 76, koalas with camels and the kangaroo rat, Dipodomys deserti, species with a celebrated ability to survive in dry places.

TABLE 76 Water turn-over in three mammals

Animal	Wt. (g)	$T\frac{1}{2}$ (days)	Flux ml/kg/ 24 hrs.	Flux ml/$g^{0.82}$/ 24 hrs.
(1) Kangaroo rat	93	11.82 ± 2.9	40	0.09
(2) Koala	7,250	12.5 ± 0.7	43.9 ± 3.0	0.20
(3) Camel	337,000	7.8	61	0.60

(1) Richmond, Langham and Trujillo (1962) cited Green, (1969)
Mean ± s.d. Laboratory determination.

(2) This study. Mean ± S.E.

(3) MacFarlane et. al. (1963)

It is clear from these data that in their water economy koalas are probably among the thriftiest of mammals. Even so, koalas exposed to hot desert conditions would differ from camels in that they could not seek water at considerable distances and would differ from the fossorial kangaroo rats in that they would have no refuge from the heat.

FEEDING TRIALS

8.1 Foliage Preference Trials

A number of koalas were brought from Flinders Chase to Adelaide for use in various feeding trials. Three or four were used at any one time. The koalas were housed separately in pens, the smallest of which measured 1.8 by 6.1 m. In each pen were several piles of timber to provide suitable resting places and shelter was available. A number of water-containers were fastened to the timber piles or walls and freshly collected branches were secured in these each day. In the intervals between experiments, the koalas were held with others in enclosures at the Cleland National Park. Here they were fed on manna gum with occasional branches of stringy-bark and blue gum, E. leucoxylon; shelter was provided, and drinking water (though none but sick animals were ever seen to drink).

The koalas adapted very quickly to their captivity and within a few days all could be approached and gently handled. The periodic transference from the Cleland National Park did not seem to disturb them; they became very familiar with their alternative quarters and when released they at once sought their usual places and fed in their accustomed manner. Notwithstanding their ready acceptance of captivity, the koalas did not thrive. One young female, BLUE U, weighed 4,800 g when caught at an age of about one and one half years. Twenty-three months later it had increased to only 5,600 g. A young female of the same generation in the wild then weighed 7,300 g and had suckled an offspring to a weight of more than 1,000 g. Another female, YELLOW Y, weighed 8,500 g when captured. Fourteen months later it weighed 7,350 g and its maximum weight during captivity was 7,950 g. This female did not breed while in captivity but it continued to suckle a pouch young it was carrying when caught. Two animals died. One did so within a few weeks but this koala was old and rather emaciated when caught. The other was young and vigorous but died suddenly after several months.

One purpose in maintaining these koalas was to quantitatively assess their responses to various eucalypt species, using manna gum as a standard, in order to grade the species in terms of acceptability. A second purpose was to test for seasonal differences in these responses. Some trials were therefore undertaken in which various species were offered, one at a time, in competition with manna gum. The results were quantified by counting the numbers of freshly bitten-off ends. Since most of the foliage eaten was in the form of single leaves bitten off at the petiole or the junction of the petiole with the stem, the method was quite accurate.

In these preliminary trials some eight species were tested. It was evident that koalas were discriminating between species but it was of some surprise that some leaves at least were usually eaten from all species and that only three were clearly rejected, while one, the brown stringy-bark, E. baxteri, seemed to be preferred by two animals to manna gum. A considerable degree of variability, both between koalas and between repeated trials was also evident. This is illustrated in the data given in Tables 77 and 78.

TABLE 77 Foliage Preference Trials. E. obliqua versus E. viminalis. Number of E. obliqua leaves eaten (as percent of total). Total number of leaves eaten in brackets.

Animal	26 Sep. 67	6 Nov. 67	7 Nov. 67	14 Nov. 67
RED U	56 (401)	32 (256)	66 (385)	39 (296)
BROWN U	46 (329)	7 (212)	71 (239)	30 (286)
BLUE U	35 (206)	4 (142)	25 (311)	17 (331)

TABLE 78 Foliage Preference Trials. *E. baxteri* versus *E. viminalis*. Number of *E. baxteri* leaves eaten (as percent of total). Total number of leaves eaten in brackets.

Animal	27 Sep. 67	8 Nov. 67	13 Nov. 67
RED U	86 (659)	88 (494)	77 (346)
BROWN U	74 (337)	79 (378)	61 (362)
BLUE U	37 (411)	69 (344)	46 (321)

The inconsistency in the results of these initial trials was a source of concern since the labour involved did not allow a large number of replications. One likely origin of inconstancy was the use of different trees since in each trial three containers were used with a branch of the test species and one of the standard, all from different trees, in each; and in the replications different trees again were used. Accordingly, some 'response consistency' trials were run in which animals were offered the same two species, the foliage being taken each time from the same trees. It was convenient to continue these trials for eight successive days and in this way to also test, if animals chose initially to feed largely from the manna gum, whether with time they became more inclined to attack an alternative species. Four animals were used in this experiment: two were given foliage from a manna gum and a stringy-bark and two were given foliage from a manna gum and a blue gum. The trials were undertaken in April of 1968 and were conducted in the same manner as the foliage preference trials done before. Terminal foliage, mainly from varied parts of the upper crowns of mature trees, was collected each day and immediately placed in water. Every evening branches were distributed and secured in the containers, each container holding a branch of manna gum and one of the test species. Branches were allocated to the right or left sides of the container by a random process and were both comparable in size and sufficiently large for the koalas to be able to satisfy their hunger on one branch, or very nearly do so. The results of this experiment are presented in graphical form in Figures 34 and 35 where the values refer to the amount of the test species eaten expressed as a percentage of the total. The numbers

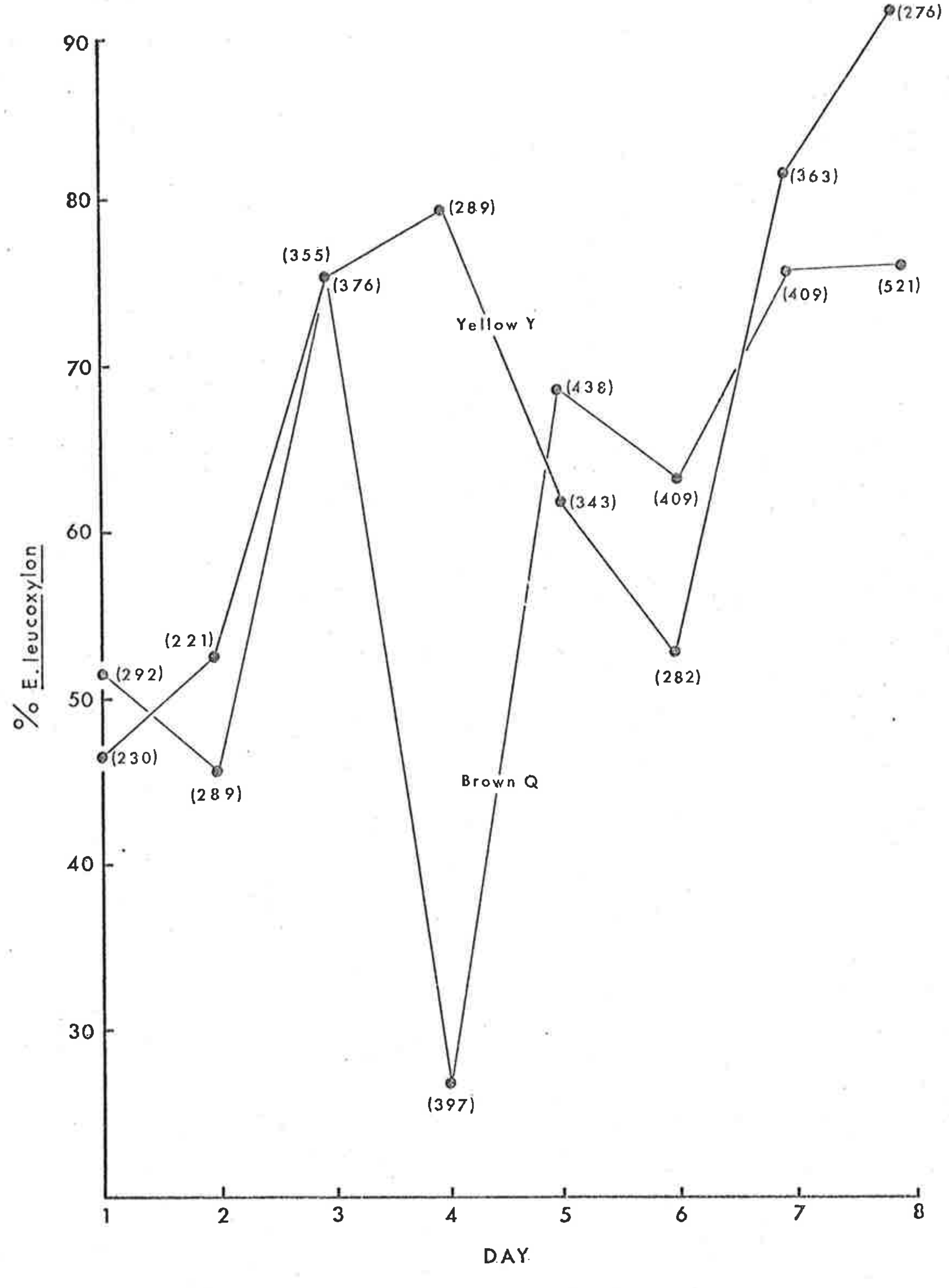


Figure 34 E. leucoxylon v. E. viminalis. No. of E. leucoxylon leaves eaten (%). Total number of leaves eaten in brackets.

