

**The ecology of the koala
(*Phascolarctos cinereus*) in over-browsed
habitats on Kangaroo Island, South Australia**

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A thesis submitted for the degree of Doctor of Philosophy in the
Faculty of Sciences

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November 2010

1 Introduction

Eucalyptus is the most abundant and widespread genus of trees throughout Australia and represents a potentially plentiful food source. However, a diet of eucalypt foliage presents a number of nutritional challenges for mammals, including low concentrations of nutrients, especially protein, high concentrations of components that interfere with digestion, especially lignin and tannins, and a range of potentially toxic secondary metabolites (Cork 1996; Cork and Foley 1997). As a consequence few herbivorous mammals take advantage of this abundant food source. Although the ringtail possum (*Pseudocheirus peregrinus*) and brushtail possum (*Trichosurus vulpecula*) consume eucalypt foliage, only the koala (*Phascolarctos cinereus*) and greater glider (*Petauroides volans*) rely entirely on the foliage of eucalypts as a source of nutriment (Cork 1996; Foley and Hume 1987; Lee and Martin 1988; Kavanagh and Lambert 1990; Munks and Green 1995; Landsberg and Cork 1997).

Not all eucalypts are palatable and koalas display dietary preferences for some species of eucalypts that are related to aspects of the nutritional quality and digestibility of foliage (and levels of secondary compounds) (Pratt 1937; Eberhard 1972; Robbins and Russell 1978; Gall 1980; Hindell *et al.* 1985; Martin 1985*a*; Hindell and Lee 1987; Gordon *et al.* 1988; Hindell and Lee 1988; White 1994; Ellis *et al.* 1995). Not surprisingly, this highly specialised diet has resulted in a close association between the distribution of koala populations and their preferred tree species. The current distribution of the koala is broken up into a number of separate populations throughout eastern and south-eastern Australia that are isolated by areas of unsuitable

habitat or cleared land. Due to restricted dispersal opportunities, high fecundity and relatively low mortality rates, some of these isolated koala populations have increased to levels where preferred tree species have come under pressure from over-browsing (Martin 1997; McLean 2003).

Circumstances of over-browsing of trees by koalas have been reported since the late 1800s and have occurred in Queensland, New South Wales, Victoria and more recently South Australia (Table 1-1). In many cases a number of management options have been considered to reduce koala numbers to sustainable levels. These include habitat protection and restoration, fertility suppression, translocation, introduction of *Chlamydia* and culling. To date fertility suppression and translocation have been the most publicly and politically acceptable, and therefore, most commonly implemented management strategies.

Table 1-1: Reports of tree defoliation by koalas in Australia

Location	Date	Author
Wilson's Promontory, VIC	1913	Kershaw 1934
French Is, VIC	1920s	McNally 1957
Quail Island, VIC	1940s	Warneke 1978
Wartook Island, VIC	1950s	Martin 1997
Goat Island, SA	1960s	Robinson 1978
Kangaroo Island, SA	1965	Philpott 1965
Kangaroo Island, SA	1966	Eberhard 1972
Tucki Tucki, NSW	1970s	Gall 1980
Walkerville, VIC	1980s	Martin 1985 ^{a,b}
Sandy Point, VIC	1983	Martin 1997
Kangaroo Island, SA	1986	Robinson <i>et al.</i> 1989
Springsure, QLD	1990s	Melzer and Lamb 1994
Kangaroo Island, SA	1996	StJohn 1997
Strathbogie Plateau, VIC	1997	Martin 1997
Framlingham Forest, VIC	1998	Martin and Handasyde 1999

Some of the earliest translocations of koalas occurred in Victoria in the 1920s when there was considerable concern surrounding the welfare of koalas in over-browsed habitats on French Island (Martin and Handasyde 1990). Implementation of a formal translocation program since that time has resulted in over 14, 000 animals being translocated from over-populated islands to more than 200 mainland sites (Martin and Handasyde 1990; Menkhorst *et al.* 1998). Availability of suitable release sites is now diminishing and many extant populations established through translocations, such as that on Kangaroo Island, are proving unsustainable (Menkhorst *et al.* 1998).

A total of 18 adult koalas and a number of young from French Island were introduced to Flinders Chase National Park on Kangaroo Island in 1923 and 1925 (Robinson *et al.* 1989; Martin and Handasyde 1990). Aside from alleviating problems associated with over-browsing on French Island, one of the objectives of these initial releases was to safeguard the species from extinction. Koalas on the mainland were threatened throughout their range from hunting, fire and extensive habitat clearing (Lewis 1934; Martin and Lee 1984; Reed and Lunney 1988). Such was the success of these translocations that by 1948 koalas were reported to be present in hundreds in areas surrounding the initial release site at Flinders Chase (Robinson *et al.* 1989) and it soon became apparent that translocations from Flinders Chase would be required to allay localised over-browsing (Philpott 1965).

Bush fires in Flinders Chase, and their perceived threat to the koala population, were the ultimate precursor to 10 koalas being translocated to Pioneer Bend on the Cygnet River on two separate occasions in 1955 and 1965 (Robinson *et al.* 1989; L. Kelly, personal communication, 1998). By the late 1980s, koalas were established along the length of the Cygnet River and its surrounds (Robinson *et al.* 1989). In 1996 the

population of koalas in the Cygnet River valley was estimated to be approximately 1300-2100 animals, with the estimate for the entire island being between 3000 and 5000 animals (StJohn 1997).

Scattered populations of koalas are now well established throughout the island from D'estrees Bay in the east through to Cape Border in the west (Masters *et al.* 2004). Of the 207,000 ha of native vegetation remaining on the island, only 1,400 ha is considered optimal koala habitat. This represents less than 1% of existing vegetation (St John 1997). This limited and patchy distribution of habitat, coupled with the koala population's propensity to increase due to the absence of disease associated with *Chlamydia*, lead to the occurrence of population densities in excess of five individuals per hectare in some areas (St John 1997; Masters *et al.* 2004). Hence, browsing pressure of koalas at higher densities on Kangaroo Island has resulted in severe defoliation and mortality of trees. Over-browsing by koalas is evident in many areas, and in riparian areas where preferred tree species occur; the majority of food trees have lost at least 50% of their foliage (St John 1997; Masters *et al.* 2004).

In 1996, publicity surrounding the koala over-population problem on Kangaroo Island, and consideration of culling as a management option, sparked widespread debate throughout the public, various interest groups, politicians, management agencies and scientists. Recognising the high level of concern and controversy, the South Australian government convened a Koala Management Task Force, comprising scientists and representatives of government and interest groups. The objectives of the Task Force were to investigate issues relating to koala management and provide recommendations on the future management of koalas in South Australia (Possingham *et al.* 1996). The principal recommendation of the Task Force was to cull

in order to ‘achieve a significant and immediate reduction in koala numbers’, followed by fertility control and translocation to maintain long-term sustainable koala densities. In contrast to this recommendation, the State and Federal governments nominated to sterilise in association with translocation to the mainland.

Throughout this process the establishment and implementation of sound management strategies aimed at addressing over-population problems were impeded by a lack of information on key aspects of koala ecology, which created uncertainty over the potential success and likely risks associated with various management options (Possingham *et al.* 1996). Research in over-populated regions has focussed primarily on the effect of over-browsing, and consequent tree defoliation, on koala condition and population dynamics (Gall 1980; Martin 1985*a*; Martin 1985*b*) with some work having also been done on koala translocations and resultant population dynamics in newly established populations (Gall 1980; Ellis *et al.* 1990; Lee *et al.* 1990; Martin and Handasyde 1990; Prevett 1991, 1996). However, there has been little investigation of the interaction between koalas and their browse trees beyond identification of preferred tree species and likely foliage selection criteria. On a broader scale, research on koalas has tended to be centred on koala biology, particularly koala physiology and the aetiology and epidemiology of *Chlamydia psittaci* (e.g. Obendorf 1983; Brown and Grice 1984; Brown *et al.* 1987; Canfield 1989; Cork 1990; Beal 1991; Osawa *et al.* 1993; White and Timms 1994; Hemsley and Canfield 1996; Augustine 1998; Krockenberger *et al.* 1998).

In its final report, the Koala Management Task Force recommended that research on koala management be expanded and identified a number of research priorities, which included:

- studies of koala browse impacts, koala demography, patterns of habitat use and the demography of preferred browse trees
- studies to establish safe and effective techniques of fertility suppression (Possingham *et al.* 1996).

This project was one of a number of concurrent research projects aimed at addressing the above research requirements. This research was supported by the South Australian Department for Environment and Heritage (DEH) as part of the Koala Rescue Program. The main focus of the project was to investigate:

- koala foraging behaviour
- tree response to extent and pattern of defoliation
- habitat use and tree preference in preferred and non-preferred habitats
- regenerative potential of over-browsed tree species
- effect of sterilisation and translocation of koalas on tree health.

Following is an outline of the structure of this thesis and a brief summary of the content of each chapter:

Chapter 1

Chapter one provides an overview of the history of koala over-population and tree defoliation throughout Australia. The history of koala introductions and translocations on Kangaroo Island is outlined and population management options reviewed. Issues surrounding over-population and tree defoliation on Kangaroo Island are discussed.

Chapter 2

Chapter two describes the climatic, topographic and vegetation characteristics of the various study sites associated with the project on Kangaroo Island and the Fleurieu Peninsula.

Chapter 3

Chapter three reports on the results of 24-hour observations of koala foraging behaviour. These observations were conducted to gain sufficient insight into the foraging behaviour of koalas to allow for the development of experimental defoliation trials to investigate the response of trees to foliage loss by koalas. This chapter also provides detailed information on daily time budgets of koalas and non-feeding behaviours such as social interaction.

Chapter 4

Chapter four discusses results of artificial defoliation experiments that were conducted to investigate the extent and pattern of browse on leaf production of manna gum and to determine how these factors contribute to the decline of tree health.

Chapter 5

Chapter five presents tree canopy condition and koala population monitoring results from Mine Creek: a tributary of the Cygnet River located near Pioneer Bend. The effect of koala sterilisation and translocation on koala numbers, sex ratios and fertility rates are discussed as is the response of over-browsed trees to fluctuations in koala numbers. The results of a tree guarding experiment aimed at investigating recovery potential of trees are also discussed.

Chapter 6

Chapter six reports on a radio-tracking study aimed at determining how koalas use vegetation communities that do not contain preferred tree species. The specific aims of this section of the study were to find out whether koalas live permanently in areas that consist of non-preferred tree species and if so, whether they establish stable home ranges within these vegetation associations.

Chapter 7

The final chapter of this thesis relates the results of this study to the management of over-abundant koala populations on Kangaroo Island and the south-east of Australia generally. This is discussed in context of current management efforts and possible future directions in management.

2 Description of Study Sites

2.1 Kangaroo Island

2.1.1 General

Kangaroo Island is located approximately 100 km south-west of Adelaide. It is separated from the mainland by Investigator Strait to the north (50 km wide) and Backstairs Passage to the east (15 km wide; Figure 2-1). The island was isolated from the mainland approximately 9,500 years ago following a rise in sea level at the end of the last glacial maximum (National Parks and Wildlife Service 1984; Clark 1976).

Kangaroo Island is 140 km from east to west, 55 km from north to south at its widest point, and has a total land area of approximately 4,400 km² (Twidale and Bourne 2002; Henschke 1997).

The climate on Kangaroo Island is cool and temperate with a distinct winter rainfall maximum (Burrows 1979). Average rainfall varies from over 900 mm in the north-west of the island to below 500 mm in the south-east. Mean monthly maxima range from 20 - 25°C in summer and 13 - 15°C in winter (Burrows 1979). Mean monthly minimum temperatures follow a similar seasonal pattern, ranging from about 13 - 16°C in February to 6 - 9°C in August.

Structurally, Kangaroo Island is an extension of the geological unit which includes the Mount Lofty Ranges and the Flinders Ranges (Northcote 1979). The dominant feature of the landscape is a large central plateau, which rises to between 100 and 300 m above sea level. The plateau gradually slopes toward limestone plains and sand

dunes to the south and is terminated by high cliffs along the north coast of the island (Northcote 1979).

Vegetation on the central plateau is dominated by mallee scrub and woodland (Ball 2002). Common tree species within these vegetation types include *Eucalyptus baxteri*, *E. obliqua*, *E. fasciculosa*, *E. cosmophylla*, *E. remota* and *E. diversifolia*. *Eucalyptus cladocaylx* is also occasionally found in open forest and woodland communities throughout the island, but is most abundant along creek lines in the west and the north of the island (Prescott 1995). Gum species such as *E. viminalis cygnetensis*, *E. leucoxyton* and *E. camaldulensis* are most common in river valleys. Coastal areas are dominated by heath and mallee scrub vegetation.

Although the eastern half of the island has been settled and farmed since the nineteenth century, wide-scale clearing and settlement of the island has only taken place since the advent of the War Service Land Settlement scheme in the 1940s (National Parks and Wildlife Service 1986). Between 1945 and 1955, 70% more land was cleared on the island than had been cleared in the preceding 109 years (National Parks and Wildlife Service 1986). Today, approximately 50% of the original vegetation cover remains, of which half occurs in conservation reserves (StJohn 1997). Kangaroo Island is free of rabbits, which have had a significant impact on vegetation on the mainland. Foxes are also absent (National Parks and Wildlife Service 1986). There is no record of a wild dog population on Kangaroo Island, however there have been anecdotal reports of domestic (farm) dogs killing koalas.

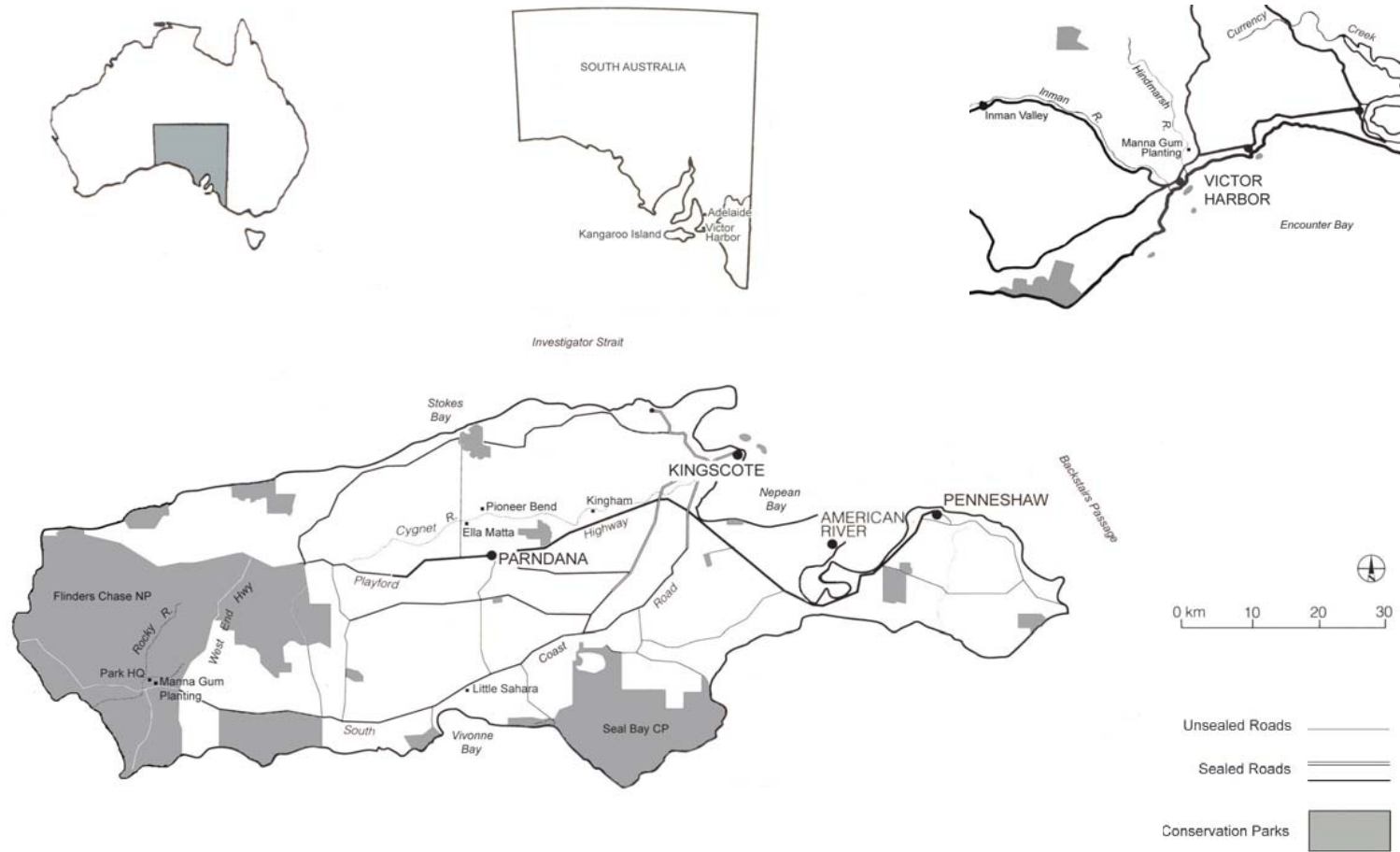


Figure 2-1: Location of study sites on Kangaroo Island and at Victor Harbor, South Australia

The economy on Kangaroo Island is primarily dependent upon rural production, fishing, tourism and related services (Kangaroo Island Tourism Working Party 1991). Most agricultural land is used for cereal cropping and grazing of sheep and cattle, however farmers are increasingly looking to industries such as timber production, aquaculture and tourism as a source of alternative income.

A number of sites on Kangaroo Island were directly associated with this study (Figure 2-1). Twenty-four hour behavioural observations (Chapter 3) were undertaken at Pioneer Bend and at Kingham's on the Cygnet River. Koala population census and tree health assessments (Chapter 5) were conducted along Mine Creek at Pioneer Bend and artificial defoliation experiments (Chapter 4) were conducted in Flinders Chase National Park. Enclosure experiments (Chapter 4) were conducted at Little Sahara on the south coast of the island. Radio-tracking (Chapter 6) was conducted primarily at Ella Matta and Pioneer Bend in the Cygnet River valley, and in areas surrounding Parndana.