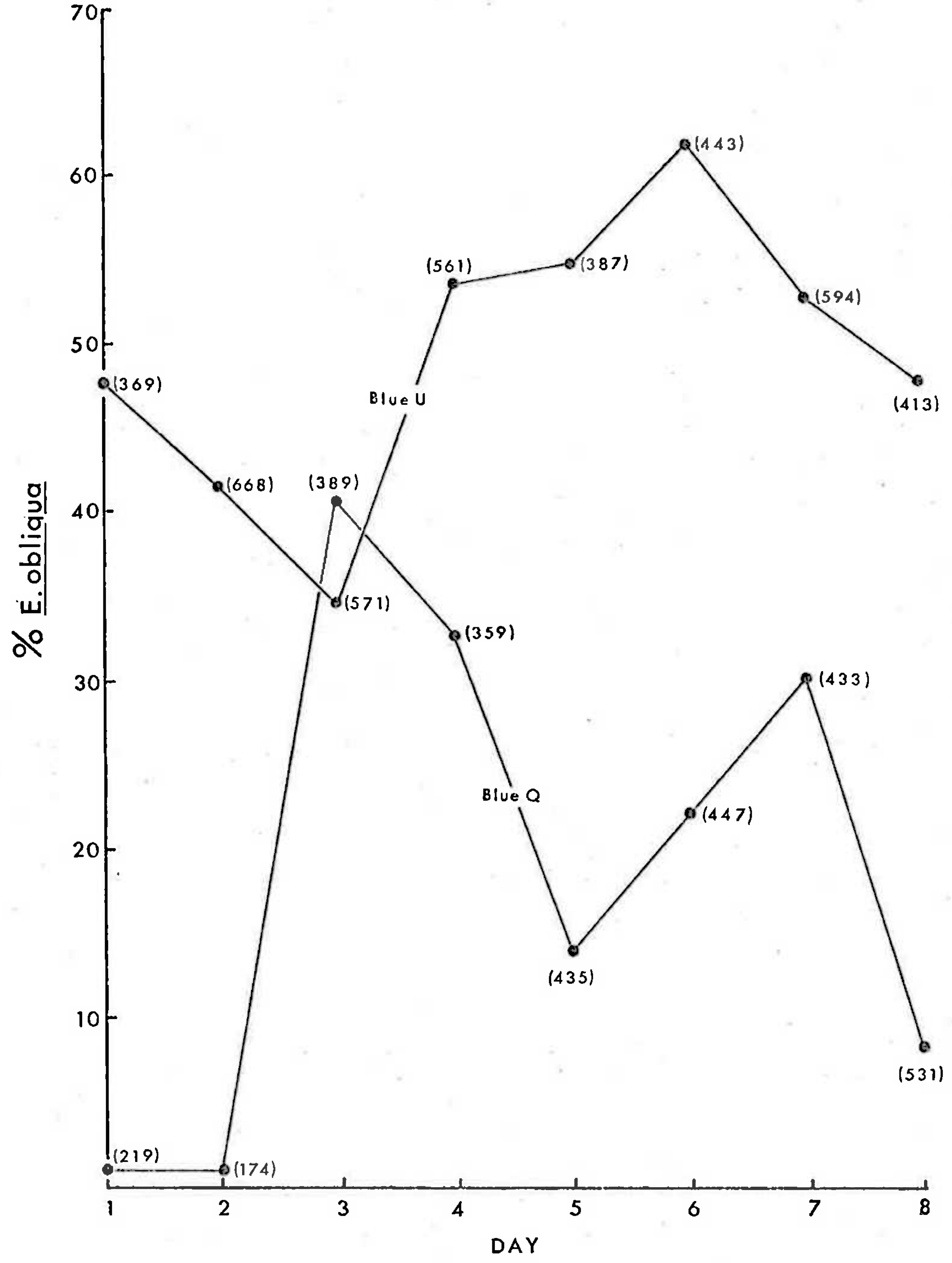


Figure 35 E.obliqua v. E.viminalis. No. of E.obliqua leaves eaten (%). Total number of leaves eaten in brackets.

in brackets in these figures are the total number of 'leaves' eaten (counted as bitten-off ends). There are a number of features to these graphs.

The most significant are:

(1.) Both BROWN Q and YELLOW Y appeared to develop a preference (for blue gum over manna gum) during the trials (Figure 34).

(2) BLUE Q and BLUE U responded very differently (Figure 35). BLUE Q maintained a general preference for manna gum over stringy-bark while BLUE U gave no indication that it was discriminating in any way between the two species. This latter result was in contrast with BLUE U's response to stringy-bark in the preliminary trials shown in Table 77, where BLUE U clearly favoured manna gum.

It was apparent from these results that koala feeding responses were indeed capricious. It was therefore decided to largely restrict further experiments to five species and to offer all five together.

The species selected were E. viminalis (manna gum), E. baxteri (brown stringy-bark), E. obliqua (messmate stringy-bark), E. fasciculosa (pink gum) and E. cladocalyx (sugar gum). They were chosen because all grew on Flinders Chase and together they formed a complementary group - the initial trials had indicated that both pink and sugar gum were likely to be rejected while brown stringy-bark seemed at least as attractive as manna gum and stringy-bark seemed to invite a rather variable response. In June and November of 1968, and February and June of 1969, foliage preference trials were undertaken in which the species were assigned daily to different containers by a random method (although these had been arranged so that koalas did not show any marked bias for particular containers). In June of 1968, the foliage representing each species and given to each of three koalas, came from four different trees, and was accordingly marked. The labour involved proved to be excessive (the daily collection of foliage alone involved the climbing of twenty large trees spread along a forty mile route) and the experiment was concluded after three trials. Since there was no indication in this June 1968 data that koalas were discriminating between foliage taken from different trees, in the subsequent experiments the foliage representing each species came from one tree only of the four. These latter experiments were continued for four trials and, as in June 1968, two days pre-feeding with all species had been given. Data are given in Tables 79 - 83.

TABLE 79 BLUE U - Foliage Preference Trials. Numbers of 'leaves' eaten from each of five species offered together.

	Jun. 1968			Nov. 1968				Feb. 1969				June. 1969			
	(1)	(2)	(3)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
E. viminalis	283	406	281	255	377	222	208	191	149	75	273	293	250	332	251
E. baxteri	216	246	154	207	8	71	191	83	63	28	70	176	250	127	191
E. obliqua	0	15	56	0	42	135	34	0	0	2	14	3	32	19	1
E. fasciculosa	0	2	1	0	0	0	3	0	0	0	0	8	4	5	20
E. cladocalyx	7	7	8	0	0	0	0	0	0	0	3	0	1	0	1

TABLE 80 YELLOW Y - Foliage Preference Trials. Numbers of 'leaves' eaten from each of five species offered together.

	Jun. 1968			Nov. 1968				Feb. 1969				Jun. 1969			
	(1)	(2)	(3)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
E. viminalis	160	171	155	185	249	293	306	258	89	65	159	156	164	165	228
E. baxteri	331	208	178	201	94	53	242	40	54	3	37	283	0	70	79
E. obliqua	19	114	111	127	165	29	37	0	0	98	44	123	211	184	123
E.fasciculosa	23	13	37	3	21	0	125	0	62	38	0	103	0	140	83
E.cladocalyx	3	18	4	1	2	0	8	0	8	0	0	2	0	0	0

TABLE 81 BROWN Q - Foliage Preference Trials. Numbers of 'leaves' eaten from each of five species offered together.

	Jun. 1968			Nov. 1968				Feb. 1969				Jun. 1969			
	(1)	(2)	(3)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
E. viminalis	127	348	262	323	228	343	296	248	138	119	140	116	67	297	351
E. baxteri	319	201	19	1	38	58	95	111	126	0	53	183	232	153	13
E. obliqua	261	59	220	0	165	124	51	45	11	34	52	350	184	202	177
E. fasciculosa	2	32	22	98	48	0	74	1	47	0	8	11	106	24	157
E. cladocalyx	1	1	6	0	0	0	0	0	0	0	0	0	10	0	0

TABLE 82 WHITE Q and WHITE F - Foliage Preference Trials. Numbers of 'leaves' eaten from each of five species offered together.

	Nov. 1968 (WHITE Q)				Feb. 1969 (WHITE F)				Jun. 1969 (WHITE F)			
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
E. viminalis	195,	256,	298,	301	241,	161,	132,	209	400,	188,	181,	218
E. baxteri	75,	211,	112,	135	0,	2,	54,	80	22,	2,	0,	66
E. obliqua	33,	0,	0,	13	70,	94,	41,	64	124,	186,	216,	157
E. fasciculosa	1,	8,	0,	6	6,	3,	15,	15	50,	84,	146,	175
E. cladocalyx	0,	4,	3,	8	1,	0,	1,	0	5,	1,	13,	5

TABLE 83 Foliage Preference Trials. Means and ranges for numbers of leaves eaten (%) from each of five species offered together.

Animal	No. of Trials	No. of leaves eaten (% Total)				
		E. vim.	E. bax.	E. obl.	E. fas.	E. cla.
BLUE U	15	62 (47-88)	32 (2-47)	6 (0-32)	0 (0-4)	0 (0-2)
YELLOW Y	15	45 (23-87)	25 (0-67)	21 (0-56)	10 (0-29)	1 (0-3)
BROWN Q	15	49 (11-78)	20 (0-45)	23 (0-53)	8 (0-23)	0 (0-2)
WHITE Q	4	64 (53-72)	31 (25-44)	4 (0-11)	1 (0-2)	1 (0-2)
WHITE F	8	53 (33-76)	8 (0-22)	27 (17-40)	12 (0-28)	1 (0-2)
TOTAL	57	53 (11-88)	24 (0-67)	17 (0-56)	6 (0-29)	0 (0-3)

From these data it is apparent that the five species fell into three categories. Manna gum stood apart as the most consistently favoured species. Brown stringy-bark and stringy-bark were sometimes eaten to a comparable extent but evidently invited much more variable responses. Pink and sugar gum were clearly rejected, although pink gum was occasionally eaten to some degree.

The separation of manna gum from brown stringy-bark and stringy-bark is perhaps of sufficient importance to warrant a probability statement. The test chosen was Friedman's non-parametric Analysis of Variance (Siegel, 1956) p. 166. Data are displayed in Table 84.

TABLE 84 Foliage Preference Trials. Frequencies of various rank orders between *E. viminalis*, *E. baxteri* and *E. obliqua*.

	Rank Order (k = 3)			
Species	E. viminalis	E. baxteri	E. obliqua	Frequency
	1	2	3	28
	1	3	2	16
	1.5	1.5	3	1
	2	1	3	5
	2	3	1	4
	3	1	2	2
	3	2	1	1
Rj	65.5	126.5	143	
N				57

$X^2_2 = 30.8 \qquad P \ll 0.001$

In view of the values for the means in Table 83 it is clear that the probability of a real difference between manna gum and the stringy-barks is of the order of 99.9%.