2.1.2 Cygnet River

The Cygnet River originates in the north-central section of the island and travels approximately 70 km east to Nepean Bay where it discharges to the sea. Flow in the river is seasonally variable, with the highest flows occurring in winter and little or no flow occurring during summer. Dryland salinity affects most of the Cygnet River catchment and in areas of the lower Cygnet River, severe and extensive salinity has resulted in the death of native vegetation (principally *E. camaldulensis*) along drainage lines and salinisation of freshwater lagoons (Henschke 1997). However, defoliation of *E. camaldulensis* and other eucalypt species in the middle to upper reaches of the

Cygnet River is not due to salinisation (Ball 2002). The majority of land within the catchment consists of freehold pastoral properties.

Vegetation consists of a narrow belt of remnant riparian vegetation, along the main river channel and tributaries, surrounded by cleared agricultural land and patches of remnant woodland and mallee scrub (Figure 2-2). Riparian vegetation is dominated by tree associations containing *E. viminalis cygnetensis*, *E. leucoxyton* and/or *E. camaldulensis* (Figure 2-3). *Eucalyptus viminalis cygnetensis* is found along the length of the river, whereas *E. camaldulensis* tends to occur in the central to lower sections of the Cygnet River where frequent floodwater inundation occurs. *Eucalyptus leucoxyton* is more abundant in the upper and central sections of the Cygnet River. Understorey species are sparse within the riparian zone and comprise mainly of scattered *Acacia retinoides*, *A. paradoxa* and *Bursaria spinosa*. In the upper and central sections of the river, remnant vegetation on surrounding farmland is dominated by associations containing *E. cosmophylla*, *E. baxteri* and/or *E. obliqua* (Figure 2-4), whereas mallee scrub comprising of a *E. cneorifolia* association predominates in the lower third of the catchment.

Soils within the catchment are predominantly sandy loams with a clay sub-soil. A feature of these soils is their winter/spring waterlogging which is related to their relatively impermeable clay sub-soils (Northcote 1979).

2.1.3 Flinders Chase

Flinders Chase National Park is located at the western end of Kangaroo Island and has a total area of 73, 000 ha making it the largest conservation area on the island (Figure 2-1; National Parks and Wildlife Service 1986). Artificial defoliation

experiments were conducted on a section of *E. viminalis cygnetensis* plantings near the Rocky River park headquarters, which is located approximately 5 km from the main entrance to the park.

Prior to 1923, the area surrounding the Rocky River park headquarters formed part of a 3,642 ha freehold pastoral property. During this time 30 ha of land was cleared around the site of the current park headquarters to promote growth of feed for sheep (National Parks and Wildlife Service 1986). Much of this area is still open pasture interspersed with clumps of *Juncus pallidus* and *Gabnia filum*. Sparse emergent *E. ovata*, *E. viminalis cygnetensis* and *E. fasciculosa* form a tree stratum within the clearing, while surrounding areas consist of regenerating open forest dominated by *E. cladocalyx*. Various sections of the clearing have been revegetated since the late 1980s and in 1991 two plots in the south-east of the clearing were planted with *E. viminalis cygnetensis* (T. Berdin, personal communication, 1999). *Eucalyptus viminalis cygnetensis* trees in one of these plots were used for the artificial defoliation experiments described in Chapter 4 (Figure 2-5).

Surface soils in the area are generally sandy loams but relatively impermeable clay sub-soils make the area subject to waterlogging in winter and spring (National Parks and Wildlife Service 1986).



Figure 2-2: Remnant riparian vegetation along Cygnet River and tributaries. The Cygnet River and tributaries are surrounded by cleared agricultural land and patches of remnant woodland



Figure 2-3: Riparian vegetation. Vegetation typically consists of associations containing *E. viminalis cygnetensis* (left), *E. leucoxydon* (right) and/or *E. camaldulensis*



Figure 2-4: Remnant woodland on farmland. Vegetation typically consists of an association of *E. cosmophylla*, *E. baxteri* and/or *E. obliqua*



Figure 2-5: *Eucalyptus viminalis cygnetensis* revegetation plot adjacent to Park Headquarters at Flinders Chase National Park

2.1.4 Little Sahara

Little Sahara is located on the south coast of Kangaroo Island approximately 6 km east of the small settlement of Vivonne Bay (Figure 2-1). A proportion of this site falls within Seal Bay Conservation Park and the remainder is privately owned land, which is managed by the National Parks and Wildlife Service under a Heritage Agreement.

The vegetation at this site is dominated by low open woodland. Common mallee species include *E. diversifolia* and *E. rugosa*. Shrub and understorey species include *Melaleuca acuminata*, *M. lanceolata*, *Correa reflexa*, *Acacia triquetra* and *A. retinoides*. A small number of remnant *E. viminalis cygnetensis* occur in the area and they are currently being submerged by a mobile sand dune (Figure 2-6). The site is bounded by deep calciferous sand dunes to the south and sand drift is usual where dunes are not vegetated (Northcote 1979).

Shallow to deep alkaline sands cover calcrete bedrock, which protrudes through the soil surface in many areas (Northcote 1979).



Figure 2-6: Remnant *E. viminalis cygnetensis* (centre) at Little Sahara with mobile dune in foreground



Figure 2-7: Hindmarsh River revegetation plot at Victor Harbor

2.2 Victor Harbor

2.2.1 General

Victor Harbor is a small seaside town located 83 km south of Adelaide on the south-eastern side of the Fleurieu Peninsula (Figure 2-1). Artificial defoliation experiments (Chapter 4) were conducted on the outskirts of Victor Harbor at a revegetation site on the Hindmarsh River.

Like Kangaroo Island, Victor Harbor has a cool and temperate climate which is moderated by its proximity to the Southern Ocean (Dowling 1997). The area has an average annual rainfall of 535 mm which falls predominantly in winter. Mean monthly maxima range from 21 - 25°C in summer and 12 - 16°C in winter (Dowling 1997). Mean monthly minimum temperatures range from 12 - 14°C in summer and 4 - 8°C in winter.

Over the past 150 years the area surrounding Victor Harbor has changed from natural woodland and grasslands to a mixture of agriculture and urban development with small patches of remnant vegetation. The only remaining native vegetation at the study site is a narrow belt of riparian vegetation, which consists of an over-storey of *E. camaldulensis* and an understorey of introduced and native grasses. Otherwise, the site consists of approximately three hectares of eucalypt and *Acacia* species, which were planted along the south-eastern side of the river in 1993 (Figure 2-7).

The site is bordered by a recently developed golf course and housing estate to the east and a commercial recreation park which is located on the western side of the river.

Soils at the site consist of sandy loams over clay subsoils.

3 Feeding Behaviour, Time Budgets and Daily Activity

3.1 Introduction

Knowledge of the behaviour of a species can contribute substantially to our understanding of its ecology (Ruckstuhl 1998; Sutherland 1998). Despite the existence of a large body of literature on various aspects of the ecology of the koala there are limited observations of the behaviour of free-ranging koalas based on continuous direct observation in natural habitat. Instead, most descriptions of daily behaviour mainly come from studies of koalas in captive (Smith 1979*a*, 1979*b*, 1980*a*, 1980*b*, 1980*c*) or semi-natural situations (Robbins and Russell 1978).

3.1.1 Feeding Behaviour

Early accounts of koala feeding habits were often unreliable. Iredale and Whitley (1934) cite an 1808 account by Home in *Philosophical Transactions* which attributes, ‘the tender shoots of the blue gum tree’ as a food source of the koala by day and ‘particular plant roots’ their source of food by night. It is now well accepted that the diet of the koala principally consists of the leaves, buds, flowers and even bark of a variety of *Eucalyptus* species (Hindell *et al.* 1985; Hindell and Lee 1988; Martin 1983; Eberhard 1972; Smith 1979*a*). Koalas have also been observed feeding on a number of non-eucalypt species including: Kapok (*Bombax malabarica*); Brush Box (*Tristania conferta*); Swamp Mahogany (*T.suaveolens*); *Acacia costata*; *A.melanoxydon*; and Monterey Pine (*Pinus radiata*) (Lithgow 1982, Robbins and Russell 1978, Pearse and Eberhard 1978, Degabriele 1973). Although there is a considerable body of quantitative data

which describes feeding behaviour at the level of tree species selection and habitat preference, little work has been done which describes the behaviour of koalas while actually foraging (i.e. specific feeding behaviour).

The few systematic observations of feeding behaviour which have been done only provide estimates of total time spent feeding and the frequency of feeding activity over 24-hours (Nagy and Martin 1985; Sharpe 1980; Mitchell 1990*a,b*; Logan and Sanson 2002). This is likely to be a consequence of most observations having occurred as an adjunct to other studies, for which detailed observation of foraging behaviour was not required. Nagy and Martin (1985), for example, calculated time budgets whilst determining field metabolic and food consumption rates of koalas and Hindell *et al.* (1985) observed koalas to confirm the reliability of using daytime occupancy of trees as an indicator of trees in which koalas feed. Likewise, Logan and Sanson (2002) used acoustically-sensitive radio-telemetry to calculate time budgets and determine the effect of tooth wear on activity patterns of free-ranging koalas.

Smith's (1979*a*) study at Lone Pine Sanctuary in Queensland is the only behavioural study that has endeavoured to describe the feeding behaviour of koalas in any detail. However, given that the koalas in Smith's (1979*a*) study were housed in brick and concrete pens and fed regularly at the same time each day, feeding behaviour in this study it is likely that the results from this study are distorted and of minimal relevance in understanding the feeding behaviour of free-ranging koalas.

Most descriptions of feeding behaviour in natural situations are based on anecdotal or opportunistic records. Many accounts suggest that koalas are highly selective when feeding. Leaves at the tips of stems are sniffed and often rejected prior to a bout of feeding (Fleay 1937; Smith 1979*a*; Eberhard 1972; Lee and Martin 1988). Martin and

Handasyde (1999) state that it is a common misconception that koalas selectively feed on juvenile foliage at the tips of branches: instead they suggest that the bulk of the diet consists of relatively mature foliage because wild koalas do not have year round access to enough young leaf tips to meet their nutritional requirements. Once leaves are accepted, and feeding has commenced, koalas are reported to become less discriminating and often strip branches of all foliage. Feeding is thought to occur more often in the outer canopy of trees where foliage is concentrated and young leaves are often abundant (Hindell *et al.* 1985; Degarbrielle 1981; Ullrey *et al.* 1981).

Despite all that is currently known about the koala there remains a lack of detailed information with respect to foraging behaviour. In particular, there is little description of the distribution of foraging effort within trees and the extent of defoliation on individual branches. This precludes confident description of koala foraging behaviour.

3.1.2 Time Budgets

Few studies have described the day-to-day behaviour of koalas through direct observation in a natural situation. Due to the difficulty in observing free-ranging koalas over long continuous periods, the most detailed time budget data come from studies in captive (Smith 1979*a*) or semi-natural situations (Robbins and Russell 1978) or via indirect recording methods (Logan and Sanson 2002).

Continuous observations in natural situations have provided limited understanding of behaviour as sampling has often been restricted to a few individuals, frequently of the same sex, over one or two consecutive days (Sharpe 1980; Hindell *et al.* 1985; Nagy and Martin 1985; Logan and Sanson 2002). Alternatively, behavioural studies of free-

ranging koalas rely on instantaneous (i.e. behaviour of koala on first sighting) observations or short periods of continuous observation (up to six hours) which are compiled to provide estimates of daily time budgets and patterns of behaviour (Parker *et al.* 1986; Mitchell 1990*b*; Sharpe 1980).

Estimates for total time spent feeding vary considerably. Values for time spent feeding range from approximately 2.8 to 4.7 hours per day (Smith 1979*a*; Hindell *et al.* 1985; Nagy and Martin 1985; Mitchell 1990*b*; Logan and Sanson 2002). Observed bouts of feeding have ranged in duration from less than five minutes to just over two hours with up to six bouts of feeding reported to occur in a day (Martin and Lee 1984; Robbins and Russell 1978).

The degree of variation amongst estimates for time spent feeding may be explained, partly, by differences in sampling strategy. Nagy and Martin (1985) observed four females for one 24-hour period in September, whereas Mitchell's (1990*b*) estimates were determined on the basis of the frequency of instantaneous observations of feeding made over many months of field work. Hindell *et al.* (1985) observed four koalas, of unspecified sex, for a single 24-hour period in March. Differences in timing and length of observation, as well as sex and age of observed animals, are all likely to have contributed to the reported differences in time budget data. Logan and Sanson (2002) also found that increased tooth wear was associated with a significant increase in the amount of time spent feeding amongst six males koalas in their study.

Estimates of the amount of time resting over 24-hours are relatively consistent and range from 19 to 20.4 hours per day (Smith 1979*a*; Nagy and Martin 1985; Mitchell 1990*b*; Logan and Sanson 2002). Behaviour other than feeding and resting make up a small proportion of the daily cycle of activity of koalas, with no more than 40 minutes

per 24-hour period spent moving and eight minutes on social interaction (Mitchell 1990*b*). There is little information reported with regard to time budget data for social behaviour as interactions between individuals have rarely been observed during continuous 24-hour observations (Sharpe 1980; Nagy and Martin 1985; Hindell *et al.* 1985).

3.1.3 Daily Cycle of Activity

Most studies have shown that feeding occurs intermittently throughout the day and night, with a peak in feeding occurring late in the evening usually one or two hours either side of sunset (Nagy and Martin 1985; Hindell *et al.* 1985; Robbins and Russell 1978; Sharpe 1980; Parker *et al.* 1986). Peaks in feeding activity have also been observed during the mid-morning (Nagy and Martin 1985; Parker *et al.* 1986) and in the three hours before dawn (Sharpe 1980). Incidental observations by Cork and Warner (1983) indicate that, for captive animals, feeding peaked between midnight and early morning.

Periods of the day when feeding is entirely absent, or unlikely, have been identified by a number of authors. Robbins and Russell (1978), Sharpe (1980) and Lee and Martin (1988) suggest that there is a trough in feeding during the middle of the day (1200-1400h) and the middle of the night (2300-0200h). Koalas are considered to have a nocturnal pattern of activity with feeding, moving and social behaviour occurring more often during the night than day (Mitchell 1990*b*; Robbins and Russell 1978). However, Nagy and Martin (1985) found little evidence in their study to suggest that the activity of koalas is restricted to either day or night.

3.1.4 Purpose of This Study

The overall objective of this study was to conduct replicated observations of the daily behaviour of koalas in natural habitat. More specific aims were to (i) construct individual time budgets and daily patterns of activity for free-ranging koalas, and (ii) describe foraging behaviour of free-ranging koalas to better understand the spatial pattern of tree defoliation (e.g. distribution of browse effort within trees and on individual branches). The second of these two aims was directed specifically at providing input to the experimental design of artificial defoliation experiments which are described in Chapter 4.

3.2 Methods

Ten tagged and radio-collared koalas were observed on one to five occasions (i.e. 24-hour period) each between August 1997 and December 1998 (Table 3-1). Two koalas were observed continuously for 24-hours by two groups of observers working in six-hour shifts. Continuous observation was undertaken as it was considered to be more efficient in terms of guaranteeing observations of feeding behaviour than occasional spot-checks. Furthermore, infrequent and limited bouts of feeding make it difficult to predict when feeding behaviour is likely to occur and therefore when to conduct observations to coincide with feeding. This approach also allowed for differences between day and night and individual patterns of activity over 24-hours to be investigated.

Sampling involved recording times when behaviour changed, to the nearest ten seconds, so that duration and percentage time spent on each activity could be calculated. Five behavioural categories were recorded: feeding; moving (either within

a tree or from one tree to another); grooming; resting (either asleep or sitting and awake); and social interaction (e.g. direct contact and vocalisations).

Table 3-1: Number of 24-hour observations of koalas at various sites and times of year. n refers to the number of 24-hour observations completed for each koala

Animal	Sex	Status	n	Sample Months	Site	Weight (kg)
M001	Male	Entire	5	Aug-Sept 97	Kingham	10.1 (Aug 97)
M002	Male	Entire	3	Nov 97	Kingham	9.5 (Aug 97)
M003	Male	Desexed	8	Jan-Oct 98	Deep Creek	9.8 (Mar 98)
M004	Male	Desexed	1	Sept 98	Mine Creek	10.5 (Mar 98)
M005	Male	Desexed	8	Jan-Oct 98	Deep Creek	13.6 (Mar 98)
F001	Female	Entire	5	Sept-Nov 97	Kingham	8.3 (Aug 97)
F002	Female	Entire	1	Nov 97	Kingham	8.9 (Aug 97)
F003	Female	Desexed	1	Nov 97	Mine Creek	8.3 (Mar 98)
F004	Female	Desexed	1	Oct 98	Mine Creek	9.0 (Mar 98)
F005	Female	Desexed	1	Oct 98	Mine Creek	9.4 (Mar 98)

Types of plant material consumed (e.g. buds, fruits and young or mature leaves) during bouts of feeding were also recorded. The position of a koala in a tree was recorded by estimating the koala's height in the tree, with the use of a clinometer (Suunto PM-5), the aspect (north, east, south, west) occupied and type of branch it was sitting on with branches categorised from 1° through to 6° (Figure 3-1). Primary branches were considered to be the first set of branches extending from the main trunk, 2° those extending from the 1° branches and so on (Figure 3-1).

Although other studies have reported no disturbance to animals when observed with conventional spotlights or torches, red filters were attached to 75 watt hand-held spotlights (Light-Force) to minimise any potential disturbance (Nagy and Martin 1985; Robbins and Russell 1978).