The data in Tables 79-82 shows a considerable difference between the responses given in both June of 1968 and June of 1969, and those given in November of 1968 and February of 1969. The difference suggests a seasonal effect in which manna gum is more attractive during the summer months. This is the exact converse of a conclusion drawn from observations made on Flinders Chase (text 5.3). However, the increase in the relative amount of manna gum eaten in November and February was associated with a greatly reduced intake on two very hot days which characterized the four day trials in both these experiments. This is shown in Figure 36 where the average total number of leaves eaten by the three koalas which were common to all experiments is plotted, as well as individual percentages of manna gum eaten. The increased relative consumption of manna gum associated with the heat-induced loss of appetite emphasises the special position of this species.

These effects must be considered artefacts of the conditions under which the experiments were done. The pens were so excellently sheltered from the wind that, with reflection from the concrete floor, hot conditions became unwarrantedly stressful. The response of the koalas to the heat was interesting. Two tardily sought the available shade but the others remained in very relaxed but immobile positions exposed to the sun, and shelter had to be constructed for them. All animals panted continuously and salivated copiously onto their forelimbs and chest, while the inner surfaces of the manus and pes became encrusted with salt. They were taught to drink from a trickling hose held against their muzzle, at which they clumsily lapped, but they would not seek water even when the hose was secured and left only inches from their snouts. Comparable conditions were only once experienced on Flinders Chase, when a maximum temperature of $42^{o}C$ was recorded. Koalas were seen panting and salivating throughout the day and some sought shelter in thick bracken at the base of trees. No animals were seen to seek water although for many the Rocky River was only a few metres distant. It is possible that the range of koalas in the more inland parts of Australia is restricted by stress imposed on their water economy by thermoregulatory needs.

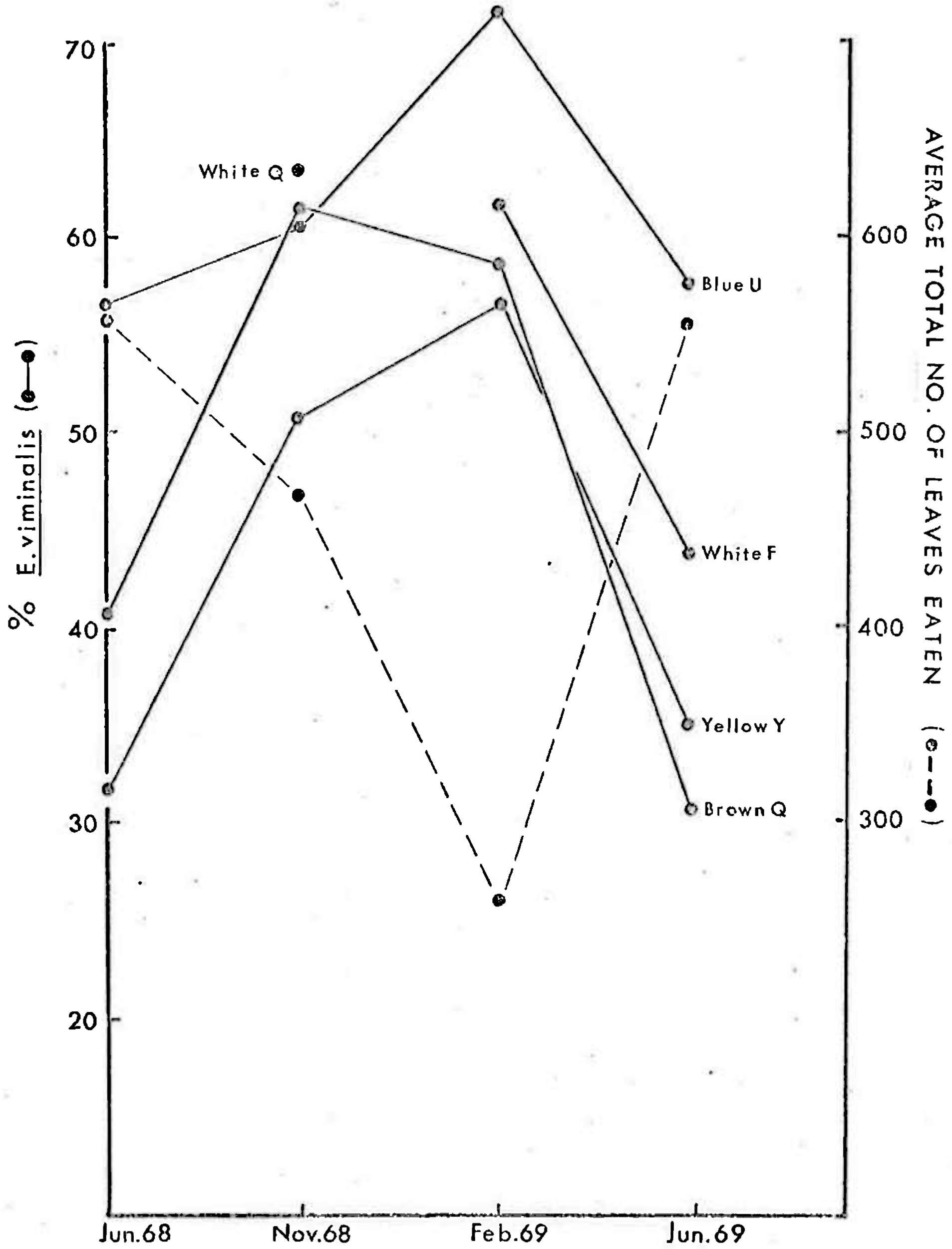


Figure 36 Foliage Preference Trials-
Average total number of leaves eaten and numbers of *E.viminalis* leaves (% Total) eaten by individual koalas.

Be this as it may, there was no evidence in these foliage preference trials of a seasonal increased attraction for manna gum such as was seen in the wild (Section 5.3.). A number of explanations might be advanced for this but it is perhaps sufficient to point out that the experimental situation necessarily differed in a number of ways from the conditions experienced by free-living koalas on Flinders Chase. Most notably, the experimental koalas were feeding on manna gum every night; since foliage from the various species was not spatially separate, the choice to begin feeding on one species did not signify the rejection of others. There was also no evidence of a seasonal variation in condition among the koalas held in captivity. However, the significance of this is likewise uncertain since, as has been pointed out, koalas in captivity were invariably in poor condition compared with many animals in the wild. The four koalas which died at the Cleland National Park between January of 1968 and June of 1969, did so during the winter period. Two animals died in the last week of May, one died early in the second week of June and the other died in the first week of September. The results of post mortems on three of these animals were inconclusive. In the remaining case, uraemia following chronic nephrosis was indicated.

In addition to the four species tested against manna gum in the foliage preference trials already cited, five other species were also tested in a similar way. During February of 1969 E. leucoxylon (blue gum), E. camaldulensis (river red gum), and E. odorata (peppermint gum) were offered together with manna gum to four koalas. Trials were run on four consecutive days following three days pre-feeding and the numbers of bitten-off ends were counted. Foliage representing each species came from different trees each day. In March of 1969 further trials were run with various combinations of species, but principally involving manna gum paired with E. elaeophora (bastard box) and E. rubida (candlebark). The conclusions drawn from these trials about the status of these additional species were also checked against more casual observations made when these species had been given in the ordinary maintenance of animals. I have summarized my findings about all species used in foliage preference trials in Table 85 where I have also listed the yields of oil obtained by distillation of these species and the groups to which they belong from Baker and Smith's (1920) analysis, in which the essential oils of 168 species of eucalypts were classified into 8 main groups according to their composition. Leaves were distilled in McKern and Smith-White's (1948) apparatus and came from shoots collected from various parts of the crowns of the particular trees used in the foliage preference trials. The values given in Table 85 are the means of replicate distillations undertaken during August of 1969, except in the cases of <u>E. elaeophora</u> and <u>E. cladocalyx</u> where the values represent single distillations done in late May of 1969.

TABLE 85 Foliage Preference and Oil Yield

Status	Species	Oil Yield (ml/100 g)	Group **
Highly favoured	*E. viminalis*	0.92	VI
	E. elaeophora *	2.62	IVa
	E. leucoxylon *	0.53	II
ACCEPTABLE			
Occasionally well favoured	*E. baxteri*	0.67	-
	E. camaldulensis *	0.73	V
	E. obliqua	0.80	VI
Sometimes eaten well	*E. odorata* *	0.20	IVa
	E. rubida *	0.02	VI
REJECTED			
Never eaten well	*E. fasciculosa*	0.18	II
	E. cladocalyx	0.27	II

* Species not occurring within Flinders Chase.

** Baker and Smith (1920) reported two 'chemical varieties', yielding oils of different composition, for both *E. viminalis* and *E. rostrata* = *E. camaldulensis*. The group given here is that 'characteristic' of the 'type'.

There is a very notable relationship in this table between the status of a species and its yield of oil. The species categorized as 'acceptable' had yields ranging from 0.53 to 2.62 ml/100 g, while those classed as 'rejected' had yields ranging from 0.02 to 0.27 ml/100 g. Within these classes, however, species are not ordered according to yield. E. leucoxylon, for instance, was much more likely to be favoured than the higher yielding E. obliqua. It is evident that other factors beside oil yield must have been important in determining the status of a species. The importance of the composition of the oil in regard to status is not apparent in this table. The three highly favoured species all represented different groups (but see part 3 of this section).

A relationship between palatability and oil yield or oil composition cannot, for the present, be established on a wider basis. Although Baker and Smith (1920) reported yields and composition for 168 species, and data for additional species are given by Penfold and Willis (1961), these values and classifications may be misleading since:

(1) there is considerable inherent variability in the yield and composition of oil characteristic of a species (see part 3 of this section).

(2) in the distillation procedures used by Baker and Smith, variable amounts of 'branchlets' were included in the charge, and the foliage of some species was transported, tightly packed in bags, for hundreds of miles by ship or rail (Baker and Smith, 1920 p. 350).

Furthermore, the exact status of other species remains equivocal (see INTRODUCTION to PART 2). Even so, it is of interest that the species E. tereticornis and E. punctata gave yields of 0.50 and 0.80 g/100 ml, while the only three species (of twenty) tested by Fleay (1937) which gave yields $<$ 0.20 g/100 ml were reported to be 'disliked', 'not liked' and 'distasteful'. The last of these was E. cladocalyx.

Some simple preference experiments were attempted in which manna gum oil was sprayed on the leaves of other species. The oil was was certainly not distasteful but no conclusions were drawn since when leaves were offered by hand to koalas they did not discriminate between species as they did when foliage was left to them overnight, while the oil evaporated from foliage left for any time, fairly quickly. It was also notable that the odour of the distilled oil differed from that of the crushed leaf.

8.2 Maintenance Trials

Shortly following the foliage preference trials undertaken in November of 1968, the four koalas were each given, for a number of days, one of the test species only. Three different responses were observed. The koala given sugar gum refused it for three successive days, after which it was fed on other species. This refusal to eat sugar gum had been seen before in both this and another koala. It was unexpected since on Flinders Chase koalas were sometimes seen in sugar gums and had a number of times been observed actively feeding on this species. In contrast, the koala given stringy-bark ate very consistently and maintained weight over the seven days of the trial. However, the koalas given, respectively, brown stringy-bark and pink gum lost weight, and this was judged to be because they were failing to eat a sufficient quantity of browse. Furthermore, the amounts eaten seemed on the way to becoming less. In all these cases the koalas' behaviour made it very evident that they disapproved of the foliage given them. They became very active in the evening but would not settle down to browse and while I was present continually importuned me. This was in great contrast to their behaviour when manna gum was also given.

The failure of koalas to eat pink gum in quantities sufficient to maintain their weight at the level reached when given manna gum, was confirmed in a subsequent experiment. Two koalas were given pink gum and two were given manna gum for three successive days and this distribution of species was then reversed over the following three days. The amount of foliage consumed was measured by weighing shoots. All the animals lost weight when given only pink gum and in two cases the quantities of pink gum eaten amounted to only 57 and 66% of the quantities of manna gum. The data for the other two animals were unreliable since each of these, when given pink gum, responded by breaking into the adjacent pen in order to get at the manna gum.

The apparent equivalence of stringy-bark and manna gum as food was thought to be important to test further, so a maintenance trial with these species was undertaken in April of 1969. The trial followed the double alternation procedure. Two koalas were fed stringy-bark for seven successive days. On the eight day they were given stringy-bark and manna gum, and were then fed manna gum for only four more days. Two other koalas were initially fed manna gum for six successive days. On the seventh day they were given both manna gum and stringy-bark and were then given stringy-bark only for five more days. On the thirteenth and last day of the experiment all animals were given a second foliage preference trial with stringy-bark and manna gum. The amounts of foliage eaten were measured by weighing shoots and several shoots, including some stripped of leaves, were used to detect independent changes in the weights of shoots. These ranged from + 16.0 g to - 51.5 but were mostly of the order of a few grams only. Leaves dropped onto the floor of the pens were collected and weighed but were usually trivial amounts. Foliage from different trees representing each species were given each day and the same trees were largely used in each half of the experiment. The trees included some of those used in previous foliage preference trials and others from the same localities. The koalas were weighed at intervals of three to four days. The weather remained equable throughout the experiment.

The koalas all maintained weight or showed slight gains during the first half of the experiment. All suffered minor losses of weight during the second half. This experiment therefore, gave no evidence that manna gum and stringy-bark are not equivalent foods <u>in the very short term</u>.* However, there was a very marked temporary failure of appetite in all animals following the change to a different species. This is shown in Figure 37 where I have plotted the quantities of foliage eaten.

---

* Fleay (1937) reported for <u>E. obliqua</u> that koalas in the Melbourne zoo 'occasionally (ate) buds and finer leaves'. According to Lewis (1934), Victorian koalas in the wild on Phillip Island do not eat the leaves of 'messmate' (= <u>E. obliqua</u>?).

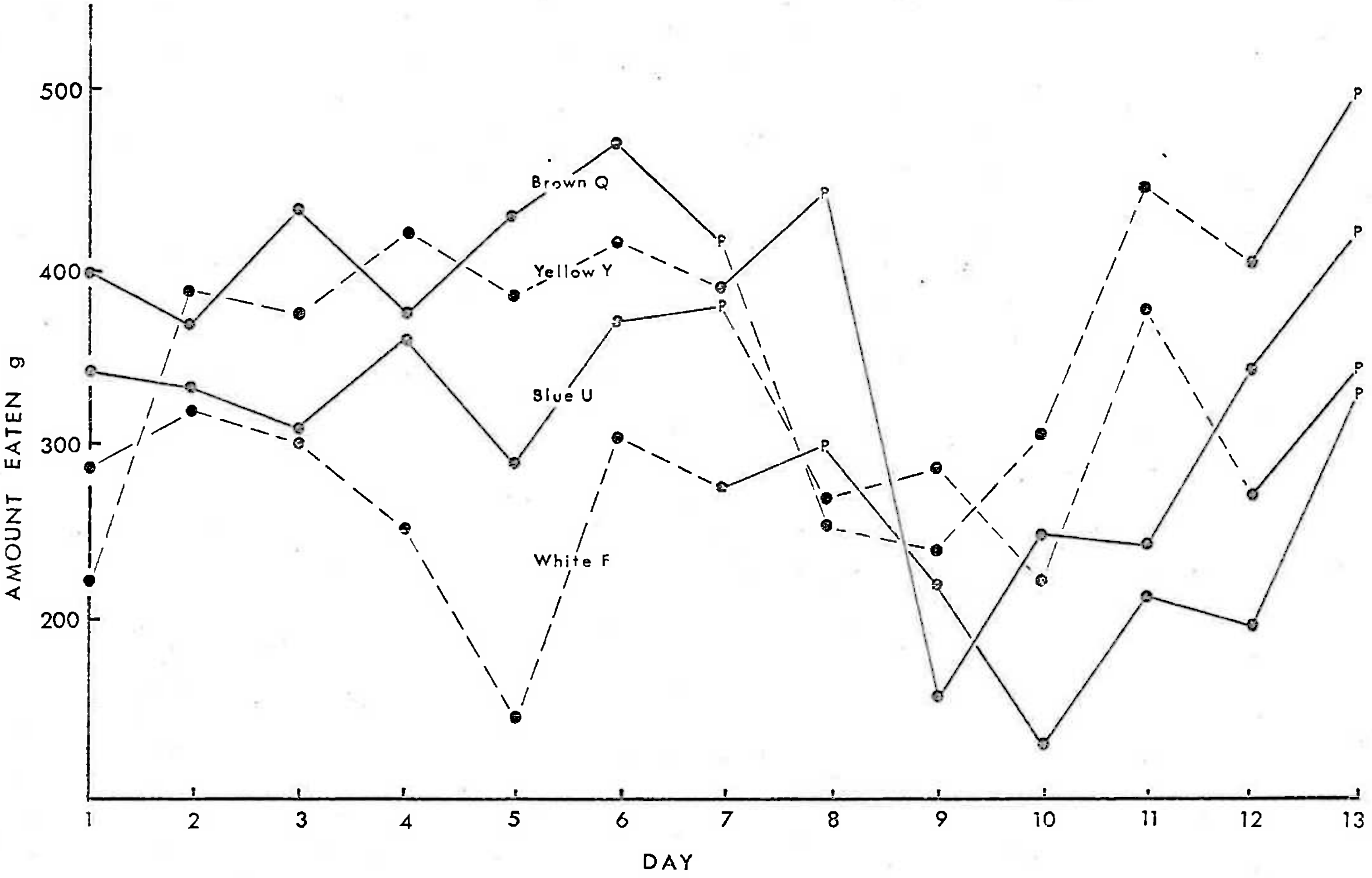


Figure 37 Maintenance Trials – Manna gum and Stringy-bark
(●——●) (●– – – –●)

The portions of the graphs during which stringy-bark was exclusively given are indicated by broken lines; the occasions when both species were given are shown by the letter 'P'. The failure of appetite is not, of course, evident in the koalas initially fed manna gum. The experiment was begun immediately after the animals had been brought from the Cleland National Park where they had been living entirely on manna gum, though they may have occasionally received a little stringy-bark.

The failure of appetite did not, in all cases, follow at once from the presentation of the 'new' species. This is shown clearly in the first half of the experiment by the graph for WHITE F, but it was also obvious in the second half since in the preference trial that preceded the change, WHITE F and YELLOW Y ate considerably more manna gum than they did on following days when it was given alone, while BLUE U and BROWN Q in a similar way nearly equalled their subsequent consumption of stringy-bark. This delay may be considered to suggest that some kind of indigestion was the origin of the appetite failure, which in turn implies an adaptation of the digestive processes to the available food. Be that as it may, recovery was rapid and the pattern for both species was the same.

The koalas, after they had fed on manna gum for a number of days, ate quantities of stringy-bark when it was also given amounting to 33, 42, 49 and 66% of the total consumed. In the converse situation the quantities of manna gum eaten amounted to 79, 89, 95 and 95% of the totals consumed. The superior status of manna gum was therefore preserved in this respect. A further maintenance experiment was undertaken with pink gum in May of 1969. Four koalas which had been fed a variety of species but most recently manna gum alone, were fed pink gum for six consecutive days. The foliage given two of these animals was liberally sprayed with oil distilled from a manna gum. Foliage was taken from trees used before, and the weather remained cool. For the rest, the experiment was similar to the previous one.