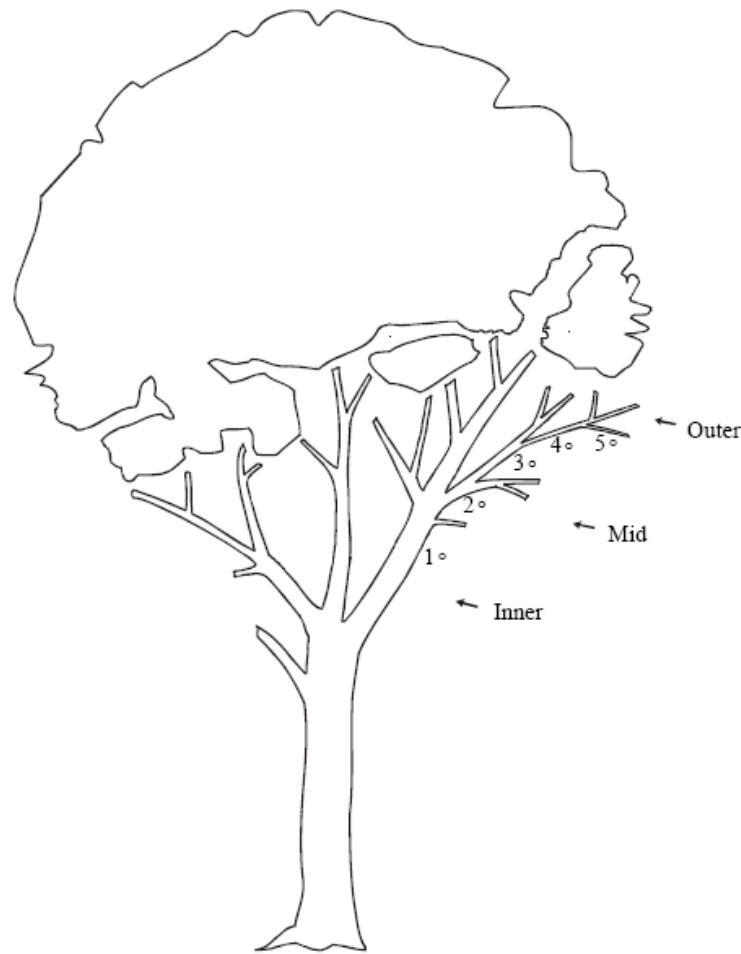


Figure 3-1: System used to record the type of branch used by a koala when recording its position in a tree. The outer-canopy usually consists of the foliage in the outermost 1-2 metres of the canopy (4° branches onward). Mid-canopy includes 2° and 3° branches. Foliage is usually absent from the inner canopy (trunk and 1° branches)

Furthermore, spotlights were adjusted to produce the minimum intensity of light required to observe animals. On many occasions there was no need for artificial lighting as animals were silhouetted well against moonlight. All observations were made using binoculars from the greatest distance practicable: typically at least 20 m.

Observations were conducted at three sites (Kingham, Mine Creek, Deep Creek) which all comprised of *E. leucoxylon*/*E. viminalis* tree associations (refer Chapter 2).

Koala M003, however, was in an *E. cosmophylla*/*E. baxteri*/*E. obliqua* tree association during six 24-hour observations.

3.3 Results

3.3.1 Feeding Behaviour

Koalas were observed feeding in seven species of eucalypt: *E. leucoxylon*; *E. cosmophylla*; *E. viminalis cygnetensis*; *E. cladocalyx*; *E. fasciculosa*; *E. camaldulensis* and *E. baxteri*. Feeding was not recorded on the two occasions when koalas were observed in *A. retinoides*. Koala F003 spent an entire 24-hour period in an *A. retinoides* without feeding. Data for this koala were excluded from further analysis (hence 33-days (i.e. 24-hour period) of observation were included in analysis). Otherwise, koalas were observed feeding in all the trees they occupied (koalas were observed in a total of 59 trees).

Feeding occurred primarily in the outer canopy of trees (79% of a total of 205 observed feeding bouts; Figure 3-2). Koalas sat as far out along branches as possible and reached out for leaves at the edge of the tree canopy. Branches were pulled in from the outer canopy and secured with a forepaw during feeding. Feeding only occurred in the mid-canopy of trees during 21% of feeding bouts and in each instance either dense branching or epicormic growth was present.

A bout of feeding was considered to be any period of feeding which was not interrupted by another activity (i.e. moving or resting) for longer than five minutes. An average of six bouts of feeding were recorded per day (range 2-19 feeding bouts per day across a total of 33 days (i.e. 24-hour period) of observation). Of these, an average of three feeding bouts occurred in each tree visited by a koala (range 1-17

feeding bouts in total of 59 trees that koalas were observed feeding in). Feeding bouts took place at one location in 67% of the 59 trees visited by observed koalas (location in tree was estimated on the basis of height in tree, type of branch and side of tree occupied). For 20% of trees, koalas fed at two different positions in the canopy and for 13% of trees feeding took place in three to five locations.

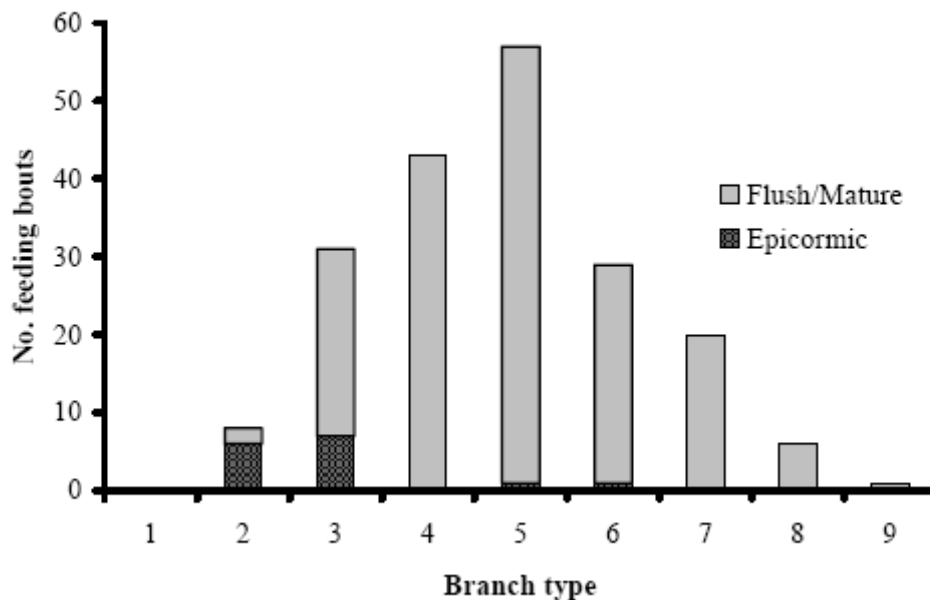


Figure 3-2: Position in tree (based on branch type(refer Figure 3-1)) and type of foliage consumed during feeding bouts (n = 205)

The concentration of foraging effort in one or two locations within a tree was often independent of resting position. Koalas rested and fed in the same position in a tree 56% of the time (i.e. koala did not move from a resting position before commencing feeding or move to another location after feeding to rest). Yet, when feeding and resting positions were different (44%) koalas were still observed returning to the

same one or two locations in a tree to feed. It was not possible to determine whether koalas fed in the same locations when trees were re-visited on a subsequent date; however on one occasion M001 was observed returning to the same tree, and same location in the tree, to feed after an absence of one month.

In 73% of 205 foraging bouts observed koalas remained stationary and browsed on branches within reach (less than one metre radius from sitting/standing position). Consequently, feeding tended to be concentrated on one branch. Koalas moved whilst feeding during 27% of feeding bouts. However, these movements were usually restricted to within 1 to 2 m of the koala's original position at the commencement of feeding. Only 28% of movements during feeding involved distances of 2 to 5 m. Of 205 observations of feeding there were only four occasions when koalas moved either throughout or across to the other side of a tree while foraging.

Koalas fed predominantly on flush (seasonal new shoot growth) and mature leaves. Epicormic growth (growth from an epicormic bud underneath the bark of a stem or a branch) was also occasionally eaten (16 of 205 feeding bouts). On 12 occasions koalas were observed sniffing leaves prior to feeding, but sniffing did not proceed all bouts of feeding. Low light intensity at night prevented observers from recording how often koalas sniffed leaves during this period of the day. Koalas consistently removed leaves from branches at the junction of the leaf and petiole and consumed leaves from base to tip. The exact proportion of leaves removed from branches could not be determined, but observers often noted that there appeared to be few leaves remaining on branches following a feeding bout.

There were no records of koalas selectively eating buds or flowers. Buds, flowers and stems did not appear to be preferentially selected for, but rather incidentally

consumed with surrounding leaves. Aside from a small number of leaves, buds were often the only part of the plant remaining on branches after koala browsing. Koala M005 was observed stripping and eating bark from branches on five occasions. Strips of bark were torn from branches with the use of the front incisors. No other koalas were observed eating bark.

Licking moisture from fur on the forearms and tree branches and trunks was observed on five occasions during rain. This usually lasted less than a minute, but on one occasion koala F001 licked water off a branch for 15 minutes. Koala M001 was observed lapping water from the Cygnet River for 15 minutes on one occasion en route from one tree to another.

Koalas fed immediately upon entering a new tree on 21 of the 31 occasions they were observed moving from one tree to another. In each of these cases koalas climbed up into the outer canopy of the new tree and did not display any other behaviour before feeding (e.g. resting or sleeping). In the remainder of instances koalas rested for between 18 minutes to almost two hours before feeding. Two observations are not included in the results, as the koala was either not re-located in time to determine its behaviour upon entering the tree or it did not feed in the tree it moved into (i.e. *A. retinoides*).

3.3.2 Non-Feeding Behaviour

Moving

Most movements within a tree occurred while animals were foraging, with only minor adjustments in position being made during rest. The exception was particularly hot or windy days when koalas moved throughout trees, apparently in an attempt to escape

the heat or find shelter from the wind. Koalas were also observed panting, drooling and licking forearms when weather conditions were hot *c.* 40°C.

Movements between trees were observed 31 times. All observed female koalas remained in one tree for the duration of 24-hour observations. Only once during a total of nine 24-hour periods that female koalas were observed did a female koala (F004) move through the canopy between two trees. All male koalas, except M004, were observed moving from one tree to another at least once during a 24-hour period of observation (male koalas were observed for a total of 25, 24-hour periods). During 80% of 24-hour observation periods male koalas made one to two movements from one tree to another. During two 24-hour periods M003 changed trees three times.

Koalas moved from one tree to another through the canopy of trees six times, but the majority of movements involved travelling across the ground (i.e. 25 of 31 observations of movement from one tree to another). The distances travelled from one tree to the next ranged from 5 m to 150 m with an average distance of 64 m. In all examples where koalas moved across the ground they travelled past other trees of the same size and species as the one they eventually occupied. Movements took place more often at night (83%) than during the day (17%). Use of the sternal gland by males to scent mark the base or trunks of trees was never observed. Nor was dribbling of urine on the ground close to visited trees. Koalas were observed urinating in trees, but never in a manner consistent with that described by Smith (1980*b*) and Martin and Lee (1984).

Social Interaction

Direct social interactions between koalas were observed on only six out of the thirty-four, 24-hour observation periods. This does not include observations of female

koalas with joeys ($n=3$). Five of the interactions involved one male and one female koala and one comprised of two males sharing a tree. Most interactions (5 observations) involved two koalas sharing the same tree while resting and occasionally feeding. Mutual sniffing and touching occurred briefly (up to 2½ minutes) during three of these observations. This behaviour primarily involved sniffing and touching the head and flanks (with forepaws) of the other koala.

A prolonged period of direct interaction between two koalas was only observed during one 24-hour watch. In January 1998 M005 and a female koala spent 22 ½ hours in the same tree during which they spent a total of 3 ½ hours sitting side-by-side. The interaction was non-aggressive and consisted of mutual sniffing, touching and nuzzling (licking and biting around the face and neck). Koala M005 and the female koala sat together on six occasions (the longest period being 1½ hours) throughout the day. No vocalisations were made during any of the encounters between koalas.

Observed males were heard bellowing during four 24-hour watches. These observations were made between the months of August and November. Numerous bellows from other male koalas in the vicinity of observed males were heard throughout the breeding season (August-March (Martin and Lee 1984)). A quarter of the bellows made by observed males appeared to be in response to other males in the area (a total of 22 bouts of bellowing were heard). Only one of the bellows made by an observed male appeared to elicit a response from another male. Sixty-seven percent of the bellows made by other males in the area drew no audible response from the male koalas being observed.

Grooming

Grooming was observed during 26 of the 24-hour observation periods and occurred up to 10 times per day. Instances of grooming usually lasted between 10 and 20 seconds and involved a series of scratches to the head, back, abdomen, arms or flanks with the use of the left or right foot. The lower body, abdomen and flanks were occasionally scratched with the forepaws. Licking or nibbling of the fur for the purpose of grooming was never observed, however, koalas did lick their forepaws during hot weather (*c.* 40°C), presumably as a means of cooling themselves. Koala F002 groomed for 27 minutes during one 24-hour observation as a response to persistent attempts by brown headed honeyeaters (*Melithreptus brevirostris*) to remove fur from her back and head.

3.3.3 Time Budgets

Data pooled over all koalas show that a large proportion of the day is spent resting with an average of only 3.2 hours of the day being allocated to feeding and moving (*n* = 33) (Figure 3-3). Little time was spent grooming with an average of 1.75 minutes per day spent on this activity (grooming was observed on 26 occasions).

Female koalas spent less time feeding (*t*-test, *df* = 32, *P* = 0.004) and moving (*df* 32, *P* = 0.001) and more time resting (*df* = 32, *P* = 0.006) than male koalas (Figure 3-4).

A considerable amount of variation occurred, for given koalas, in the amount of time spent feeding from one observation period to another. Feeding times ranged from: 2.5 - 4 hours for M001; 0.8 - 2 hours for F001; 1.5 - 4.5 for M005; and 1.5 - 3.5 hours for M003. There was an overall decline in feeding time for M005 from January 1998 through to October 1998.

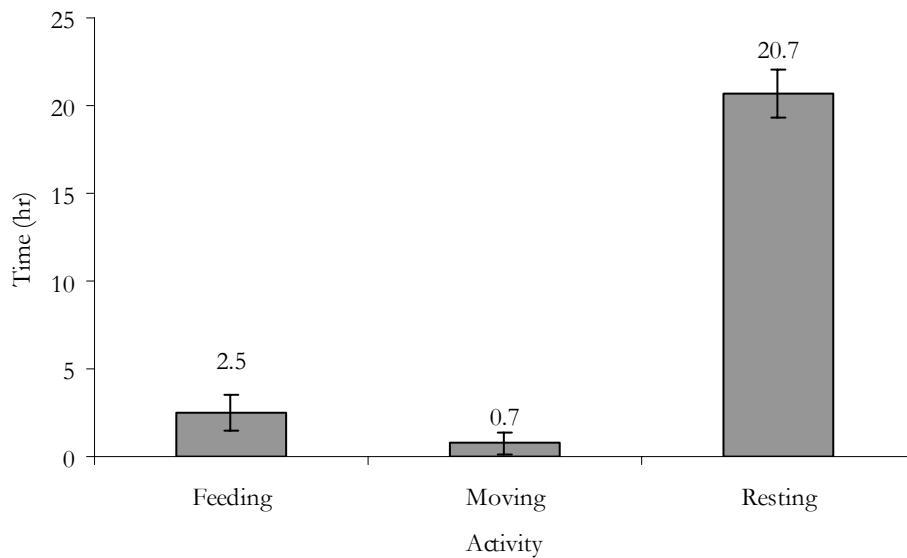


Figure 3-3: Average time spent (\pm SD) per 24-hour day on various activities for all koalas during 24-hour observations ($n = 33$). Data for F003 was excluded from analysis as it did not feed during the one 24-hour period it was observed

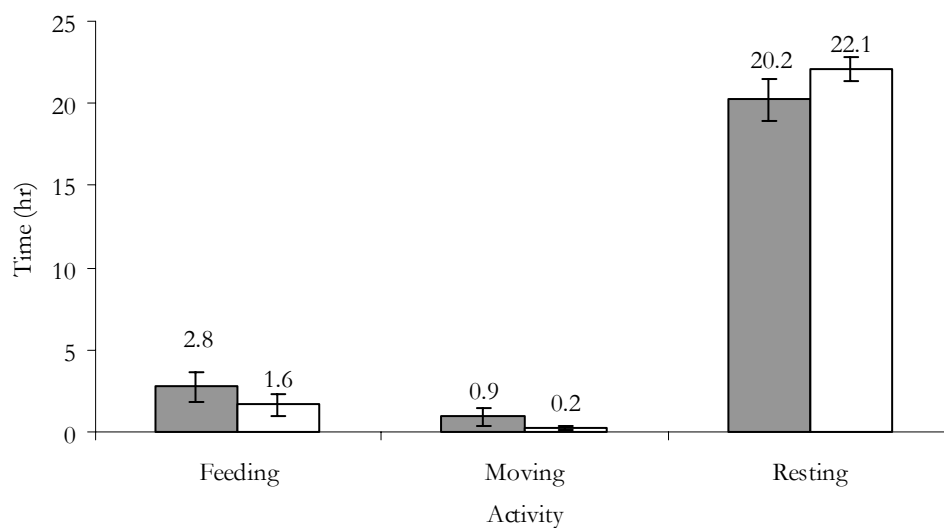


Figure 3-4: Average time spent (\pm SD) per 24-hour day on various activities for male ($n = 26$) and female koalas ($n = 7$). Grey columns denote values for male koalas; white columns denote values for female koalas. Data for F003 was excluded from analysis as it did not feed during the one 24-hour period it was observed

3.3.4 Daily Cycle of Activity

Data pooled for all koalas shows that feeding was observed at all times of the day (Figure 3-5). There was a gradual increase in feeding frequency from the late afternoon through to the middle of the night, before a decline in feeding through to the early morning. Feeding frequency was at its lowest from 0800h in the morning through to midday. Of 205 observed bouts of feeding only 13 were recorded during this period of the day. The frequency of feeding, as shown in Figure 3-5, was the total time spent feeding for any given hour divided by the overall time spent feeding, for all 24-hour observations.