The amounts of foliage eaten are plotted in Figure 38 where the broken lines indicate when pink gum was given. All animals ate from this species little more than about 50% of their usual intake, and lost weight. Of course, this weight loss might also have reflected a difference in the

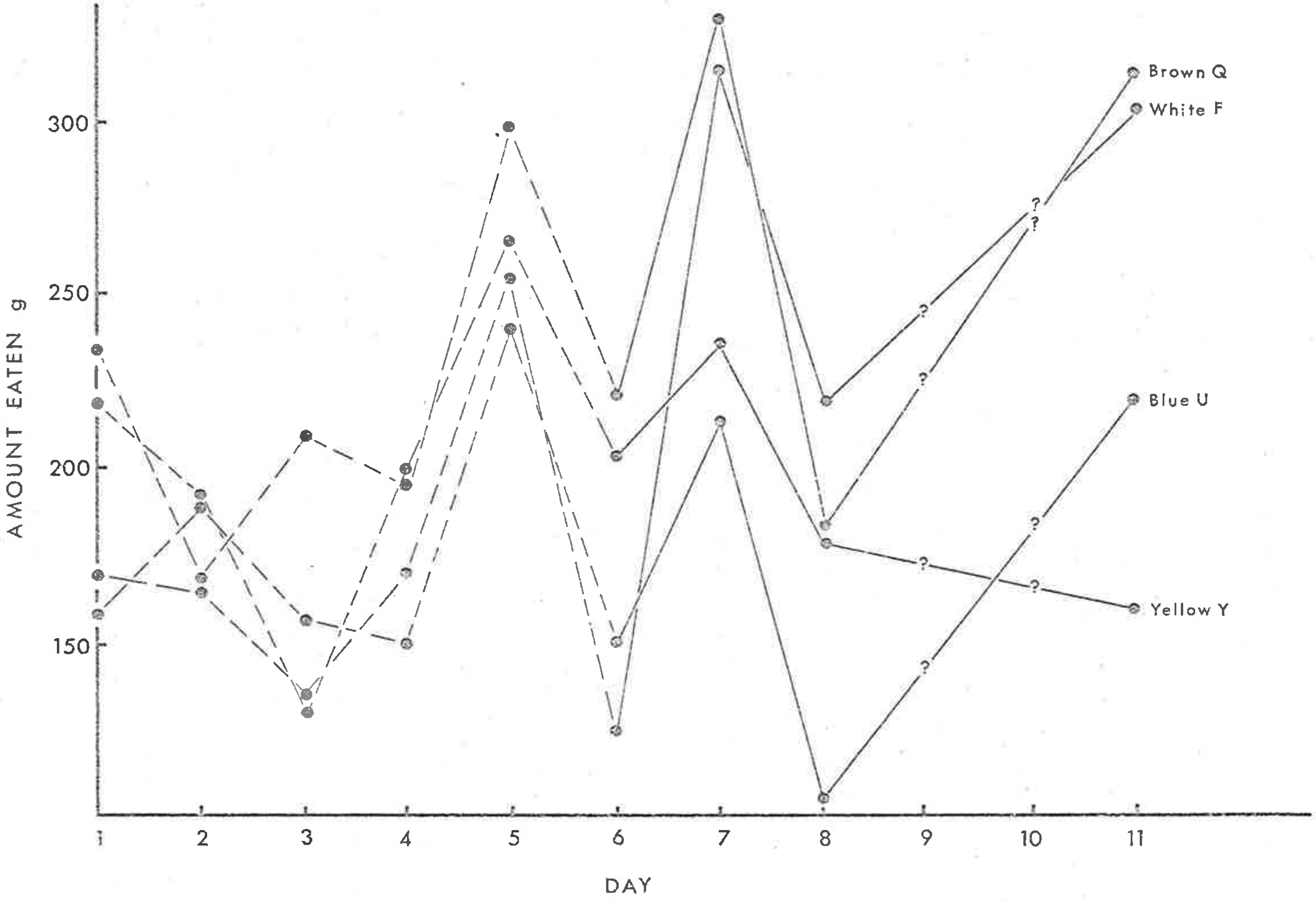


Figure 38 Maintenance trials – Pink & Manna gum

(●– – –●) (●———●)

digestibility as well as level of the intake. This could be checked since in both this and the stringy-bark-manna gum maintenance trial faecal pellets dropped by each koala were collected daily and allowed to air-dry for several months in the laboratory before weighing. Thus an index of the digestibility (wet weight of foliage eaten per gram of air dry pellet produced) of these two diets could be calculated for each animal. Values are given in Table 86.

TABLE 86 Differences in the values of a digestibility index for two diets.

Animal	Digestibility Index Manna gum/Stringy-bark	Manna gum/Pink gum
U	4.60	3.77
F	5.38	3.41
Y	4.88	3.44
Q	4.88	3.87
Mean	5.03	3.62
S.E.	0.18	0.12

$\bar{d} = 1.41$ $S_{\bar{d}} = 0.2867$ $t_3 = 4.9$ $.02 > P > .01$

The mean difference is significant at the 2% level. It may therefore be judged that the manna gum/pink gum diet was less digestible than the manna gum/stringy-bark diet.

Apart from a relatively sharp increase on the fifth day, there was no indication that the koalas were likely to develop an appetite for pink gum, and their behaviour made their dislike of this species very evident. The oil sprayed on the foliage given to animals did not make any apparent difference but this was to some extent expected since though a little was adsorbed on the surface of the leaf, most evaporated relatively quickly. The koalas' appetites did not markedly revive when they were given manna gum, and they continued to lose weight. After eleven days (see Fig. 38) the animals were returned to the Cleland National Park, where for a number of days at least two of the four continued to feed very poorly. Their condition caused considerable concern.

This quite prolonged carry-over from only six days' feeding suggests that the pink gum was more than just unpalatable and possibly inadequate food, but that it was in some way injurious or toxic. Of course, the essential oil of this species is unlikely to have produced such symptoms since E. fasciculosa yields very little oil (Table 85). On the other hand, the association between palatability and oil yield shown in Table 85 suggests that this very lack of oil might be an explanation i.e., the koalas actually require the oil and its absence over a relatively short period of time can have a deleterious effect that takes some time to make good. The suggestion becomes more tenable if it is supposed that the caecal flora or its dominant forms are in some way adapted to the presence of considerable quantities of essential oil. Of course, this hypothesis cannot be invoked to explain why species on Flinders Chase such as E. obliqua or E. baxteri are inadequate for survival in the long term, since they have oil yields comparable to that of E. viminalis. But perhaps differences in the composition of the oils in these species become important.

8.3 Koalas and Ethereal Oils

'In Australia cases of poisoning by eucalyptus oil are common... The minimum fatal dose for an adult (in several cases) has been a teaspoonful (four to five mil.). Rapid death followed the drinking (during a drunken orgy) of five hundred and sixty-eight mils (a pint) .... In one case pronounced collapse ensued upon the taking of twelve drops. In another case the skin, breath, faeces and urine smelt of the oil for two weeks.' MacPherson (1925).*

---

* MacPherson presumably referred to cases of the ingestion of refined eucalyptus oil. The British Pharmacopeia standard for eucalyptus oil in 1920 (cited Baker and Smith) was a minimum content of 55% cineole. The crude oil of several species has a cineole content ranging as high as 70%.

Ethereal plant oils may be composed of some of an enormous range of compounds. Haagen-Smit (1948 : 18) classified a large number of these into four main groups, viz:

1. Terpenes, related to isoprene or isopentene;
2. Straight-chain compounds, not containing any side branches;
3. Benzene derivatives;
4. Miscellaneous.

The principal compounds present in many oils of eucalyptus on which Baker and Smith (1920) classified them into eight main groups are pinene, cineole, phellandrene, aromadendral and piperitone.

Cleland (1946) measured the toxicity of cineole in guinea pigs, rabbits, rats and possums. Symptoms of cineole poisoning usually appeared within two or three hours and included ataxic gait and shivering, followed by circulatory and, more particularly, respiratory failure. The L.D. 50 per 2/3 power of body weight in kilos was 1.2, 2.3, 2.5 and 2.5 g cineole respecitvely. The M.L.D. (minimum lethal dose) was 0.7, 1.2, 1.6 and 1.2 g cineole per kilo of body weight. There was therefore no apparent special resistance to cineole poisoning in the possum, Trichosurus vulpecula, a marsupial which feeds to some degree on eucalyptus foliage. Cleland calculated that koalas feeding on E. elaeophora, a high yielding species with a relatively high cineole content, might ingest daily about 0.2 g per kilo of body weight which would very conservatively be about one quarter of the probable minimum lethal dose. Cleland therefore concluded that a specific resistance to cineole in koalas was unnecessary. However, if E. radiata 'type' (70% cineole, yield 3.5%) is substituted for E. elaeophora in Cleland's calculation, the daily ingestion rises to about 1.0 g per kilo of body weight. This value suggests that a diet exclusively of E. radiata 'type' might be toxic to koalas, particularly since Cleland cited evidence that there are cumulative effects with cineole doses in excess of 1 g per kilo given on successive days. Pratt (1937) reported that koalas in Victoria 'relished' E. australiana = E. radiata as a 'change-of-diet species', while Fleay (1937) said of this species that it was 'eaten sparingly but enjoyably throughout the year'.

Even so, a direct toxic effect of cineole, or some other component of eucalyptus oil, is an unlikely explanation for the majority of preferences displayed by koalas. Few species have yields comparable to that of *E. radiata* (3.5%). Indeed, of the 168 species tested by Baker and Smith only 7 gave a yield exceeding 2%.

However, the consequence for gut flora of essential oil in a diet of eucalyptus foliage is another matter. Nagy, Steinhoff and Ward (1964) found the essential oils of big sagebrush to have broad antibacterial properties and to inhibit the growth of cultured micro-organisms from the rumen of mule deer, *Odocoileus hemionus*. Their studies suggested that cellulose digestion would be slowed down slightly if the diet contained 15 - 30% of big sagebrush (oil content 1 - 2%) and that a definite depression of microbial activity would follow a diet entirely of big sagebrush. Appetite and rumen movement in a steer ceased completely following the introduction of 21 pounds of sagebrush in 7 pound daily portions through a rumen fistula. Recovery did not take place until the seventh day when the contents of the rumen were replaced with that from fistulated cows fed alfalfa hay. Penfold and Grant (1922; 1923) reported the germicidal values of the principal commercial eucalyptus oils and their pure constituents (in Rideal-Walker carbolic acid co-efficients). They found the crude oils to have values comparable to those of tar oil products, activity depending largely on the ketone, alcohol, aldehyde and phenol content (see also Greig-Smith, 1919).

The production of essential oils by plant species can be most variable. Among the eucalypts, 'physiological forms' or 'chemical varieties' have been found in some species (Penfold and Willis, 1961) pp. 279 - 280. McKern *et al.*, (1951) showed large variation in yield and composition between individual trees belonging to the same population in two species. They also showed significant differences in yield and composition between young and old leaves from *E. dives*. Berry *et al.*, (1937) found a wide variation in yield and composition of oils distilled from growing tips of *E. cneorifolia* at different seasons, though the sampling procedure used in this study was criticised by McKern *et al*. Gaponenkov and Aleshin (1933 cit. Haagen-Smit, 1948) p. 69 reported large daily fluctuations in the oil content of nutmeg sage and variations in yield associated with weather.

There is therefore both strong a priori grounds for thinking that the essential oils of eucalypts are likely to be significant to the koalas feeding on them, and evidence that variations in their yield and their composition are sufficient to account for much of the capriciousness of the koalas' responses. In view of an association between palatability and oil yield shown in part 1 of this Section, the general hypothesis that the responses of koalas to different species of eucalypt are related to the effect of oil on the caecal flora, would seem a promising line of research to pursue.

APPENDIX

GENETIC AND SYSTEMATIC STATUS OF MANNA GUM

All the manna gums on Kangaroo Island and in the Mount Lofty Ranges near Adelaide which I examined, had at least some flower clusters with more than three flowers and rough bark varying from a relatively small amount at the butt to a large amount extending to the secondary branches. They therefore fitted the description of *E. viminalis* var. *huberiana* given by Burbidge (1947). However, Pryor (1955) suggested that most of the trees in South Australia and Victoria generally referred to *E. viminalis* var. *huberiana* Burbidge or *E. huberiana* Naudin should be considered members of a segregating hybrid swarm of *E. viminalis* x *E. aromaphloia*. The uncertain genetic status of South Australian manna gum did not overly concern me in this study. Foliage taken from different manna gums was always similar in appearance, taste and smell and clearly differed from that of other eucalypts. In view of the doubt attached to the varietal rank, I have retained the name *E. viminalis* for all manna gums growing on Kangaroo Island and in the Mount Lofty Ranges.

Hybridization is not uncommon in eucalypts. Boomsma (1949) has reported the occurrence of isolated hybrid trees as well as segregating hybrid swarms of various kinds in the Mount Lofty Ranges. The trees used in the foliage preference and maintenance trials undertaken during this study were all ones readily assignable to species.

BIBLIOGRAPHY

Andrewartha, H.G. (1957)
The Use of Conceptual Models in Population Ecology.
Cold Spring Harbor Symposia on Quantitative Biology:
XXII, 219-236.

Andrewartha, H.G. (1959)
Density-Dependent Factors in Ecology.
Nature: 183, 4655, 200.

Andrewartha, H.G. (1970)
Introduction to the Study of Animal Populations. 2nd ed.
London: Methuen and Co. Ltd.

Andrewartha, H.G., and Birch, L.C. (1954)
The Distribution and Abundance of Animals.
Chicago: The University of Chicago Press.

Andrewartha, H.G. and Browning, T.O. (1961)
An analysis of the idea of "resources" in animal ecology.
Journal of Theoretical Biology: 1, 83-97.

Asdell, S.A. (1946)
Patterns of Mammalian Reproduction.
New York: Comstock Publishing Co.

Backhouse, T.C., and Bolliger, A. (1960)a
Cryptococcosis in the Koala (Phascolarctos cinereus).
The Australian Journal of Science: 23, 3, 86.

Backhouse, T.C., and Bolliger, A. (1961)
Morbidity and Mortality in the Koala (Phascolarctus cinereus).
Australian Journal of Zoology: 9, 1, 24 - 37.

Baker, R.T. and Smith, H.G. (1920)
A Research on the Eucalypts especially in regard to their
Essential Oils (2nd ed.).
Sydney: Government Printer.

Bartholomai, A. (1968)
A New Fossil Koala from Queensland and a Re-assessment of the
Taxonomic position of the Problematical Species, Koalemus
ingens De Vis.
Memoirs of the Queensland Museum: 15, 2, 65 - 71.

Bauer, F. (1959)
The Regional Geography of Kangaroo Island, South Australia.
Ph. D. thesis. The University of Adelaide.

Bensley, B.A. (1903)
On the Evolution of the Australian Marsupials; with Remarks on the Relationships of the Marsupials in General.
The Transactions of the Linnean Society of London:
IX, III, 83 - 217.

Berger, P.J. (1966)
Eleven-month "Embryonic Diapause" in a Marsupial.
Nature: 211, 5047, 435 - 436.

Berger, P.J. (1970)
The Reproductive Biology of the Tammar Wallaby, Macropus eugenii Desmarest (Marsupialia).
Ph. D. Thesis. Department of Biology, Graduate School of Tulane University.

Berry, P.A., Macbeth, A.K., and Swanson, T.B. (1937)
The carbonyl constituents of Eucalyptus oils.
Part II. The seasonal variation of E. cneorifolia.
Journal of the Chemical Society: 1443 - 7.

Bolliger, A. (1953)
The Adrenals of the Koala (Phascolarctos cinereus) and their Alleged Relationship to Eucalyptus Leaf Diet.
The Medical Journal of Australia: June 27, 917.

Bolliger, A. (1962)
Gravel in the Caecum of the Koala (Phascolarctos cinereus).
The Australian Journal of Science: 24, 10, 416.

Bolliger et al. (1960)a See Backhouse and Bolliger.

Bolliger, A., and Backhouse, T.C. (1960)b
The Blood of the Koala (Phascolarctos cinereus).
Australian Journal of Zoology: 8, 3, 363 - 370.

Bolliger et al. (1961) See Backhouse and Bolliger.

Bolliger et al. (1962) See Finckh and Bolliger.

Bolliger et al. (1963) See Finckh and Bolliger.

Bolliger, A., and Shorland, F.B. (1963)
Investigation on Fats of Australian Mammals.
The Australian Journal of Science: 25, 11, 453 - 456.

Boomsma, C.D. (1949)
Nomenclature of Eucalypts with Special Reference to Taxonomic Problems in South Australia.
Transactions of the Royal Society of South Australia:
72, 2, 221 - 227.

Bradshaw, S.D., and Shoemaker, V.H. (1967)
Aspects of Water and Electrolyte Changes in a Field Population of Amphiboluvus lizards.
Comparative Biochemistry and Physiology: 20, 855 - 865.

Briese, D. (1970)
The Oestrous Cycle of the Koala (Phascolarctos cinereus).
Hons. Research Project Report: Department of Zoology, The University of Adelaide.

Brown, G.D. (1968)
The Nitrogen and Energy Requirements of the Euro (Macropus robustus) and Other Species of Macropod Marsupials.
Proceedings of the Ecological Society of Australia: 3, 106 - 112.

Burbridge, N.T. (1947)
Key to the South Australian Species of Eucalyptus L'Herit.
Transactions of the Royal Society of South Australia: 71, 2, 137 - 167.

Burnet, N.M. (1934) See Sutton (1934).

Burnet, N.M. (1938)
The Case for the Koala.
Wildlife: Nov.-Dec., 9 - 10.

Burt, W.H. (1943)
Territoriality and Home Range Concepts as Applied to Mammals.
Journal of Mammalogy: 24, 346 - 352.

Calaby, J.H. (1958)
Studies on Marsupial Nutrition II. The Rate of Passage of Food Residues and Digestibility of Crude Fibre and Protein by the Quokka, Setonix brachyurus (Quoy and Gaimard).
Australian Journal of Biological Sciences: 11, 571 - 580.

Calaby, J.H., and Poole, W.E. (1971)
Breeding Kangaroos in Captivity.
International Zoo Yearbook: 11, 5 - 12.

Catchpole, C.K. (1972)
A Comparative Study of Territory in the Reed Warbler (Acrocephalus scirpaceus) and Sedge Warbler (A. schoenobaenus).
Journal of Zoology (London): 166, 213 - 231.

Chapman, T.E., and Black, A.L. (1967)
Water Turnover in Chickens.
Poultry Science: 46, 761 - 765.

Chitty, D. (1967)
The Natural Selection of Self-Regulatory Behaviour in
Animal Populations.
Proceedings of the Ecological Society of Australia: 2, 51-73.

Christian, J.J. (1950)
The Adreno-Pituitary System and Population Cycles in Mammals.
Journal of Mammalogy: 31, 247 - 259.

Christian, J.J., and Davis, D.E. (1964)
Endocrines, Behaviour and Population.
Science: 146, 1550 - 60.

Church, R.L. (1966)
Water Exchanges of the California Vole, *Microtus californicus*.
Physiological Zoology: 39, 4, 326 - 340.

Clark, M.J. (1967)
Pregnancy in the Lactating Pigmy Possum,
Cercatetus concinnus.
Australian Journal of Zoology: 15, 673 - 683.

Clark, M.J., and Poole, W.E. (1967)
The Reproductive System and Embryonic Diapause in
the Female Grey Kangaroo, *Macropus giganteus*.
Australian Journal of Zoology: 15, 441 - 459.

Cleland, J.B. (1946)
Cystinuria.
M.Sc. Thesis: The University of Adelaide.

Crook, J.H. (1970)
Social organization and the environment: aspects of contemporary
social ethology.
Animal Behaviour: 18, 197 - 209.

Dawson, T.J., and Hulbert, A.J. (1970)
Standard Metabolism, Body Temperature, and Surface
Areas of Australian Marsupials.
American Journal of Physiology: 218, 4, 1233 - 1238.

De Vis, C.W. (1889)
On the Phalangistidae of the Post-Tertiary Period in Queensland.
Proceedings of the Royal Society of Queensland: 6, 105 - 114.

Ealey, E.H.M., and Main, A.R. (1967)
Ecology of the Euro, *Macropus robustus* (Gould), in North-Western
Australia III. Seasonal Changes in Nutrition.
C.S.I.R.O. Wildlife Research: 12, 53 - 65.

Faulkner, A.S. (1922)
The Life of a Native Bear (Koala) in Captivity.
The Australian Zoologist: 3, 332.

Finckh, E.S., and Bolliger, A. (1962)
The Prevalence of Cryptococcosis in the Koala
(Phascolarctos cinereus).
The Medical Journal of Australia: April 14, 545 - 547.

Finckh, E.S., and Bolliger, A. (1963)
Serous Cystadenomata of the Ovary in the Koala.
The Journal of Pathology and Bacteriology: 85, 2, 526 - 528.

Finnemore, H., Reichard, S.K., and Large, D.K. (1935)
Cyanogenetic Glucosides in Australian Plants.
Part 3 - E. cladocalyx.
Proceedings of the Royal Society of New South Wales: 69, 209 - 214.

Fleay, D. (1937)
Observations on the Koala in Captivity.
The Australian Zoologist: 9, 1, 68 - 80.

Fleay, D. (1947)
Gliders of the Gum Trees.
Melbourne: Bread and Cheese Club.