There is considerable variation in timing of feeding amongst individual koalas (Figure 3-6). Individuals were observed feeding at all times of the day, except mornings (dawn to midday) when feeding either did not occur or was rarely observed. Distinct peaks in feeding are not apparent, but some individuals did feed more frequently at particular times of the day (e.g. M001 early to late afternoon, F001 middle of the night, M002 early morning).

All koalas fed less during the day (average 29%) than at night (average 71%) except for koala M001 which spent almost equal time feeding during the day (53%) and night (47%).

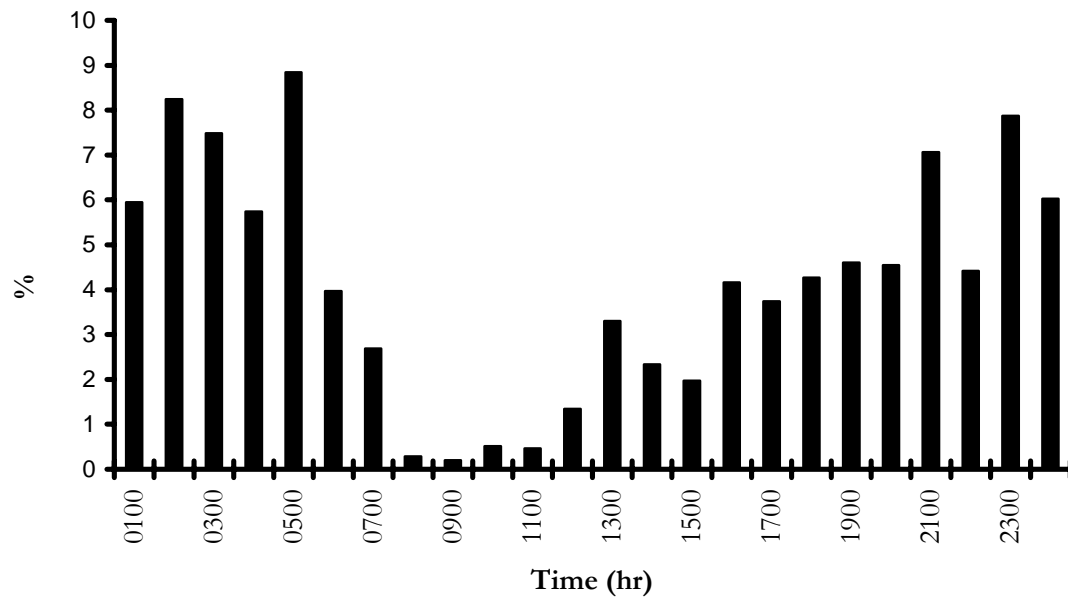


Figure 3-5: Average percentage of time spent feeding in each hour of the day for nine koalas observed feeding over 33 days. F003 was excluded from analyses as it did not feed during the one 24-hour period it was observed

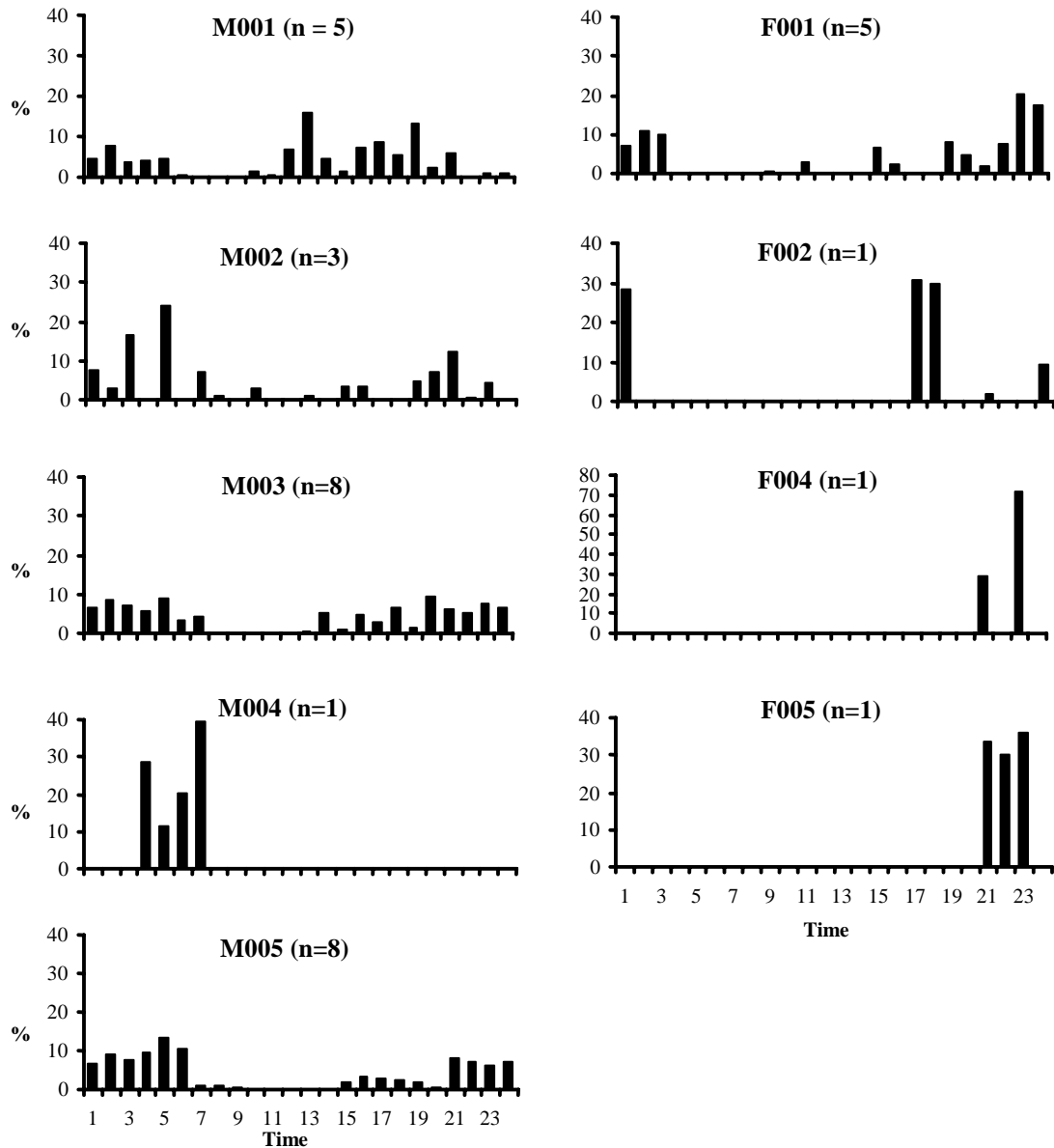


Figure 3-6: Average percentage of time spent feeding in each hour of the day for nine koalas observed feeding over 33 days. F003 was excluded from analyses as it did not feed during the one 24-hour period it was observed

3.4 Discussion

3.4.1 Feeding Behaviour

Koalas were found to restrict feeding bouts to one or two locations within the outer canopy of each tree they visited. Feeding was concentrated at these locations with browsed branches being almost completely defoliated. There are no other known reports of the distribution of feeding effort within trees for free-ranging koalas. One of the limitations of the observations was that confident estimation of the proportion of leaves removed from branches was not possible. This is due to the considerable difficulty in seeing individual leaves from the ground plus the obvious limitations associated with conducting night-time observations. Nonetheless, observers did report that the majority of leaves on a browsed branch were removed leaving branches visibly thinned. The proportion of leaves removed from branches was further investigated in subsequent captive feeding observations and enclosure experiments (Chapter 4).

Koalas in this study readily ate young leaves when they were present. Young growth is thought to be preferred by koalas over mature foliage (Fleay 1937; Hindell *et al.* 1985; Martin and Lee 1984). The common ringtail possum and greater glider have also been found to show a distinct preference for young foliage when available (Pahl 1990; Comport *et al.* 1996). The ratio of nitrogen to fibre is considered an important predictor of koala acceptance of eucalypt foliage (Cork *et al.* 1983; Lee and Martin 1988; Hume and Esson 1993). Young foliage typically has a higher concentration of available energy, moisture, N, P, K and lower lignified fibre content than mature foliage, which may contain up to 50% lignified fibre (Degabriele 1981; Ullrey *et al.* 1981; Cork *et al.* 1983; Cork and Pahl 1984; Comport *et al.* 1996). Koalas derive most

of their nutriment from cell contents which consist of easily digested carbohydrates, proteins and lipids (Cork *et al.* 1983; Robbins 1993). Cell walls, on the other hand, are difficult to break down and digest due to their lignin content (Robbins 1993). Large amounts of fibrous material in the diet also has a 'gut filling' effect which reduces the potential intake of food and, hence, available nutrients (Cork and Warner 1983). The consumption of young leaves is therefore advantageous as young leaves have a high cell content to wall ratio and contain little lignified fibre (Lee and Martin 1988; Comport *et al.* 1996). Nagy and Martin (1985) also suggest that selective consumption of young, succulent leaves by koalas increases water intake.

Buds, flowers, stems and even bark have been reported to be eaten, but do not make up a substantial proportion of the diet of koalas (Eberhard 1972; Smith 1979a; Hindell *et al.* 1985). Hindell *et al.* (1985) observed koalas eating bark and Eberhard (1972) noted evidence of bark stripping during his study at Finders Chase on Kangaroo Island. Neither of these authors provides any details of their observations of this behaviour (e.g. sex and age of animal or amount of bark removed). One young male koala (1-2 years) in this study was observed eating bark on several occasions. Koala attendants at Cleland Conservation Park have noted that many young animals in captivity commonly eat bark and suggest that it may possibly be linked to some nutritional requirement which is otherwise not met during growth of young animals (H. Mitchelmore, personal communication, 1999). Observations of koalas eating gravel and dirt have similarly been related to mineral requirements which are not met by a diet of leaves (Smith 1979a).

The observation that koalas fed in all eucalypts they visited lends additional support to the assumption that daytime occupancy of trees predicts koala use of trees as a

food source (Robbins and Russell 1978; Hindell *et al.* 1985). There has been some speculation concerning the validity of this assumption (Ellis *et al.* 2002). Results from Ellis *et al.* (2002) study at Blair Athol in central Queensland indicated that diet choice and day-time tree use by koalas may not always be correlated and that inferences regarding diet composition based on daytime observation maybe misleading. Ellis *et al.* (2002) does qualify this by suggesting for koala populations inhabiting more homogeneous *Eucalyptus* communities, such as that described by Eberhard (1972) at Flinders Chase on Kangaroo Island, daytime roosting observations may more closely resemble the diet preferences. In this study bouts of feeding were recorded in nearly all trees occupied by koalas during 24-hour observations. The only times that koalas did not feed in trees they occupied, was two occasions when they were observed in *A. retinoides*. In one instance, the tree was only occupied for a short period of time and in the other the koala appeared to be highly aware of the presence of observers and may not have been behaving normally. Hence the latter observation was not included in analyses. Although other species of *Acacia* have been reported to be eaten by koalas, there are no reports of *A. retinoides* being eaten by koalas on Kangaroo Island.

Rates of water turnover in koalas are closely related to the moisture content of available food (Ellis *et al.* 1995). Although koalas in captivity are capable of maintaining water balance without access to free water, free-ranging koalas have been observed drinking dew and rain on leaves and eating leaves wetted by rain (Nagy and Martin 1985; Ellis *et al.* 1995). Observations in this study of koalas drinking rainwater from trunks, branches and in one case a river also support the notion that koalas do opportunistically drink water from time to time. Ellis *et al.* (1995) attribute this behaviour to a need, at times, for koalas to make up for inadequate water intake from

leaves. Gordon *et al.* (1988) found that during drought and heatwave conditions in south-west Queensland many koalas in trees which were not close to permanent water either died or showed poor body condition due to a combination of malnutrition and dehydration. Koalas that were in trees that grew by large permanent water-holes, on the other hand, were in good condition and experienced low rates of mortality. This indicates that, depending on prevailing environmental conditions, leaf water content may not always provide sufficient water intake for koalas. In less extreme conditions than that reported by Gordon *et al.* (1988) this shortfall may well be overcome by opportunistically drinking water.

Ranging behaviour has usually been closely linked with mating and/or territorial behaviour in males (Eberhard 1972; Mitchell 1990*b*). It is generally assumed that there is a distinct difference in resource priorities between sexes, with males actively seeking to secure access to mates and females seeking out optimal food resources (White 1994). The observation that males fed immediately upon entering trees in 68% of observations of movements suggests that feeding criteria also influences ranging behaviour in males. This is also supported by the observation that male koalas fed in all the trees they visited.

3.4.2 Non-Feeding Behaviour

Male koalas in this study made fewer movements per day from one tree to another, than that reported by Robbins and Russell (1978) (1 to 2 compared with an average of 3.1 moves per day). No other studies provide estimates of movements per 24-hour period, but Mitchell (1990*b*) does state that koalas in his study moved at least once per day. The discrepancy in results may be due, in part, to day to day and individual variation in movement which confound results when sample sizes are small.

Nonetheless, the observation that males can occupy a number of trees per day has implications for radio-tracking studies which are usually based on one observation or locations per day. Because koalas can occupy a number of trees in a day, Robbins and Russell (1978) concluded that tree usage is only a reliable guide to feeding at the level of tree species preference ranking.

Mitchell (1990*b*) found that frequency of movements from one tree to another was related to sex, with male koalas changing location more frequently than females. This is supported by the results of this study in which only one female was observed moving from one tree to another (through the canopy of a tree) on a single occasion. In contrast, all males changed locations each day. Males may move more frequently to maintain larger home ranges, which contain more trees. This is likely to not only allow male koalas increased opportunity for social interaction, which Mitchell (1990*b*) observed was initiated by adult males, but also to meet potentially increased nutritional requirements associated with greater body weight. The average body weight of male koalas in southern Australia is 12 kg whereas the average body weight of females is 8.5 kg (Martin and Handasyde 1999).

Signalling systems involving olfactory senses are not unusual amongst arboreal marsupials (Ralls 1971; Comport *et al* 1996). The koala possesses three scent glands: the sternal gland on the chest; and two paracloacal glands. Smith (1980*b*) frequently observed scent marking during his study at Lone Pine Sanctuary. Males would grasp the trunk of a tree with the hands, flatten the chest against the trunk and rub the sternal gland along it up to half a dozen times. Although scent marking is considered an important means of communication between individual koalas, it was never observed during this study (Nagy and Martin 1988). Similarly, Eberhard (1972) never

observed scent marking and Sharpe (1980) only observed the behaviour three times during a year long study. Sharpe (1980) explains her lack of observations of scent marking by suggesting that scent marking is more a means of stimulating the scent gland so that the koala itself has a strong odour, rather than a method of marking objects and territory. As scent marking has been observed to occur principally during social contact, Sharpe (1980) suggests that the frequency of Smith's (1980*b*) observations is explained by the high density of animals in his study (20 to 30 koalas in an 18.2 * 5.6 m pen). Eberhard (1972) proposed that the usual method of climbing is such that it results in incidental transfer of secretion to trees. In either case scent marking was never observed during this study despite numerous observations of males during the breeding season.

Males were frequently heard bellowing during the breeding season. Although Eberhard (1972) reported that calls from one male are commonly followed by responses from other males, only one bellow by a male in this study was followed by a bellow from another male in the area. Eberhard (1972) states that calls are only occasionally heard in isolation without any response from other males. Observations in this study are more consistent with Sharpe's (1980) findings which indicate that, for the most part, males show no interest in surrounding males when they bellow. It may be that koalas in an area recognise each others calls and do not generally bellow unless an unfamiliar bellow is heard.

None of the attack-defence behaviours associated with attempted copulations described by Mitchell (1990*b*) were observed during the one observation of social interaction between a male (M005) and a female koala. Neither was the interaction between the two koalas ignore-ignore, which made up 80% of Mitchell's (1990*b*)

male-female interactions. Given that the interaction did not consist of aggressive behaviour or ignore-ignore behaviour and involved a juvenile male and adult female, it is likely that the interaction was similar to that described for juveniles and females by Sharpe (1980). Sharpe (1980) observed adult females being completely tolerant of juvenile males which spent considerable time with resident females at her study site on Phillip Island. Koala M005 was a juvenile at the time of the interaction, none of the behaviour was aggressive and the female koala was highly tolerant of M005 for many hours.

3.4.3 Daily Time Budgets

Koalas spend most of their time resting. On average koalas in this study spent 20.7 hours per day resting. Other estimates of the duration of rest are consistent with this and range from 19 to 20.4 hours per day (Smith 1979*a*; Sharpe 1980; Nagy and Martin 1985; Mitchell 1990*b*; Logan and Sanson 2002). A combination of the low nutritive value of leaves, gut filling effect of leaf fibre, slow rate of passage of digesta and cost of detoxifying secondary plant compounds interact to limit the koala's available energy (Cork and Warner 1983; Robbins 1993). Consequently koalas, like many other arboreal herbivores, remain stationary for long periods to conserve energy and aid digestion (Comport *et al.* 1996).

Although times reported for the amount of time spent feeding by other authors vary, they generally fall within the range of values recorded in this study (0.8 to 4.5 hours per day). The wide range in values is likely to be due to the high level of variation found between sexes and individuals. There was a significant difference in the amount of time males and females spent feeding. Differences in feeding times between males and females are essentially allometric. Metabolic rates, and therefore

food requirements, increase with body size (Comport *et al.* 1996). Hence, males with larger body weights were observed feeding for longer than smaller female koalas (Table 3.1). Interestingly koala M005's feeding times gradually declined from approximately 4 to 2 hours per day over ten months. Concurrently, this young koala was going through a period of growth with body weight increasing from 4.5 to 9.76 kg. Added nutritional costs incurred by young growing animals require greater food intake and therefore more feeding time.

As mentioned earlier, sampling strategies of previous studies of daily time budgets have differed considerably. Robbins and Russell (1978) and Logan and Sanson (2002) observed only males, Nagy and Martin (1985) only females, Mitchell (1990*b*) males and females and Hindell *et al.* (1985) did not specify the sex of the animals they observed. Differences between estimates of time spent feeding might therefore be a feature of sex bias in sampling. It is apparent from results in this study that there is also considerable individual variation in the amount of time spent feeding. It is likely that these variations coupled with limited sampling account for differences in results between studies.