Foot, J.Z., and Romberg, B. (1965)
The Utilization of Roughage by Sheep and the
Red Kangaroo, Macropus rufus (Desmarest).
Australian Journal of Agricultural Research: 16, 429 - 435.

Forbes, W.A. (1881)
On Some Points in the Anatomy of the Koala (Phascolarctus cinereus).
Proceedings of the Zoological Society of London: Jan. 18, 180 - 195.

Forbes, D.K., and Tribe, D.E. (1970)
The Utilization of Roughages by Sheep and Kangaroos.
Australian Journal of Zoology: 18, 247 - 256.

Gaebler, O.H., and Choitz, H.C. (1964)
Studies of Body Water and Water Turnover
Determined with Deuterium Oxide Added to Food.
Clinical Chemistry: 10, 1, 13 - 19.

Gilmore, D.P. (1970)
The Rate of Passage of Food in the Brush-tailed Possum,
Trichosurus vulpecula.
The Australian Journal of Biological Science: 23, 515 - 518.

Glauert, L. (1910)
The Mammoth Cave.
Records of the West Australian Museum: 1, 1, 11 - 36.

Gosse, J.H. (1939)
Flinders Chase Sanctuary.
The Koala Magazine: 1, 3, 12 - 13.

Green, B. (1969)
Water and Electrolyte Balance in the Sand Goanna
Varanus gouldii (Gray).
Ph. D. Thesis: The University of Adelaide.

Greig-Smith, R. (1919)
The Germicidal Activity of the Eucalyptus Oils.
Parts i and ii.
The Proceedings of the Linnean Society of N.S.W.:
XLIV, 72 - 92 and 311 - 347.

Haagen-Smit, A.J. (1948)
The Chemistry, Origin and Function of Essential Oils in
Plant Life: in, The Essential Oils.
Volume 1, 17 - 77, Guenther. (Ed.)
New York: D. Van Nostrand Co.

Hamilton, W.D. (1964)
The Genetical Evolution of Social Behaviour.
I and II.
Journal of Theoretical Biology: 7, 1, 1 - 52.

Heinsohn, G.E. (1966)
Ecology and Reproduction of the Tasmanian Bandicoots
(Perameles gunni and Isoodon obesulus).
University of California Publication in Zoology: 80.
Berkeley and Los Angeles: University of California Press.

Hill, J.P., and Hill, W.C.O. (1955)
The growth stages of the pouch young of the native cat
(Dasyurus viverrinus) together with observations on the
anatomy of the new born young.
Transactions of the Zoological Society of London: 28, 349 - 452.

Hinde, R.A. (1956)
The Biological Significance of the Territories of Birds.
Ibis: 98, 3, 340 - 69.

Hughes, R.L. (1965)
Comparative Morphology of Spermatozoa from Five Marsupial
Families.
Australian Journal of Zoology: 13, 533 - 543.

Hughes, R.L., Thomson, J.A., and Owen, W.H. (1965)
Reproduction in Natural Populations of The Australian Ringtail Possum, Pseudocheirus peregrinus (Marsupialia: Phalangeridae), in Victoria.
Australian Journal of Zoology: 13, 383 - 406.

Iredale, T., and Troughton, E. Le G. (1934)
A Check-list of the Mammals Recorded from Australia.
Memoir of The Australian Museum, Sydney: VI, 1 - 122.

Jacobs, M.R. (1936)
The Primary and Secondary Leaf Bearing Systems of the Eucalypts and their Silvicultural Significance.
Commonwealth Forestry Bureau: Bulletin No. 18.

Jacobs, M.R. (1955)
Growth habits of the eucalypts.
Canberra: Commonwealth Government Printer.

Jewell, P A. (1966)
The Concept of Home Range in Mammals.
In, Jewell, P.A., and Loizos, C. (Eds.).
Play, Exploration and Territory in Mammals.
Symposium of the Zoological Society of London: 18, 85 - 109.

Kaufmann, J.H. (1971)
Is Territoriality Definable?
In, Behaviour and Environment. A.H. Esser (Ed.).
New York: Plenum Press: 36 - 40.

Kershaw, J.A. (1934)
The Koala on Wilson's Promontory.
Victorian Naturalist: LI, 3, 76 - 77.

Kikkawa, J., and Walter, M. (1968)
Distribution of Koalas in Queensland.
Wildlife in Australia: 5, 4, 100 - 103.

Kirsch, J.A.W. (1968)
Prodromus of the Comparative Serology of Marsupialia.
Nature: 217, 5217, 418 - 420.

Knox, K.L., Nagy, J.G., and Brown, R.D. (1969)
Water Turnover in Mule Deer.
Journal of Wildlife Management: 33, 2, 389 - 393.

Lack, D. (1954)
The Natural Regulation of Animal Numbers.
Oxford: Clarendon Press.

Lack, D. (1960)
Population Studies of Birds.
Oxford: Clarendon Press.

Lewis, F. (1934)
The Koala in Victoria.
Victorian Naturalist: 51, 3, 73 - 76.

Leyhausen, P. (1971)
Dominance and Territoriality as Complemented in Mammalian Social Structure.
In, Behaviour and Environment. A.H. Esser (Ed.)
New York: Plenum Press: 22 - 33.

Lifson, N., and McClintock, R. (1966)
Theory of Use of the Turnover Rates of Body Water for Measuring Energy and Material Balance.
Journal of Theoretical Biology: 12, 46 - 74.

Lucas, A.H.S. and Le Souef, W.H.D. (1909)
The Animals of Australia.
Melbourne: Whitcombe and Tombs Ltd.

MacFarlane, W.V. (1968)
Adaptation of Ruminants to Tropics and Deserts;
In, Adaptation of Domestic Animals, E.S.E. Hafez (Ed.),
164 - 182.
Philadelphia: Lea and Febiger.

MacFarlane, W.V., Morris, R.J.H., and Howard, B. (1963)
Turn-over and Distribution of Water in Desert Camels, Sheep, Cattle and Kangaroos.
Nature: 197, 270 - 271.

McIntosh, D.L. (1966)
The Digestibility of Two Roughages and the Rates of Passage of Their Residues by the Red Kangaroo, Megaleia rufa (Desmarest) and the Merino Sheep.
C.S.I.R.O. Wildlife Research: 11, 125 - 135.

MacKenzie, W.C. (1918)
The Gastro-Intestinal Tract in Monotremes and Marsupials.
Australia: Critchley Parker Pty. Ltd.

MacKenzie, W.C., and Owen, W.T. (1919)
The Glandular System in Monotremes and Marsupials.
Australia: Critchley Parker Pty. Ltd.

McKern, H.H.G., and Smith-White, S. (1948)
An improved distillation apparatus for the determination of the essential oil content of plant material.
Journal and Proceedings of the Australian Chemical Institute: 25, 276 - 8.

McKern, H.H.G., Spies, M.C., and Willis, J.L. (1951)
Critical Studies on Variations in Essential Oil Yield and Composition within and between Individual Trees of various Eucalyptus Species.
Paper presented to the Brisbane meeting of the Australian and New Zealand Association for the Advancement of Science held in May, 1951.

Mackerras, I.M. (1958)
Catalogue of Australian Mammals and Their Recorded Internal Parasites. Part 3. Monotremes and Marsupials.
Proceedings of the Linnean Society of New South Wales: 83, 101 - 125.

MacMillen, R.E., and Nelson, J.E. (1969)
Bioenergetics and Body Size in Dasyurid Marsupials.
American Journal of Physiology: 217, 4, 1246 - 1251.

McNally, J. (1957)
A Field Survey of a Koala Population.
Proceedings of the Royal Zoological Society of New South Wales, 1955 - 56: 18 - 27.

McNally, J. (1960)
Koala Management in Victoria.
The Australian Museum Magazine: XIII, 6.

MacPherson, J. (1925)
The Toxicology of Eucalyptus Oil.
The Medical Journal of Australia: July 25, 108 - 110.

Main, A.R. (1968)
Physiology in the Management of Kangaroos and Wallabies.
Proceedings of the Ecological Society of Australia: 3, 96 - 105.

Marlow, B.J. (1962)
Marsupials of Australia.
Brisbane: The Jacaranda Press.

Martin, P.G., and Hayman, D.L. (1967)
Quantitative Comparisons Between the Karyotypes of Australian Marsupials From Three Different Superfamilies.
Chromosoma: 20, 290 - 310.

Merchant, J.C., and Sharman, G.B. (1966)
Observations on the Attachment of Marsupial Pouch Young to the Teats and on the Rearing of Pouch Young by Foster-Mothers of the Same or Different Species.
Australian Journal of Zoology: 14, 593 - 609.

Milne, A. (1957)
Theories of Natural Control of Insect Populations.
Cold Spring Harbor Symposia on Quantitative Biology: XXII, 253 - 272.

Minchin, K. (1937)
Notes on the Weaning of a Young Koala Phascolarctos cinereus.
Records South Australian Museum: 6, 1, 1 - 3.

Minnich, J.E. (1970)
Water and Electrolyte Balance of the Desert Iguana, Dipsosaurus dorsalis, in its natural habitat.
Comparative Biochemistry and Physiology: 35, 921 - 923.

Moir, R.J., Somers, M., and Waring, H. (1956)
Studies on marsupial nutrition I. Ruminant-like digestion in a herbivorous marsupial Setonix brachyurus (Quoy and Gaimard).
Australian Journal of Biological Sciences: 9, 293 - 304.

Mountford, C.P. (1965)
see Roberts and Mountford (1965).

Mullen, R.K. (1970)
Respiratory Metabolism and Body Water Turnover Rates of Perognathus formosus in its Natural Environment.
Comparative Biochemistry and Physiology: 32, 259 - 265.

Munday, K.A. (1961)
Aspects of Stress Phenomena.
Symposium of the Society for Experimental Biology: 15, 168 - 189.

Myers, K., Hale, C.S. Mykytowycz, R., and Hughes, R.L. (1971)
The Effects of Varying Density and Space on Sociality and Health in Animals. In, Behaviour and Environment. A.H. Esser (Ed.).
New York: Plenum Press. 148 - 187.

Nagy, J.G., Steinhoff, H.W., and Ward, G.M. (1964)
Effects of Essential Oils of Sagebrush on Deer Rumen Microbial Function.
The Journal of Wildlife Management: 28, 4, 785 - 790.

Nicholson, A.J. (1933)
The Balance of Animal Populations.
Journal of Animal Ecology: 2, 132 - 178.

Ogilby, J.D. (1892)
Catalogue of Australian Mammals with Introductory Notes on General Mammalogy.
Australian Museum Sydney Catalogue No. 16.

Oldfield Thomas (1887)
On the Milk Dentition of the Koala.
Proceedings of the Zoological Society of London: Pt. 3, 338 - 339.

Oldfield Thomas. (1888)
Catalogue of the Marsupialia and Monotremata in the Collection of the British Museum (Natural History).

Oldfield Thomas (1923)
On Some Queensland Phalangeridae.
Annals and Magazine of Natural History: (9), xi, 246 - 250.

Pearson, J. (1949)
Placentation of the Marsupialia.
Proceedings of the Linnean Society of London: 161, 1 - 3.

Penfold, A.R., and Grant, R. (1922)
The Economic Utilization of the Residues from the Steam Rectification of the Essential Oil of Eucalyptus cneorifolia and The Germicidal Values of the Crude Oil and the Pure 'Active' Constituents.
Proceedings of the Royal Society of New South Wales: 56, 219 - 226.

Penfold, A.R., and Grant, R. (1923)
The Germicidal Values of the Principal Commercial Eucalyptus Oils and Their Pure Constituents, with Observations on the Value of Concentrated Disinfectants.
Proceedings of the Royal Society of New South Wales: 57, 80 - 89.

Penfold, A.R., and Willis, J.L. (1961)
The Eucalypts.
London: Leonard Hill (Books) Ltd.

Philpott, C.M. (1965)
The Ecology of the Koala, Phascolarctos cinereus (Goldfuss), on Flinders Chase, Kangaroo Island.
Thesis: Department of Zoology, The University of Adelaide.

Pilton, P.E., and Sharman, G.B. (1962)
Reproduction in the marsupail Trichosurus vulpecula.
Journal of Endocrinology: 25, 119.

Pocock, R.I. (1921)
The External Characters of the Koala (Phascolarctos) and Some Related Marsupials.
Proceedings of the Zoological Society of London:
Pt. 3, 591 - 607.

Pratt, A. (1937)
The Call of the Koala.
Melbourne: Robertson and Mullens.

Pryor, L.D. (1955)
The Genetic and Systematic Status of Eucalyptus huberiana Naudin, E. viminalis Labill. and E. aromaphloia Pryor and Willis.
Transactions of the Royal Society of South Australia: 78, 156 - 164.

Ride, W.D.L. (1970)
A Guide to the Native Mammals of Australia.
Melbourne: Oxford University Press.

Roberts, A., and Mountford, C.P. (1965)
The Dreamtime.
Adelaide: Rigby Limited.

Roberts, J.E., Fisher, K.D., and Allen, T.H. (1958)
Tracer Methods for Estimating Total Water Exchange in Man.
Physics in Medecine and Biology: 3, 7 - 15.

Robinson, K. (1954)
Heat Tolerance of Australian monotremes and marsupials.
Australian Journal of Biological Science: 7, 348 - 360.

Rowley, I. (1956)
Individual marking of the rabbit Oryctolagus cuniculus (L).
C.S.I.R.O. Wildlife Research: 1, 1, 40 - 44.

Schmidt-Nielsen, K. (1964)
Desert Animals.
Oxford: Clarendon Press.

Schultze-Westrum, T. (1965)
Innerartliche Verstandigung Durch Dufte Beim Gleitbeutler
Petaurus breuiceps papuanus Thomas (Marsupialia,
Phalangeridae).
Zeitschrift fur Vergleichende Physiologie: 50, 151 - 220.

Sharman, G.B. (1961)
The Mitotic Chromosomes of Marsupials and Their Bearing
on Taxonomy and Phylogeny.
Australian Journal of Zoology: 9, 38 - 60.

Sharman, G.B., and Calaby, J.H. (1964)
Reproductive Behaviour in the red kangaroo, Megaleia rufa,
in captivity.
C.S.I.R.O. Wildlife Research: 9, 58.

Sharman, G.B., Calaby, J.H., and Poole, W.E. (1966)
Patterns of Reproduction in Female Diprotodont Marsupials;
In, Comparative Biology of Reproduction in Mammals.
Symposia of The Zoological Society: 15.
London and New York: Academic Press.

Sharman, G.B., Frith, H.J., and Calaby, J.H. (1964)
Growth of the Pouch Young, Tooth Eruption and Age
Determination in the Red Kangaroo, Megaleia Rufa.
C.S.I.R.O. Wildlife Research: 9, 1, 20 - 49.

Siegel, S. (1956)
Non-Parametric Statistics for the Behavioural Sciences.
New York: McGraw-Hill Book Co., Inc.

Simpson, G.G. (1945)
The Principles of Classification and A Classification of Mammals.
Bulletin of the American Museum of Natural History: 85, 350 pp.

Smith, R.F.C. (1969)
Studies on the Marsupial Glider, Schoinobates volans (Kerr)
I. Reproduction.
Australian Journal of Zoology: 17, 625 - 636.

Snedecor, G.W., and Cochran, W G. (1967)
Statistical Methods.
Ames: Iowa State U.P.

Solomon, M.E. (1964)
Analysis of Processes Involved in the Natural Control of Insects.
In, J.B. Cragg (Ed.), Advances in Ecological Research, 2, 1 - 58.
London: Academic Press.

Sonntag, C.F. (1922)
On the Myology and Classification of the Wombat, Koala and Phalangers.
Proceedings of the Zoological Society of London: 2, 863 - 896.

Stead, D.G. (1934)
The Koala or Native Bear.
Australian Wildlife: 1, 1, 13 - 22.

Stead, D.G. (1939)
Further Notes on the Koala with Special Reference to Some Recent Discussions.
Australian Wildlife: 1, 5, 45 - 56.

Stirton, R.A. (1957)
A New Koala from the Pliocene Palankarinna Fauna of South Australia.
Records of the South Australian Museum: 13, 1, 71 - 81.

Stirton, R.A., Tedford, R.H., and Miller, A.H. (1961)
Cenozoic Stratigraphy and Vertebrate Palaeontology of the Tirari Desert, South Australia.
Records of the South Australian Museum: 14, 1, 19 - 61.

Stirton, R.A., Tedford, R.H., and Woodburne, M.O. (1967)
A New Tertiary Formation and Fauna from the Tirari Desert, South Australia.
Records of the South Australian Museum: 15, 3, 427 - 462.

Sutton, C.S. (1934)
The Koala's Food Trees.
Victorian Naturalist: 51, 3, 78 - 80.

Tester, J.R., Warner, D.W., and Cochran, W.W. (1964)
A radio-tracking system for studying movements of deer.
The Journal of Wildlife Management: 28, 42 - 45.

Thomson, J.A., and Owen, W.H. (1964)
A Field Study of the Australian Ringtail Possum <u>Pseudocheirus peregrinus</u> (Marsupialia: Phalangeridae).
Ecological Monographs: 34, 1, 27 - 52.

Thomson and Owen (1965)
see Hughes, Thomson and Owen (1965)

Troughton, E. Le G. (1935)
<u>Phascolarctos cinereus victor</u>.
Australian Naturalist: 9, 139.

Troughton, E. (1941)
Furred Animals of Australia.
Sydney: Angus and Robertson Ltd.

Troughton, E. Le G. (1955)
The Koala.
Australian Museum Magazine: 11, (12), 396 - 401.

Turnbull, W.D., and Lundelius, E.L. (1970)
A Late Pliocene Mammalian Fauna from the Grange Burn, Victoria, Australia.
Fieldiana: Geology 19: 1 - 163.

Tyndale-Biscoe, C.H. (1968)
Reproduction and Post-Natal Development in the Marsupial Bettongia lesueur (Quoy and Gaimard).
Australian Journal of Zoology: 16, 577 - 602.

Tyndale-Biscoe, C.H., and Smith, R.F.C. (1969)a
Studies on the Marsupial Glider, Schoinobates volans (Kerr) II. Population Structure and Regulatory Mechanisms.
Journal of Animal Ecology: 38, 637 - 650.

Tyndale-Biscoe, C.H., and Smith, R.F.C. (1969)b
Studies on the Marsupial Glider, Schoinobates volans (Kerr) III. Response to Habitat Destruction.
Journal of Animal Ecology: 38, 651 - 659.

Wakefield, N.A. (1970)
Notes on the Glider-possum, Petaurus australis (Phalangeridae, Marsupialia).
Victorian Naturalist: 87, 8, - 236.

Walker, E.P. (Ed.) (1964)
Mammals of the World I.
Baltimore: John Hopkins Press.

Waring, H., Moir, R.J., and Tyndale-Biscoe, C.H. (1966)
Comparative Physiology of Marsupials.
Advances in Comparative Physiology and Biochemistry: 2, 237 - 376.

Waterhouse, G.R. (1846)
A Natural History of the Mammalia.
Vol. 1. Marsupiata, or Pouched Animals.
London: Hippolyte Baillière.

Watson, A., and Miller, G.R. (1971)
Territory Size and Aggression in a Fluctuating Red Grouse Population.
Journal of Animal Ecology: 40, 2, 367.

Watson, A., and Moss, R. (1970)
Dominance, Spacing Behaviour and Aggression in Relation to Population Limitation in Vertebrates.
In; Animal Populations in Relation to their Food Resources.
A. Watson (Ed.) 167 - 220.
Oxford: Blackwell.

Weiss, M., and Richards, P.G. (1970)
Adrenal Steriod Secretion in the Koala (Phascolarctos cinereus).
Journal of Endocrinology: 48, 145 - 6.

Williamson, M.H. (1957)
An Elementary Theory of Interspecific Competition.
Nature: 180, 1, 422 - 425.

Wood, J.G. (1930)
An Analysis of the Vegetation of Kangaroo Island and the Adjacent Peninsulas.
Transactions of the Royal Society of South Australia:
LIV, 105 - 139.

Wood Jones, F. (1923-25)
The Mammals of South Australia. Parts I - III.
Adelaide: Government Printer.

Wynne-Edwards, V.C. (1962)
Animal Disperson in Relation to Social Behaviour.
Edinburgh: Oliver and Boyd.