3.4.4 Daily Cycle of Activity

Feeding was observed at all times of the day. Unlike results from other studies, no obvious peaks in feeding were observed. Reported peak periods of feeding include: 0930 - 1030h; 1800 - 1900h; and 1600 - 2000h (Eberhard 1972; Robbins and Russell 1978; Sharpe 1980; Hindell *et al.* 1985; Parker *et al.* 1986). For koalas observed during 24-hour observations, feeding was observed during all these times, but there were no consistent distinct peaks surrounded by an absence or particularly low frequency of feeding, as has been reported. Feeding was however at its lowest from 0930 to 1030h

which is consistent with the peak feeding time identified by Parker *et al.* (1986). Hindell *et al.* (1985) and Eberhard (1972) also recorded an absence of feeding from 0900 to 1100h in the morning. Robbins and Russell (1978), Hindell *et al.* (1985) and Sharpe (1980) all note an absence or low frequency of feeding in the middle of the night, whereas a substantial proportion of feeding bouts occurred at this time of the day in this study. As with time budget data, individual variation, coupled with limited sampling, may account for differences in results between studies.

Movements and feeding took place more often during night than day. Mitchell (1989) also reported that koalas in his study moved more often at night than during the day. Although Robbins and Russell (1978) found no difference in the frequency of movements between day and night they did observe that approximately a third of feeding took place during the day. Unlike some other arboreal folivores (e.g. brushtail and ringtail possums and greater gliders (Smith *et al.* 1989)), koalas are not strictly nocturnal and are occasionally active during the day.

3.5 Summary

The primary purpose of conducting the 24-hour observations of individual koalas was to document patterns of foraging within trees to better understand the likely impact of koala browsing on tree condition.

Koalas were found to restrict feeding bouts to one or two locations within the outer canopy of each tree they visited. Feeding was concentrated at these locations with browsed branches being almost completely defoliated. For some plant species concentrated damage has been found to have a greater effect on plant growth than dispersed damage (Marquis 1996). An investigation of the effect of both the extent and pattern of damage on leaf production of manna gum was undertaken to better

understand the process of tree defoliation and mortality on Kangaroo Island, using artificial defoliation experiments as discussed in the following chapter.

4 Assessment of Koala Browse Impact Using Artificial Defoliation

4.1 Introduction

Most plant-herbivore studies investigate the effect of the removal of plant tissue by herbivores on subsequent growth, reproduction and/or defensive strategies of plants (Owen and Wiegert 1976; Adjei *et al.* 1980; Detling *et al.* 1980; McNaughton 1979, 1983, 1985, 1986; Coppock *et al.* 1983; Coughenour *et al.* 1984; Wallace *et al.* 1985; Belsky 1986*a*, 1986*b*, 1987; Paige and Whitham 1987; Oesterheld and McNaughton 1988; Barker *et al.* 1989; Georgiadis *et al.* 1989; Mills *et al.* 1989; Bergelson and Crawley 1992; Paige 1992). The levels and attributes of plant responses to herbivory have been found to vary depending on plant species (Bilbrough and Richards 1993), timing of herbivory (Gedge and Maun 1992; Marquis 1992), extent of damage (Abbott *et al.* 1993), spatial scale investigated (Brown and Allen 1989), type and pattern of herbivore damage (Gold and Caldwell 1989; Mauricio *et al.* 1993; Honkanen and Haukioja 1994) and plant life history traits (Coley 1980). As a consequence, the concept of a continuum in reactions of plants to herbivory is developing, and more recent studies have endeavoured to understand the mechanisms and factors affecting plant responses to herbivory, rather than focus on the net outcome of compensation itself (Doak 1991; Prins and Verkaar 1992; Bilbrough and Richards 1993; Honkanen *et al.* 1994; Honkanen and Haukioja 1994; Marquis 1996; McLaren 1996; Honkanen *et al.* 1999).

Plant tolerance is the ability of plants to regrow and/or reproduce after herbivory (Strauss and Agrawal 1999). Compensation is the degree of tolerance observed. A number of intrinsic and extrinsic factors influence the capacity of plants to compensate for herbivory. These include: resource availability (Houle and Simard 1996); intra-specific competition (Mabry and Wayne 1997); photosynthetic rate (Rosenthal and Kotanen 1994); plant nutrient uptake (Houle and Simard 1996); phenological state (Rosenthal and Kotanen 1994); and plant architecture (Lehtilä and Syrjänen 1995). However, probably the most important factor influencing compensation is the complexity and variability of resource allocation in plants (Trumble *et al.* 1993; Lehtilä and Syrjänen 1995).

Unlike animals, plants are not well integrated physiologically (Watson 1986; Marquis 1991). Plants are modular organisms which are made up of repetitive multicellular units (e.g. branches), none of which are essential to the survival of the whole individual (Haukioja 1991). Resource movement is often restricted between plant parts, with modules varying in the level that they depend on each other and the remainder of the plant for resources. A branch, for example, is not as completely autonomous as a ramet of a clonal plant, as branches depend on the root system for water and nutrients (Sprugel *et al.* 1991). However, branches can be completely autonomous with regard to carbohydrates, if all necessary carbon is fixed within a branch, and they can also be independent of other branches for water and nutrients (Sprugel *et al.* 1991).

Autonomy has important implications for woody plant structure and function, and hence, the way plants respond to herbivore damage (Marquis 1991; Strauss and Agrawal 1999). Where complete autonomy exists, plant response to herbivore

damage may be localised to the affected plant part (e.g. branch; Honkanen and Haukioja 1994). Hence, the pattern of defoliation that herbivores impose on plants, and not just the extent of defoliation, is an important consideration when determining the effects of herbivores, such as the koala, on plant growth (Strauss and Agrawal 1999).

Although most studies have focussed on the effect of damage level on the ability of plants to compensate for herbivory (Kulman 1971; Hendrix 1988; Whigham 1989; Abbott *et al.* 1993; Cornelissen 1993; Bergström and Danell 1995; Gedge and Maun 1992; Edenius *et al.* 1993; Abbot and Wills 1996; Quin and Hall 1996) a number have also considered the relationship between spatial pattern of defoliation and subsequent plant regrowth and reproduction. Patterns of spatial variation in herbivory have been investigated at the level of individual leaves (Lowman 1982; Marquis 1988; Mauricio *et al.* 1993; Coleman and Leonard 1995), branches (Tuomi *et al.* 1988; Marshall 1989; Haukioja *et al.* 1990; Marquis 1991; Honkanen *et al.* 1999), and whole trees (Marquis 1992; Honkanen and Haukioja 1994). Of particular relevance to this study are results from investigations of the effects of herbivory at the tree level. As discussed in Chapter 3, koalas restrict feeding bouts to one or two locations within the outer canopy of a tree. This feeding results in browsed branches being almost completely defoliated.

For some plant species concentrated damage has been found to have a greater effect on plant growth than dispersed damage (Marquis 1996). For example, Marquis (1992) found that when 10% leaf area was removed from a single branch of *Piper arieianum* (an understorey tropical wet forest shrub), growth and total plant seed production were reduced to a greater extent than when 10% leaf area loss was scattered evenly

throughout the plant. Similarly, Honkanen and Haukioja (1994) also found that consequences of defoliation for branch growth in Scots Pine (*Pinus sylvestris*) depended less on extent of damage than on the pattern of damage. When a single branch of a tree was defoliated its ability to produce needles was retarded more than in cases where other branches were also defoliated. Fresh needle mass dropped by almost half on branches that were defoliated on their own (Honkanen and Haukioja 1994).

Results from studies which have looked at the impact of varying levels of defoliation on plant growth and reproduction are less consistent. A number of studies have found that plant growth rates decline in proportion to the quantity of foliage lost (Payton 1983; Whigham 1989; Edenius *et al.* 1993; Bergström and Danell 1995; Quin and Hall 1996; Kaitaniemi *et al.* 1999). For example, Abbott *et al.* (1993) reported that manual defoliation of Jarrah (*E. marginata*) saplings resulted in growth loss that correlated linearly to defoliation severity. Similarly, Abbott and Wills (1996) also found that a single 50% defoliation, or less, of *E. globulus* was tolerable throughout much of the year, but that 100% defoliation was not tolerable at any time. However, some studies have also reported either negligible or highly variable responses to defoliation. Lyytikäinen-Saarenmaa (1999) defoliated Scots Pine at three levels (50, 75 and 100%) and found no significant differences, in subsequent growth of shoots, between controls and any of the treatment groups. In a study of two beach annuals Gedge and Maun (1992) also found only slight (non-significant) differences in plant growth between different treatments (0, 25, 50, 75, 100% leaves removed). They also noted that plant response to defoliation, even within treatments, was highly variable. Cornelissen (1993) found that compensatory response varied amongst three species

of sub-tropical evergreen saplings that were defoliated at three levels (50, 75 and 90%). *Castanopsis fargesii* compensated well for all levels of defoliation, whereas *Pinus massoniana* showed no compensatory growth at all. On the other hand *Elaeocarpus japonicus* only showed strong compensatory growth at the 50% defoliation level (Cornelissen 1993). These results suggest that different plant species, and in some cases individuals within species, can vary in their ability to tolerate herbivore damage.

In order to define the impact of leaf eating herbivores, the effect of both the extent and pattern of damage must be measured (Marquis 1996). An investigation of the effect of these variables on the growth of manna gum was considered to be particularly important to understanding the process of tree defoliation and mortality on Kangaroo Island because of the observed patchy distribution of koala browse within tree canopies and the lack of knowledge concerning manna gum tolerance to herbivory.

The aim of this part of the study was to investigate the effect of koala browse on the growth of manna gum. Artificial defoliation experiments were used to determine what effect the pattern and extent of defoliation had on leaf production and to determine how these factors contributed to the decline of tree health. The experiment addressed three specific questions: (i) how do trees respond to simulated koala herbivory, (ii) what level of defoliation can be tolerated by manna gum (*Eucalyptus viminalis*), and (iii) does the pattern of browse affect the ability of trees to compensate for defoliation?

4.2 Methods

The effect of spatial pattern and level of defoliation on regrowth of manna gum (*E. viminalis cygnetensis*) was examined using artificial defoliation. Spatial pattern was

investigated through comparison of canopy-wide and branch-wide (localised) defoliation treatments. Pattern effects were investigated because, unlike other eucalypt herbivores such as leaf-eating insects (e.g. Coleoptera and Lepidoptera), koalas do not distribute feeding throughout the canopy, but rather concentrate their efforts on one or two branches.

To examine the effect of extent of defoliation on tree health, trees were subjected to two different levels of leaf removal. This was done to determine what level of defoliation can be tolerated by manna gum trees. However, before artificial defoliation experiments could commence additional behavioural data were required to further develop the experimental design.

One of the limitations of the 24-hour behavioural observations (Chapter 3) was that it was not always possible to confidently estimate the proportion of leaves removed from branches during feeding bouts. This was due to the considerable difficulty in seeing individual leaves from the ground, especially at night. Consequently, it was not possible to determine what proportion of leaves that should be artificially removed from branches in treatments aimed at mimicking koala browse. Therefore, enclosure experiments were conducted to determine the proportion of leaves removed on branches browsed by koalas. Enclosure experiments were initially chosen in preference to observations of captive animals, as it allowed for free-ranging koalas to be observed in entire, naturally occurring trees.

4.2.1 Enclosure Experiments

Six foot high corrugated iron fences were constructed around the drip line of two medium sized (height approx. 6m) manna gums at Little Sahara in January 1998.

These trees were selected because they were healthy and showed no signs (e.g. scats or scratches on the trunk) of prior koala browse. In addition, trees at this site had a stunted growth form, due to the growing conditions in the area, which allowed for easy observation of koalas and access to the tree canopy.

Ten outer canopy branches were selected and tagged in each tree prior to the initial release of koalas into the enclosures. All leaves (mature and flush), buds and fruits on each branch were counted. Branches were initially tagged with flagging tape, but this was removed before koalas were released into the enclosures to ensure that the koalas were not deterred from feeding on branches. During observation periods the branches were labelled using permanent ink markers.

Two radio-collared male koalas were captured at Pioneer Bend and relocated to the enclosures in January and March 1998 (refer Table 3.1 Chapter 3; M003 and M005). On each of these occasions, one koala was placed in each enclosure and observed continuously for 48-hours by two groups of observers working in eight hour shifts. Drinking water was provided in each enclosure due to the hot weather conditions at the time. Koalas were placed in the same enclosure for both observation periods. Behavioural data were recorded as outlined in Chapter 3. The only alteration to these methods was the inclusion of the location of the observer when the position of a koala was recorded. This was achieved by designating a number to each panel of both fences and recording the number of the panel the observer was standing next to when recording the position of a koala. This ensured that the branches in which koalas fed could be accurately relocated at the end of each observation period.

At the conclusion of each 48-hour observation period both koalas were removed from the enclosures and returned to Pioneer Bend where they were released. Leaves,

buds and fruits on all tagged branches were recounted. At the conclusion of the first observation period in January 1998 any branches that koalas had fed in, but that were not already tagged, were tagged and included in the second round of observations. At the beginning of the second observation period in March 1998 there were 16 tagged branches on one tree and 15 on the other.

4.2.2 Captive Feeding Observations

The enclosure experiments did not prove to be an efficient means of collecting data as only a small number of the tagged branches were fed upon by koalas during the observation periods (i.e. seven of 31 tagged branches). For this reason, and because of concerns about the welfare of the koalas used in the enclosure experiments, it was decided that feeding trials would be conducted with the use of captive koalas at Cleland Wildlife Park. The aim of these trials was to collect additional data to further develop the design of the artificial defoliation experiments.

Two koalas (1 male; 1 female) were used in the feeding trials over five consecutive days in early February 1999. Each koala was housed separately in a large (2.5 x 3 x 2.5 m) outdoor cage. Koalas were provided with fresh branches from a variety of local eucalypt species every day. Tree species, as well as the number of leaves (flush and mature), buds and fruits on each branch were recorded before branches were placed into the cages. Each cage contained two pots of water (front and back of cage), into which the branches were placed. Branches were left in the cages for 24-hours before being removed and replaced with new branches. Once removed from the cages, browsed branches were identified and the number of leaves, buds and fruits recounted. Leaves that had fallen onto the floor of the cages (as a result of

koala foraging) were not collected because there were often relatively few leaves on the floor and it was not possible to determine which branch leaves had come from.

4.2.3 Artificial Defoliation

The true effects of herbivory can be difficult to assess, especially when plants damaged naturally are used to quantify these effects (Strauss 1988). Often there is little known about the effects of herbivore selectivity and this can confound analysis when random sampling is assumed in analysis (Baldwin 1990). Additionally, there are practical difficulties associated with carrying out measurements of leaves and branches in large mature trees, which in the study area were up to 27 m in height. One way of circumventing these problems was to estimate the effects of herbivory using simulated herbivory treatments by manually clipping leaves from smaller trees. The value of using simulated herbivory is great, since it approximates the effects of natural herbivory and can be assigned at random to individual plants (Strauss 1988). The amount of defoliation can also be measured, controlled and kept constant throughout treatments (Danell *et al.* 1994). Therefore, it was considered that artificial defoliation would provide more detailed information on the amounts of foliage being produced under different levels and patterns of herbivory than could have been determined from observations of naturally defoliated trees.

A total of 50 manna gum trees were selected and tagged at Flinders Chase National Park and Victor Harbor in May and September 1998 respectively. Manna gum was chosen as this is the preferred browse species of koalas and hence the worst affected by defoliation on Kangaroo Island (Chapter 5). Five treatments were assigned randomly to each member of five groups of five trees at each site. Defoliation treatments consisted of:

- (i) 75% defoliation of the whole tree canopy
- (ii) 25% defoliation of the whole tree canopy
- (iii) 75% defoliation of only two branches per tree
- (iv) 25% defoliation of only two branches per tree
- (v) control (i.e. no artificial defoliation).

Due to concerns that trees may be killed as a result of complete defoliation, not more than 75% of foliage was removed from any tree. As koalas were not observed feeding on flowers, buds or fruits none of these plant parts were removed. Based on 24-hour observations (Chapter 3), enclosure trials, and captive observations of feeding behaviour treatment (iii) was considered to best mimic natural koala browse. Two branches of similar size and position (i.e. northern side of each tree) were chosen for defoliation in treatments (iii) and (iv).

Trees at each site varied slightly in size and reproductive status. Trees at Victor Harbor were not reproductively mature, whereas some trees at Flinders Chase were producing buds, flowers and fruits. Unfortunately, not all trees at Flinders Chase were producing buds and fruits so it was not possible to investigate the effect of defoliation on the reproductive fitness of trees. Trees at Flinders Chase were planted in 1991 and trees at Victor Harbour were planted in 1993. Due to logistical

difficulties (i.e. inaccessibility of tree canopies and excessive time required to defoliate large trees) experiments were not conducted on mature eucalypt trees.

At the beginning of the experiment 20 branches were selected and tagged in each tree, including controls. Similar sized branches were selected randomly from throughout the tree canopy. In treatments (iii) and (iv) this represented ten branches in non-defoliated sections of the canopy and ten branches in defoliated sections.

Whole leaves were manually clipped at the junction of the leaf base and petiole using secateurs. This simulated the removal of leaves by koalas (Chapter 3). Leaves were removed systematically along tree branches. In treatments which required 75% defoliation, all leaves, except every fourth leaf encountered, were removed. Where 25% defoliation was necessary every fourth leaf encountered was removed and the remainder of leaves were left intact. Trees at Flinders Chase were defoliated over a period of three months (May - July 1998). Trees at Victor Harbor were defoliated over a period of three weeks (September 1998). Trees at Flinders Chase took considerably longer to defoliate due to the greater size of the experimental trees. A single tree in the 75% whole-canopy defoliation took approximately two days to defoliate at Flinders Chase, whereas the same treatment at Victor Harbor took approximately half a day to complete. All leaves on tagged branches were counted prior to and following defoliation. Trees were defoliated prior to the summer growing season and final leaf counts were conducted six months later after the growing season was complete.

Additional defoliation of experimental trees by koalas could not be controlled at Flinders Chase even though trees were fenced-off from surrounding koala habitat. Therefore, visitation of trees by koalas was monitored by removing scats from

beneath trees and recording whether or not new scats appeared. Scats were removed immediately after artificial defoliation and every six weeks thereafter for the duration of the experiment. All of the experimental trees (including controls) were visited at least once by koalas during the six months of the experiment. However, none of the experimental trees were visited regularly and they were not considered to be suffering substantial defoliation by koalas. Nonetheless, the experiment was repeated at Victor Harbor, where koalas are absent, due to concerns that koala browse may confound the results of the experiment at Flinders Chase.

Treatments which involved defoliation of leaves from throughout the entire canopy of trees (treatments (i) and (ii)) are referred to as canopy-wide treatments. Treatments in which leaves were only removed from two branches per tree are referred to as localised defoliation treatments.

Repeated Defoliation

One of the original objectives of this study was to investigate the effect of repeated defoliation on the growth of trees. However, after the initial artificial defoliation experiment was conducted it became apparent that a considerable amount of time (i.e. many months) would be required to re-defoliate trees. This was mainly due to the substantial growth that had occurred on many experimental trees since the initial defoliation experiment was conducted. Many tagged branches had in excess of one thousand leaves, which would have made it time consuming and difficult to clip and count leaves accurately (initial averages were 150 and 100 leaves per branch at Flinders Chase and Victor Harbor respectively).

4.2.4 Statistical Analyses

A small number of branches on trees at Flinders Chase were omitted from the analyses because tags had perished, and they could not be relocated, or there was a substantial amount koala browse or damage on branches (e.g. branches were broken). Data for all tagged branches in the defoliation experiments were used to generate mean values for each tree. Individual branches of a tree were not considered independent. Mean values for treatments were analysed by Tukey HSD using the SPSS statistical analyses package.

4.3 Results

4.3.1 Enclosure Experiment

Daily feeding times in the enclosures were comparable to observed feeding times for koala M003 and koala M005 during 24-hour observations, however feeding bouts were shorter and more numerous than previously observed. Furthermore, the occasional long bouts of feeding (i.e. 40 – 60 min), which were usually observed at least once per day during 24-hour observations, were absent during the enclosure experiments. Nonetheless, branches were often revisited from one feeding bout to another and the number of branches visited by koalas did not differ greatly from previous observations. If anything the following results may represent a conservative estimate of the number of leaves removed from branches by koalas.

Koalas within the enclosures browsed on seven of the 31 tagged branches (Table 4-1). Four of these branches (B4-B7) were tagged following the first round of observations and were also fed on by koalas during the second observation period (i.e. the same branches were fed on during both observation periods). Koalas

removed a substantial proportion of leaves from branches, with a median of 77% of leaves removed during feeding bouts (Table 4-1).

Mature foliage was eaten to a greater extent than flush (young) foliage, however, examination of the results shows that there was considerable variation, from branch to branch, in the amount of flush and mature foliage eaten (Table 4-1). Flush and mature foliage was present on all tagged branches.

Bark was eaten by koala M003 on three occasions. Strips of bark were removed from outer canopy branches with the front incisors. There were fewer buds and fruits on tagged branches following browsing by koalas. Observers noted that buds and fruits were frequently knocked off branches as a result of branches being handled by koalas (i.e. pulled in toward koalas from the outer canopy). Immature buds that had recently emerged along the stems of flush growth were also consumed with flush growth. It did not appear as though fruits and buds were eaten deliberately.

Based on observations of koalas in the enclosures, it was concluded that 75% defoliation of foliage would be used to mimic koala browse in artificial defoliation experiments. This was close to the overall median value and easier to implement than 77%. As trees were clipped prior to the growing season there was little flush growth present on branches, therefore 75% of all foliage on the trees was removed.

Table 4-1: Proportion of leaves removed from tagged branches by koalas in enclosures

Branch	Date	Koala ID	# Leaves	# Eaten	% Eaten Total	% of Eaten Leaves	
						Flush	Mature
B1	Jan-98	M003	496	386	78	18	82
B2	Jan-98	M003	294	194	66	29	71
B3	Jan-98	M003	305	152	50	2	98
B4	Mar-98	M005	474	387	82	75	25
B5	Mar-98	M005	728	563	77	89	11
B6	Mar-98	M003	112	89	79	17	83
B7	Mar-98	M003	388	144	38	94	6
Median					77	29	71

4.3.2 Captive Feeding Observations

Fifteen of the 35 branches that were placed in the cages were fed on by the two captive koalas. The extent of leaf consumption on branches was similar across all species of eucalypts used in the experiment (Table 4-2). A median of 70% of leaves were removed from branches. This supports the design of treatment (iii) in the artificial defoliation trials in which 75% of foliage was removed from focal branches to mimic the browsing of a koala.

Table 4-2: Proportion of leaves removed from tagged branches by captive koalas at Cleland Wildlife Park. BG: *E. leucoxylon*; MG: *E. viminalis*; RG: *E. camaldulensis*; SB: *E. obliqua*

Date	Koala	Branch	Tree Species	# Leaves	# Eaten	% Eaten
8-Feb-99	Vivonne	1	BG	703	560	80
9-Feb-99	"	2	SB	274	181	66
10-Feb-99	"	3	MG	591	513	87
11-Feb-99	"	4	BG	550	322	59
12-Feb-99	"	5	RG	1820	865	48
8-Feb-99	Blacky	6	BG	791	572	72
9-Feb-99	"	7	SB	222	188	85
9-Feb-99	"	8	MG	169	134	79
10-Feb-99	"	9	MG	999	526	53
10-Feb-99	"	10	MG	343	177	52
11-Feb-99	"	11	MG	796	595	75
11-Feb-99	"	12	BG	485	313	65
11-Feb-99	"	13	BG	315	242	77
11-Feb-99	"	14	BG	285	181	64
12-Feb-99	"	15	BG	1362	947	70
Median						70

4.3.3 Artificial Defoliation

Victor Harbor

Although mean leaf production increased by at least two to three times on branches in which 75% of foliage was removed (either localised or canopy-wide) compared to leaf production on control trees, this difference in leaf production was not statistically significant ($P = 0.225$; Figure 4-1). This lack of statistical difference is likely to be due to large variation in response to defoliation recorded within treatments. Future experiments would benefit from a substantially increased number of replicates per treatment.

There was also some increase in leaf production on branches in treatments in which 25% of foliage was removed, but again this was not significantly higher than for branches from control trees. There were no significant differences in leaf production between any of the treatment groups. Leaf production did not fall below that of the control trees in any of the treatments and in no cases did epicormic growth take place.

There were no significant differences in the total number of leaves on branches before and after defoliation when compared to control trees (Figure 4-2).

Although the results are not statistically significant, comparison of Figure 4-1 and Figure 4-2 indicates that trees at Victor Harbor did increase leaf production and compensate for removal of leaves.

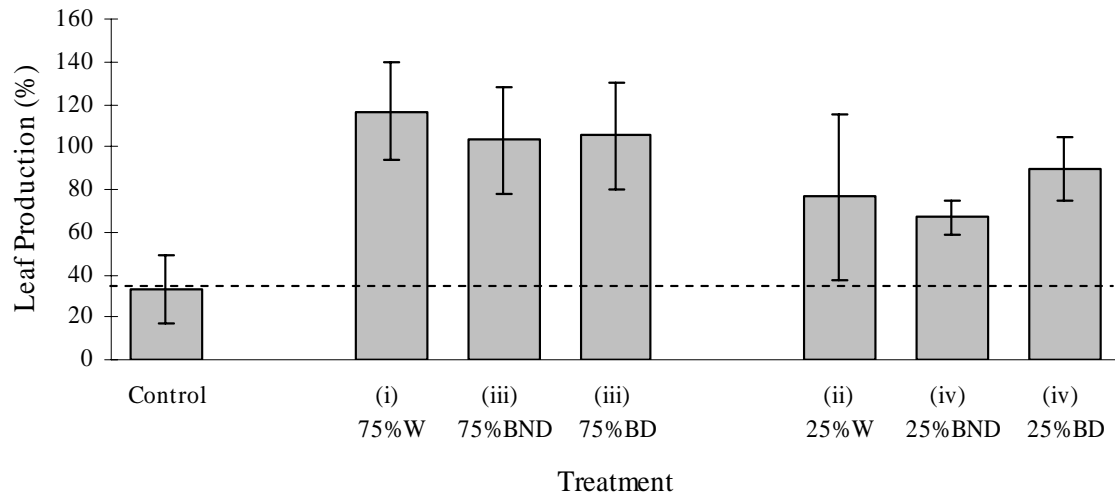


Figure 4-1: Mean leaf production (\pm SE) at Victor Harbor. The number of new leaves (post-treatment) is presented as a percentage of the number of pre-treatment leaves on each branch. The dashed line represents the level of leaf production on control trees that were not subject to any treatment. BND: branch not defoliated; BD: branch defoliated; W: tree-wide removal of foliage

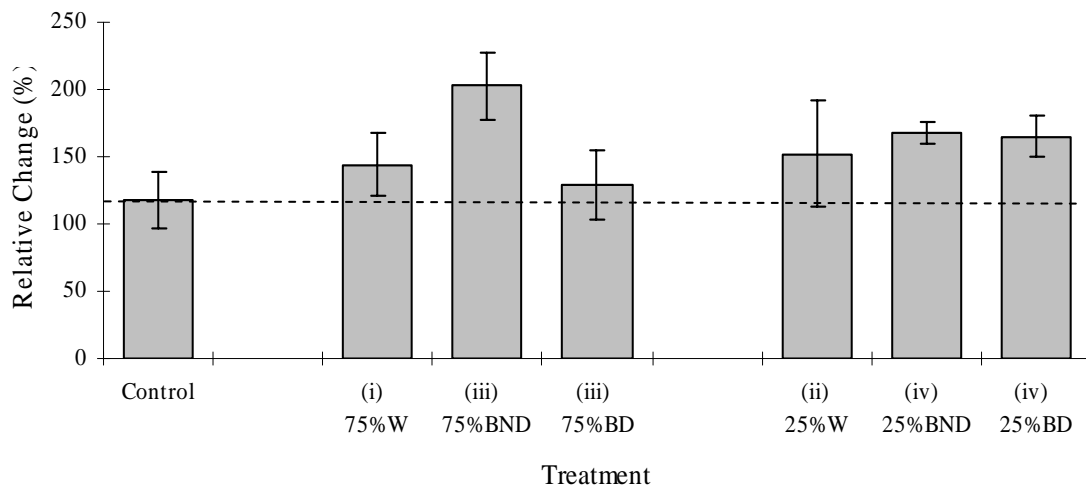


Figure 4-2: Relative change in the total amount of foliage on tagged branches at Victor Harbor (Mean \pm SE). Relative change was measured as the total number of leaves on branches following defoliation (post-treatment) relative to the total number of leaves prior to defoliation (pre-treatment). This provides a measure of recovery of defoliated branches. The dashed line represents the control level of leaf production. BND: branch not defoliated; BD: branch defoliated; W: tree-wide removal of foliage

Flinders Chase

At Flinders Chase none of the trees in treatments had significantly higher leaf production than control trees (Figure 4-3). The greatest increase in leaf production was recorded for branches from trees which had 75% of leaves removed from throughout the canopy, with mean leaf production (number of new leaves compared to number of leaves prior to defoliation) of 116% compared to 51% on control trees.

Unlike Victor Harbor, defoliation at Flinders Chase did have a deleterious effect on leaf production in some treatments. When localised defoliation occurred, leaf production on treated branches was lower than on control trees (Figure 4-3; 75%BD and 25%BD). However, this difference was not significant for either the 75% or 25% localised defoliation treatments (i.e. treatments in which defoliation was only applied to two branches).

Branches on trees in the 75% canopy-wide treatment had significantly higher levels of leaf production than defoliated branches in the 75% localised defoliation treatment ($P = 0.016$) and defoliated branches in the 25% localised defoliation ($P = 0.02$; Figure 4-3).

The results indicate that some trees at Flinders Chase were not able to increase leaf production to levels which fully compensated for removal of leaves. Although not statistically significant, branches on trees in the localised defoliation treatments (75% BD and 25% BD) were not able to fully compensate for foliage loss when compared to control trees (Figure 4-4).

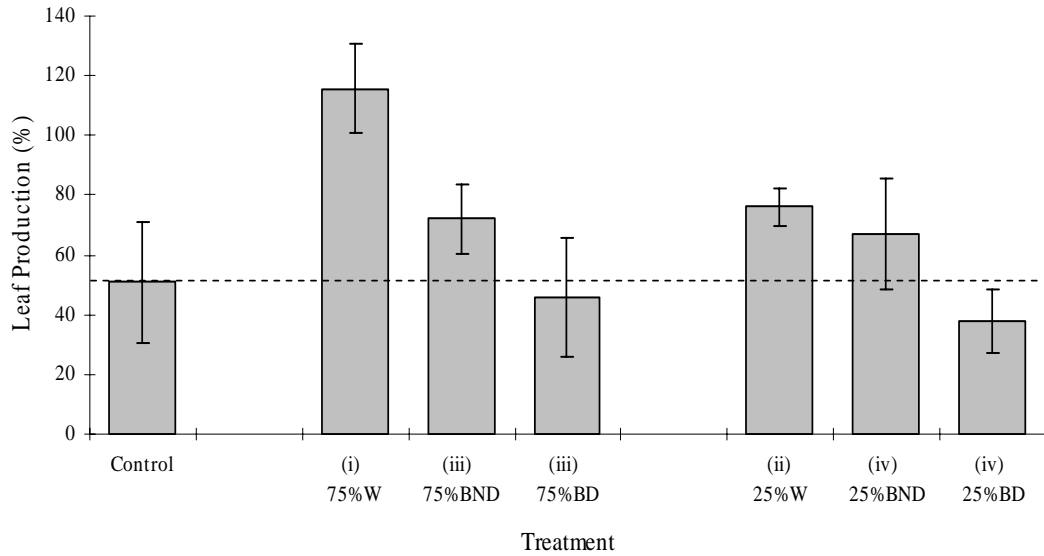


Figure 4-3: Mean leaf production (\pm SE) at Flinders Chase. The number of new leaves (post-treatment) is presented as a percentage of the number of pre-treatment leaves on each branch. The dashed line represents the control level of leaf production on trees that were not subject to any treatment. BND: branch not defoliated; BD: branch defoliated; W: tree-wide removal of foliage

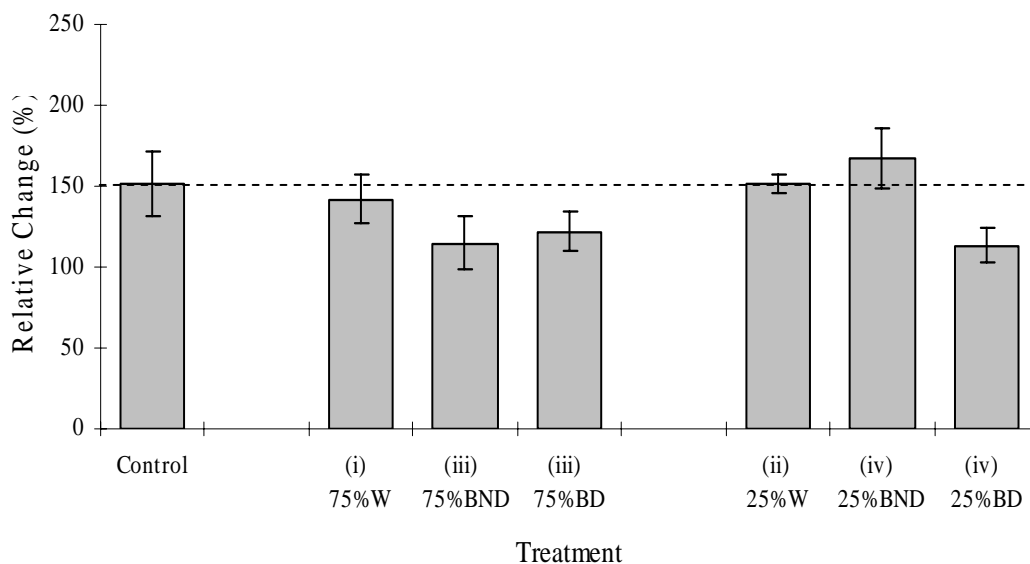


Figure 4-4: Relative change in the total amount of foliage on tagged branches at Flinders Chase (Mean \pm SE). Relative change was measured as the total number of leaves on branches following defoliation (post-treatment) relative to the total number of leaves prior to defoliation (pre-treatment). This provides a measure of recovery of defoliated branches. The dashed line represents the control level of leaf production. BND: branch not defoliated; BD: branch defoliated

4.4 Discussion

Manna gum trees showed strong compensatory growth following artificial defoliation. New leaf production was particularly high on trees that were subjected to canopy-wide defoliation. All branches on these trees compensated well for herbivory and did not show any loss in terms of growth. In contrast, branches which experienced localised damage produced comparatively fewer leaves than branches on trees which had experienced canopy-wide defoliation. This was apparent at Flinders Chase where localised defoliation resulted in lower leaf production than canopy-wide treatments and undamaged controls. These results suggest that pattern, and not just level of damage, can significantly affect leaf production following defoliation. Although branches in canopy-wide treatments had high levels of leaf production, especially when 75% of leaves were removed, leaf production declined when high levels of defoliation were localised. Consequently, pattern of defoliation also had an effect on the ability of branches to fully recover from defoliation.

Branches on trees in canopy-wide defoliation treatments did not experience significantly more or less relative change in the number of leaves before and after defoliation than control branches. All branches on trees in canopy-wide treatments were able to compensate fully for loss of foliage and normal growth was not compromised. At Victor Harbor, similar results were found for branches in treatments where localised defoliation occurred. On many trees, enhanced leaf production resulted in full recovery of branches and maintenance of similar net growth levels (i.e. relative change) as undamaged controls. The only branches which did not fully compensate for leaf removal and which consequently did not recover entirely from foliage loss were branches at Flinders Chase which experienced

localised removal of 75% and 25% of foliage. Therefore it appears that manna gum can be highly tolerant of one-off defoliation of the entire canopy, even when substantial quantities of foliage are lost, but that branches may not be as tolerant of high levels of herbivory if defoliated in isolation. The original intent of this study was to consider the effects of repeated defoliation on leaf production, but due to practical constraints (Section 4.2.3) this was not possible. Abbot *et al.* (1993) found that repeated artificial defoliation of Jarrah (*Eucalyptus marginata*) at varying levels and frequency significantly reduced growth with no compensatory growth evident. It is possible that the high levels of compensatory growth observed in this study are a feature of the one-off defoliation applied to trees.

The high rates of leaf production on branches in the 75% canopy-wide defoliation treatments suggests that they were not suffering from a deficiency of carbon. Either these branches were able to produce sufficient carbon for regrowth through increased photosynthesis of remaining leaves, or they imported carbon from elsewhere in the tree. Although removal of leaves decreases the leaf area available for photosynthesis, it can also increase light levels to previously shaded portions of the tree canopy, thereby increasing the photosynthetic capacity (and carbon fixing potential) of remaining leaves (Mabry and Wayne 1997; Strauss and Agrawal 1999). As a consequence, the net photosynthetic rate of branches may actually increase and allow for greater leaf production (Gold and Caldwell 1990). Carbon may have also been allocated to above ground leaf production from pre-existing carbon reserves in the stem or roots of trees. Although reserves in stems and roots have been found to play a relatively minor role in annual shoot growth in evergreen tree species, branches

are thought to be capable of drawing carbon from reserves to support growth of new foliage under stress conditions (Kozlowski and Winget 1964; Sprugel *et al.* 1991).

It was not entirely surprising that manna gum trees recovered so well after one-off defoliation of the whole canopy. Many eucalypts are noted for their ability to produce regrowth foliage from epicormic buds or lignotubers, and in some species, from rhizomes or root suckers (Landsberg and Cork 1997). This capacity for regrowth has evolved as a response not merely to herbivory, but also fire which is widespread in Australia (Bell and Williams 1997; Gill 1997). There have been few studies of mortality rates of eucalypts following fire, but Gill (1997) found an initial rate of 13% followed by a further 2% after sprouting in a forest near Canberra. There was no mortality of experimental trees in this study probably because defoliation only occurred once and did not involve the removal of all leaves in the canopy. Indeed, Abbott and Wills (1996) found that death of blue gum (*E. globulus*) trees was rare even when single large (100%) defoliations occurred. Similarly, epicormic growth probably did not develop on experimental trees in this study because defoliation levels were not particularly severe and only took place once. Epicormic growth usually occurs as a response to fire, during which the whole canopy is destroyed leaving no remaining foliage for photosynthesis. Epicormic growth has also been observed on trees on Kangaroo Island which have suffered long-term and repeated heavy defoliation by koalas.

Plants may be limited in their ability to respond to localised damage by herbivores because carbon does not flow freely from undamaged to damaged plant parts, particularly between branches (Marquis 1996). Locally defoliated branches at Flinders Chase must have lacked the carbon resources required to adequately compensate for

damage for there to be decreased growth on these branches following foliage loss. Unlike branches on trees in canopy-wide treatments, locally defoliated branches would have received little benefit from foliage loss in terms of increased light availability and photosynthesis. Honkanen and Haukioja (1994) also suggested that when a branch is the single one defoliated in a tree its transpiration capacity may be weakened compared to that of non-defoliated branches, and that consequently it is unable to increase its nutrient intake to compensate for the loss of foliage. In this way, other branches within the tree may indirectly prevent the damaged branch from compensating for lost foliage (Honkanen and Haukioja 1994).

There has also been some speculation that there is a mechanism which actively hinders compensation for locally damaged branches (Honkanen and Haukioja 1994). An unexpected result of the defoliation experiment was the enhanced growth of non-defoliated branches on trees in localised defoliation treatments. In some cases, non-defoliated branches on trees subjected to localised defoliation (i.e. where only two branches were defoliated) showed higher levels of new leaf production than the locally defoliated branches and branches on control trees. Haukioja (1991) suggested that plant units (e.g. branches) in the best condition and/or position obtain more resources (e.g. nutrients) than those in an inferior condition and/or position. Redirecting resources away from damaged branches which are a net drain on the tree to healthier branches may benefit the tree by increasing the net photosynthetic capability of the tree (Honkanen and Haukioja 1994). This may also explain why shaded branches in trees eventually die (Sprugel *et al.* 1991).

As has been discussed, a number of factors may contribute to high compensatory ability in plants including increased photosynthetic rates and resource allocation

patterns (Rosenthal and Kotanen 1994). However, the age of a tree can also be an important determinant of plant resilience to herbivory (Larcher 1980; Coley *et al.* 1985). Over the lifespan of trees, the ratio of leaf (net energy producing) tissue to stem and root (net energy utilising) tissue is progressively reduced (Payton 1983). In the first years of life the leaf mass can make up half of the overall dry matter of the plant, but with increasing size the ratio of leaf mass to stem is altered, the leaf mass growing only slightly while trunk and branches become steadily thicker and heavier (Larcher 1980). Foliage often comprises only 1-5% of the total mass of mature trees and these leaves must supply the materials for maintenance and growth to parts of the tree amounting to many times their own weight (Larcher 1980). Young trees, therefore, have higher relative growth rates, accompanied by greater potential for compensatory carbon gain and subsequent growth, than mature trees (Bryant *et al.* 1991). In a study on the effects of herbivory on southern rata (*Metrosideros umbellata*) Payton (1983) considered whether young trees were able to withstand defoliation better than more mature trees and found that young trees were indeed more resilient to foliage loss than older trees. Similarly, trees at Flinders Chase showed slightly lower new leaf production than younger reproductively immature trees at Victor Harbor. Furthermore, the only branches to under-compensate for defoliation were on locally defoliated trees at Flinders Chase. These results suggest that the age of trees may have an effect on defoliation resilience and that trees at Flinders Chase may provide a better representation of the effect of herbivory on mature trees, but still potentially under represent the impact of localised heavy defoliation on large mature trees.

4.5 Summary

Pattern of defoliation does appear to affect the response of trees to defoliation.

Although branches on manna gum trees can be highly tolerant of up to 75% removal of leaves from the entire canopy, they do not appear to be as tolerant of high levels of herbivory if defoliation is localised to only one or two branches in the canopy.

This is a crucial consideration when determining carrying capacities of riparian habitats both during the recovery phase of already heavily defoliated trees and the long-term carrying capacities of these habitats if and when the trees recover.

Estimation of the carrying capacity for koala habitat should not be based on direct correlations between the amount that koalas eat and the 'standing crop' of leaves on trees within a given area of habitat. It is clear that the impact of herbivory on trees is not always directly proportional to the amount of foliage removed via herbivory and that equal amounts of foliage removal can have different consequences for the tree depending on the pattern of foliage removal.

5 Tree Response to Sterilisation and Translocation of Koalas

5.1 Introduction

This chapter presents tree canopy condition and koala population monitoring results from Mine Creek: a tributary of the Cygnet River located near Pioneer Bend (Chapter 2, Figure 2-1). Mine Creek was been the site of an intensive koala population control program conducted by the South Australian Department for Environment and Heritage (DEH) between 1997 and 1999 and therefore presented an opportunity to test the effect of koala management techniques on tree health.

Since 1997, the key component of DEH's koala management program on Kangaroo Island has been the use of fertility control (i.e. sterilisation) to reduce birth rates. In areas where koala numbers were particularly high and tree defoliation severe, sterilisation was combined with translocation, to immediately reduce koala numbers and alleviate browse pressure on trees.

The overall aim of the koala management program on Kangaroo Island was to achieve and maintain a 70% sterilisation rate and a target density of 1 koala/ha in high quality riverine habitat (Possingham *et al.* 1996; StJohn 1998). The target density of 1 koala/ha was based on results from studies in other states which indicated that sustainable koala densities are approximately 0.5-1.0 koala/ha in suitable habitat (Possingham *et al.* 1996).

In 1996, the density of koalas at Mine Creek was estimated to be as high as 5 koalas/ha and over 60% of *E. viminalis cygnetensis* were severely defoliated (StJohn

1997, Masters *et al.* 2004). Sterilisation and translocation commenced in late 1997 and over the next four years 121 koalas were sterilised and 58 of these translocated from Mine Creek to the southeast of South Australia (T. Duka, personal communication, 26 March, 2003) (Table 5-1).

Table 5-1: Numbers of sterilised and translocated koalas at Mine Creek 1997-2000. NB: figures are for sterilised (and re-released) and translocated koalas captured within a 10 ha area at Mine Creek

Year	No. Sterilised and Released	No. Sterilised and Translocated
1997	105 (64F, 41M)	13 (4F, 9M)
1998	15 (6F, 9M)	45 (26F, 19M)
2000	5 (1F, 4M)	0
2002	2 (2M)	6 (2F, 4M)

Source: T. Duka, personal communication, 26 March, 2003

Between 1997 and 1999 koala numbers and tree health were monitored at Mine Creek as part of this study to determine the effectiveness of sterilisation and translocation in reducing koala numbers and improving tree condition. The specific aims of the monitoring study were to:

- investigate the effect of koala sterilisation and translocation on koala numbers, sex ratios and fertility rates at Mine Creek
- determine the response of over-browsed preferred tree species (*E. viminalis cygnetensis* and *E. leucoxydon*) to fluctuations in koala numbers
- determine if severely defoliated trees were capable of recovering from over-browsing following substantial reduction in koala browse pressure.

5.2 Methods

Population census and tree health assessments were conducted at Mine Creek from December 1997 through to March 2000. Mine Creek was selected for the monitoring study for a number of reasons including:

- the area was considered to represent some of the most severely over-browsed koala habitat on Kangaroo Island
- the area was subject to one of the most intensive sterilisation and translocation efforts undertaken by DEH on Kangaroo Island
- the Mine Creek study site corresponds with DEH's annual monitoring site - CYG114. Hence, there was good historical tree health and koala population data for the area.

The Mine Creek site was considered to present an ideal opportunity to test the effectiveness of koala management techniques (i.e. sterilisation and translocation) in severely defoliated habitat.

A tree guarding experiment was carried out in conjunction with the monitoring study primarily in areas along the main channel of the Cygnet River and Deep Creek (i.e. mostly outside of the Mine Creek site). The Mine Creek monitoring site and location of trees in the tree guarding experiment can be seen in Figure 5-1.



Figure 5-1: Mine Creek koala population and tree monitoring site. Locations of guarded (yellow) and control (blue) trees used in tree guarding experiment are also shown

5.2.1 Population Census

Population censuses were used to provide an estimate of the koala population size at Mine Creek before, during and after sterilisation and translocation of koalas.

A total of 12 population censuses were conducted at Mine Creek between December 1997 and March 2000. Additional data for December 1996, November 2000 and September 2002 have been provided by DEH.

A two-count census method, as described by Caughley and Sinclair (1994), was used to estimate population size. This method involved two observers (or two groups of observers) searching the census area independently and recording the number of koalas seen. The second observer (or group of observers) also recorded whether the koalas they observed were sighted by the first observer; as indicated by an inconspicuous chalk mark at the base of trees in which koalas were found. The total size of the population (Y) was then estimated using the following formula:

$$Y = \frac{[(B + S_1 + 1)(B + S_2 + 1)]}{(B + 1)} - 1$$

Where:

S1 - is the number of koalas seen by the first observer, but not the second observer

S2 - is the number of koalas seen by the second observer, but not the first observer

B - is the number of koalas that were observed by both observers one and two.

Observers also recorded the tree species that koalas were observed in, the sex of sighted koalas, presence or absence of young and whether koalas had an ear tag

(sterilised koalas were ear tagged). Sex ratios and fertility rates were calculated on the basis of data collected by the first observer.

5.2.2 Canopy Condition

The canopy condition of preferred tree species was monitored to determine whether canopy condition changed in response to koala sterilisation and translocation.

In August 1997 all mature *E. viminalis cygnetensis* and *E. leucoxydon* trees within a 1 × 0.1 km (10 ha) section of Mine Creek were tagged with individually numbered galvanized iron tags.

A total of 311 trees were tagged of which 97 were *E. viminalis cygnetensis* and 214 were *E. leucoxydon*. Canopy condition was assessed visually with each tree assigned a level of defoliation as per Martin (1983):

- Category 1 – crown normal
- Category 2 – crown thin (up to 50% defoliation)
- Category 3 – crown very thin (approx. 50 - 80% defoliation)
- Category 4 – epicormic growth only
- Category 5 – tree dead.

Trees were revisited and defoliation levels assessed once per year (December 1997, November 1998 and December 1999). Initially trees were revisited and assessed at quarterly intervals, however it was difficult to overcome observer bias due to familiarity with the condition of trees at this frequency, hence the shift to annual observations.

5.2.3 Tree Guards

Almost a year after monitoring commenced at Mine Creek it was apparent that the canopy condition of many severely defoliated trees (i.e. category 3 and 4) was not showing any obvious improvement despite translocation and sterilisation of substantial numbers of koalas in the area. An experiment in which koalas were excluded from trees was conducted to provide an indication of whether canopy condition in severely defoliated trees was not improving because: a) trees were no longer physiologically able to produce compensatory growth, or b) remaining koalas at Mine Creek imposed sufficient browse pressure to prevent trees from improving in condition (i.e. koalas were continuing to suppress compensatory growth).

Koalas were excluded from seven *E. leucoxylon* and eight *E. viminalis cygnetensis* trees by fitting corrugated iron guards around the trunk/s of each tree (Appendix A). All guarded trees were considered to be category 4 trees (i.e. severe defoliation with mainly epicormic growth). Each tree guard was 1.5 m in height and was secured with rivets which were flush with the outside surface of the guards to ensure that there was no opportunity for koalas to grip the outside of the guards and climb up trees. Where necessary, access to guarded trees was also prevented by pruning branches from surrounding trees to isolate the canopy of guarded trees. The number of trees that were suitable for this experiment was limited by the need to achieve canopy isolation and a high level of defoliation. For each guarded tree a control tree of similar condition and size was selected and tagged nearby. Seven *E. leucoxylon* and nine *E. viminalis cygnetensis* trees were selected as controls.

Both guarded and control trees were photographed in October 1998 and revisited and re-photographed in November-December 1999. This allowed one full growing

season for trees to respond in the absence of browsing by koalas. On both occasions trees were photographed from the same point (identified by a peg in the ground), at approximately the same time of day and using the same camera settings. The relative condition of trees in 1998 and 1999 was assessed qualitatively based on visual comparison of photographs using the same defoliation categories used in tree health assessments.

5.2.4 Tree Species Preferences

Tree species preferences were determined by comparing the observed proportion of sightings of koalas in tree species with the expected proportion of sightings based on the availability of tree species within the census area. Further details of methodology used are presented in Chapter 6, Section 6.2.5.

5.2.5 Statistical Analyses

Changes in tree canopy condition and koala tree preferences at Mine Creek were assessed using chi-squared analysis.

A linear regression was fitted to the natural logarithms of each of the census population estimates to determine the average rate of increase following the peak period of control. (1997-98).

Tree guard data for *E. viminalis* was analysed using the Somer's d test for ordinal association. This tests whether there is a monotone (i.e. consistently positive or consistently negative) association between the independent variable (tree-guarding: guarded vs. unguarded control) and the dependent variable (change in tree condition: increase, no change, decrease).

The Somer's d test could not be applied to tree guard data for *E. leucoxydon*, because there were no trees that declined in condition (i.e. the data were realised as a 2 x 2 table). Due to low cell counts (all 4 cells had expected values less than 5) a Fisher's Exact test was used to test for an association between tree-guarding and tree condition.

5.3 Results

5.3.1 Population Census

Population Size

Figure 5-2 presents koala population size and densities at Mine Creek between December 1996 and September 2002. Results show that there was a considerable decline in koala numbers within the first couple of years of control. DEH estimated that there were approximately 50 koalas within the 10 ha site in December 1996, however by October 1998 it was estimated that there were only 12 koalas remaining at the Mine Creek site. This decline corresponds closely with the peak of DEH's sterilisation and translocation efforts in 1997 and 1998.

Despite a fall in population size of almost 75% the density of koalas at Mine Creek did not reach the target of 1 koala/ha and began to gradually increase again in mid-1999. By September 2000, the koala population at Mine Creek was estimated to be in the order of 34 koalas – almost 70% of the initial population size and over three times the density considered sustainable. The average annual population growth rate for koalas at Mine Creek following control was 27% per year (SE \pm 0.7%). This represents a potential doubling in the koala population at Mine Creek every three years following sterilisation and translocation.

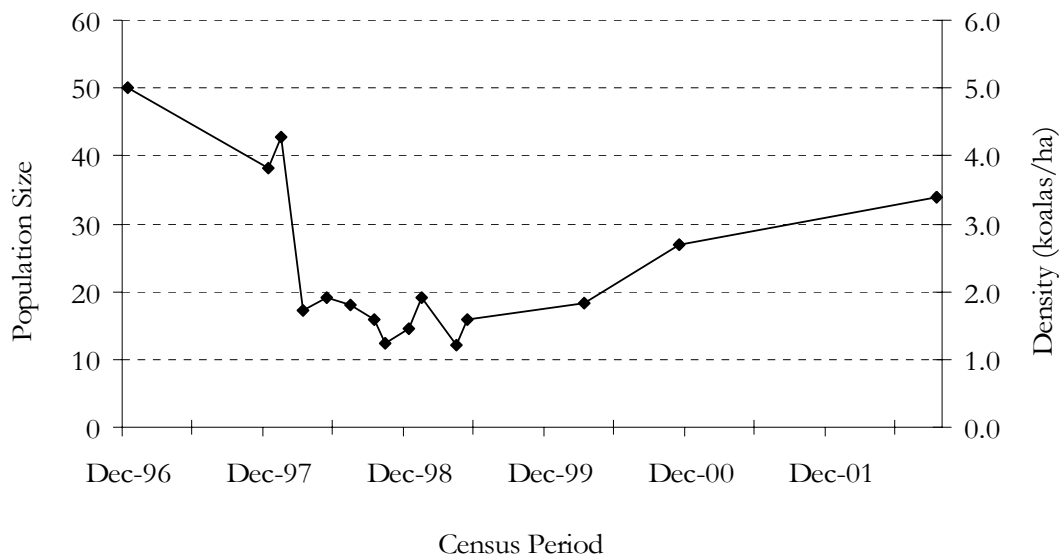


Figure 5-2: Koala census results December 1996 to September 2002. Shaded area represents the peak period of sterilisation and translocation effort at Mine Creek (data for December 1996, November 2000 and September 2002 have been provided by DEH)

Population Demographics

The fertility rate of the Mine Creek koala population recorded prior to sterilisation was 70% (fertility rate is expressed as percent of females with joeys) (Table 5-2). The fertility rate declined to approximately half this level in 1997 and 1998 and almost no joeys were observed during censuses conducted from mid-1999 onward (the exception was a single female with a joey recorded in June 1999).

Overall the sex ratio favoured females, particularly in the first year following commencement of the control program when up to five times more female koalas were recorded than males. Tag rates indicate that around 80% of male and female koalas within Mine Creek were sterilised after the most intensive sterilisation effort in mid to late 1997 (all sterilised koalas were ear tagged). The proportion of sterilised

koalas then fluctuated considerably from one census period to another through to March 2000 (Table 5-2).

Tree Preferences

Koalas were observed primarily in *E. viminalis cygnetensis* and *E. leucoxylon*. In 36% of observations koalas were sighted in *E. viminalis cygnetensis* with 56.5% of observations associated with *E. leucoxylon*. There were 12 observations of koalas in *Acacia retinoides*, representing 7.5% of all observations during censuses. Data relating to observations in *A. retinoides* were not included in chi-squared analyses due to small sample size and associated low expected values.

Observed frequencies of use of tree species were found to differ significantly from availability of tree species when data for all censuses were pooled. Results suggest that koalas selectively used *E. viminalis cygnetensis* and were found in *E. leucoxylon* less than expected ($\chi^2 = 4.16$, df 1, $P < 0.05$).

5.3.2 Tree Condition

Tree monitoring results are summarised in Figure 5-3 and Figure 5-4. These figures show that at the commencement of monitoring in 1997, *E. viminalis cygnetensis* trees showed a greater amount of defoliation overall than *E. leucoxylon* trees. Almost three quarters of *E. viminalis cygnetensis* trees were found to be heavily defoliated in 1997 (i.e. greater than 50% defoliation), whereas only 14% of *E. leucoxylon* trees showed a similar degree of defoliation.

Table 5-2: Koala sex ratios and fertility rates observed during censuses at Mine Creek, 1996 - 2002. Fertility rates are expressed as the percentage of females observed with joeys in each census period. Joeys can be expected to emerge from the pouch in early spring and remain dependant for approximately 6-months. Sterilised koalas were ear-tagged: tag rate provides an indication of proportion of sterilised koalas

Census Date	No. Males	No. Females	Sex Ratio (proportion females)	Fertility Rate (%)	Tag Rate (%)		Population Estimate
					M	F	
Dec-96	16	27	0.63	70	NA	NA	50
Dec-97	11	25	0.69	30	72	80	38
Jan-98	14	19	0.58	26	93	79	43
Mar-98	2	10	0.83	0	0	80	17
May-98	3	13	0.81	0	33	92	19
Jul-98	3	11	0.79	0	33	64	18
Sep-98	4	14	0.78	7	100	71	16
Oct-98	2	5	0.71	40	100	20	12
Dec-98	8	5	0.38	40	50	40	14
Jan-99	5	6	0.55	16	100	33	19
Apr-99	4	8	0.67	0	25	38	12
Jun-99	5	11	0.69	9	80	73	16
Mar-00	4	9	0.69	0	25	33	18
Nov-00	4	11	0.73	0	-	-	27
Sep-02	7	11	0.61	0	-	-	34

NB: Sex ratios, fertility rates and tag rates were calculated on the basis of data collected by the first observer as opposed to collective data for both observers. Data for Dec-96, Nov-00 and Sep-02 provided by DEH.

There was a significant shift in the number of *E. viminalis cygnetensis* trees from category 3 to category 2 defoliation levels between 1997 and 1999 ($\chi^2 = 18.2$, df 8, $P < 0.05$). Category 4 trees however did not appear to recover with almost a quarter of the trees in this category dying. There was no net increase in the number of trees in category 1. Overall *E. viminalis cygnetensis* showed little improvement with 59% of

trees remaining in defoliation categories 3 to 5, two years after population control and monitoring commenced at Mine Creek.

Eucalyptus leucoxylon appears to have responded better to the decline in koala numbers at Mine Creek with fewer trees in higher defoliation categories (i.e. 3 and 4) and a 30% increase in the number of trees in category 1 between 1997 and 1999. Only 7.5% of *E. leucoxylon* trees were found to have category 3 or 4 levels of defoliation in October 1999.

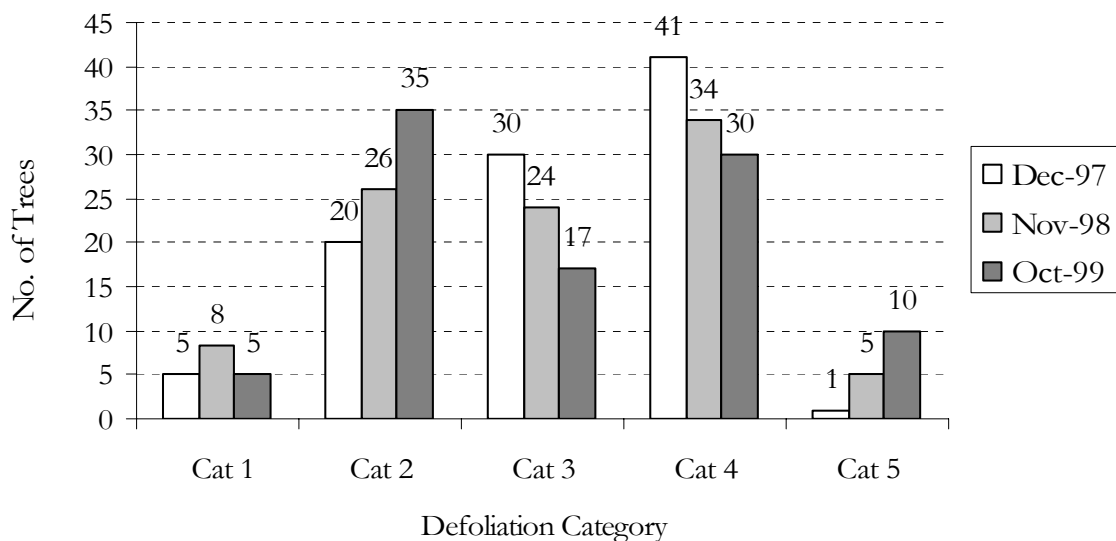


Figure 5-3: Changes in canopy condition of 97 *E. viminalis cygnetensis* trees at Mine Creek between 1997 and 1999. There was a significant shift in numbers of trees in each category of defoliation over the monitoring period which is largely attributed to the increase in numbers of trees in category 2 and 5 ($\chi^2 = 18.2$, df 8, $P < 0.05$)

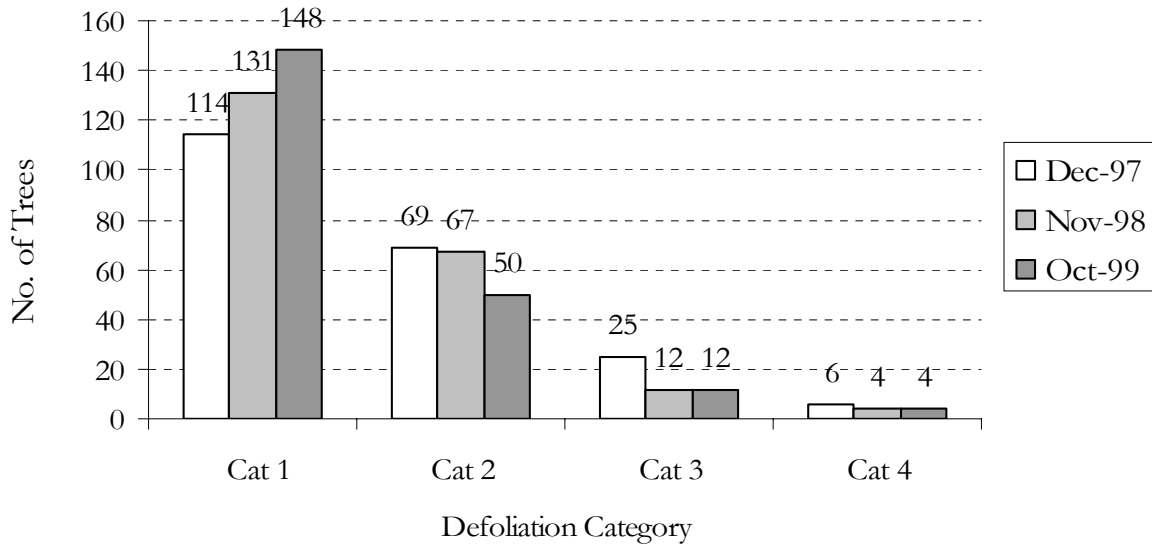


Figure 5-4: Changes in canopy condition of 214 *E. leucoxylon* trees at Mine Creek 1997 – 1999. There was a significant shift in numbers of trees in each defoliation category over the monitoring period which is largely attributed to the decline in number of trees in category 3 and increase in number of trees in category 1 ($\chi^2 = 15.4$, df 6, $P < 0.05$)

5.3.3 Tree Guards

Photographs of guarded and control trees, taken in October 1998 and one year later in December 1999, are presented in Appendix A. These photographs were used to provide a visual assessment of the relative condition of trees before and after installation of guards (Table 5-3). The condition of trees was assessed qualitatively based on visual comparison of photographs using the same defoliation categories used in tree health assessments.

Eucalyptus viminalis cygnetensis trees responded well to the exclusion of koalas and showed significant improvement in condition following installation of guards (Somers' d statistic -0.806; $P = 0.000$). All but one of the guarded *E. viminalis*

cygnetensis trees improved in condition. In contrast, control trees either showed no change in canopy condition or showed further thinning of their canopies. Only one control tree showed some improvement in canopy condition.

Canopy condition in the majority of guarded *E. leucoxydon* trees showed some improvement but this was not statistically significant ($P = 0.592$; two-sided Fisher's Exact test). Two of the five guarded trees showed no discernable change in canopy condition. Flush growth was observed on three of the control *E. leucoxydon* trees while canopy condition in the remaining four controls did not appear to change.

Table 5-3: Condition of guarded and control trees Oct 98 – Nov/Dec 99

Treatment	Tree Condition		
	Improved	No Change	Decline
Manna gum control	1	5	3
Manna gum guarded	7	1	0
Blue gum control	3	4	0
Blued gum guarded	5	2	0

5.4 Discussion

Population estimates between 1997 and 2000 demonstrate that koala numbers at Mine Creek did fall in response to control measures. However, the reduction in koala density at Mine Creek was short-term and due largely to translocation rather than the effect of sterilisation. Sterilisation in itself is not considered effective when immediate relief from browsing is required (Possingham *et al.* 1996; Martin and Handasyde 1999). Fertility suppression affects future birth rates only and without translocation

the standing population of koalas at Mine Creek, and associated levels of browse pressure, would have remained at pre-control levels over the duration of the study (Possingham *et al.* 1996). Sterilisation may be usefully applied to maintain low koala densities after an initial population reduction via alternative control methods, but sterilisation alone is unable to affect much change in severely over-browsed habitats in the immediate term (Possingham *et al.* 1996). Translocation has long been used in Victoria to reduce population densities in over-browsed habitats and since the inception of a formal translocation program over 14, 000 animals have been translocated to over 200 release sites (Martin and Handasyde 1990; Menkhorst *et al.* 1998). While this program has been successful in significantly reducing koala densities in over-browsed habitats it has often lead to the establishment of additional populations of koalas which also eventually become overpopulated. South Australia also faces the problem of having few suitable release sites on the mainland. The potential applicability, and capacity, of translocation is therefore limited.

The average annual local population growth rate for koalas following control was 27% per year, representing a potential doubling in the population every three years. Given the timeframe of the study and the noticeable decline in the fertility rate of the post-control population at Mine Creek, the increase in koala numbers subsequent to control was unlikely to be due to *in situ* breeding, but instead immigration from surrounding uncontrolled areas of habitat (or areas where only sterilisation was undertaken and population densities remained high). Although there was considerable fluctuation in tag rates from one census to another, low tag rates in some census periods do suggest that there was some immigration of non-sterilised individuals into the Mine Creek area.

Recolonisation of an area of habitat in which population density has been reduced through control, also known as a vacuum effect, has been documented in studies of *Peromyscus leucopus* (Stickle 1946), *Microtus pennsylvanicus* (Van Vleck 1968), *Perognathus parvus* (Verts and Carraway 1986) and *Clethrionomys gapperi* (Schieck and Millar 1987, Nakata and Satoh 1994). More recently, Efford *et al.* (2000) attempted to induce vacuum effect dispersal of known resident adult common brushtail possums (*Trichosurus vulpecula*) by creating a neighbouring area of reduced density. Their study found that during the year after control, 29% of possums within 100 m of the boundary of the removal area shifted their range centre at least 50 m towards it. Efford *et al.* (2000) concluded that individuals move to maximise their access to resources when no longer constrained by the behaviour of neighbours. As Mine Creek represents an area of regionally preferred habitat, due to the relative abundance of the preferred browse species *E. viminalis cygnetensis*, it is possible that koalas in surrounding less preferred habitat were attracted to this site following removal of some of the koalas. These results highlight the importance of understanding the spatial dynamics of populations and its potential influence on the outcome of control programs.

One of the key factors considered to favour a vacuum effect is a small, isolated removal or control area (Efford *et al.* 2000). To some extent this may explain some of the challenges that have been faced when localised areas of severely browsed habitat have been targeted for control on Kangaroo Island. Both Mine Creek, and Scotch Thistle Flat in Flinders Chase National Park, are relatively small areas of highly preferred habitat that have been targeted for control and in both cases long-term reduction in koala population density and subsequent habitat recovery have proved

difficult to achieve. After five years of control, including a substantial translocation program, koala densities at Scotch Thistle Flat remained unsustainably high and the majority of *E. viminalis cygnetensis* have died (Masters *et al.* 2004). Given the widespread distribution of koalas on Kangaroo Island, it is likely that populations of koalas in less preferred habitats will provide a significant contribution to population growth in areas of preferred habitat that are targeted for control.

The main objective of the koala management program on Kangaroo Island was, ‘to reduce the impact of koala over-browse on native preferred browse species so that at least 80% of manna gum is in good condition’ (DEH 2001). When the koala management program was initially established in 1997 it was considered that in order to meet this objective the population of koalas in preferred, highly suitable habitat would need to be reduced to a target density of 1 koala/ha. The lowest density of koalas recorded at Mine Creek following control was 1.2 koalas/ha in October 1998 and April 1999. Consequently, tree health monitoring data shows that there was limited recovery in the canopy condition of over-browsed trees in the study area. Two years after the commencement of the management program 59% of *E. viminalis cygnetensis* trees at Mine Creek remained severely defoliated. Results from the tree guard experiment support the suggestion that this may have been due to continued browse pressure by koalas rather than a physiological inability of trees to produce compensatory growth. Exclusion of koalas from guarded trees produced flush growth in 88% and 71% of *E. viminalis cygnetensis* and *E. leucoxylon* trees respectively. In a similar trial Geard and Burbury (1997) guarded thousands of eucalypts that were heavily browsed by brushtail possums and found that short-term re-foliation was observed in all cases, with approximately 50% of trees making a long-term recovery.

The strong capacity for regrowth in eucalypts, as observed in this study (Chapter 4) and others, suggests that long-term recovery of eucalypt communities on Kangaroo Island is achievable if koala densities are reduced to, and held at, low enough levels.

The initial koala management program, which commenced in 1997, was based on an island-wide population estimate of 5 000 koalas (StJohn 1997). A review of koala distribution and abundance on Kangaroo Island in 2001 indicated that the koala population size on the island was more likely to be approximately 27 000 (Masters *et al.* 2004). These discrepancies were predominantly due to the extended range of the population, which was not fully recognised when management of koalas began in 1997 (Duka and Masters 2005). Prior to 2000-2001 the majority of koalas were thought to be located within Flinders Chase National Park and the Cygnet River catchment. However, over half the estimated population of koalas on Kangaroo Island resides outside of these areas (Chapter 6). Approximately 3 500 koalas were sterilised between 1997 and 2000, and of these approximately 1 100 koalas were translocated to south-east South Australia (Masters *et al.* 2004). Based on the initial population estimate of 5 000 this control effort was anticipated to have targeted 70% of the koala population. It is now evident that less than 15% of the island's koala population have been targeted by control and that the koala over-population problem, and the task of addressing it, is much greater and more extensive than initially thought.

5.5 Summary

There was a decline in koala population density at Mine Creek; principally in response to translocation rather than sterilisation. The reduction in koala density at Mine Creek was short-term and did not reach the target density of 1 koala/ha.

Subsequently, tree canopy condition, particularly for the preferred browse species *E. viminalis cygnetensis*, did not improve substantially and remained severely defoliated two years after the commencement of control. An increase in the population size of koalas was observed from mid-1999 onward, representing a potential doubling in the population every three years. Immigration of animals from surrounding uncontrolled areas is a potentially important mechanism of localised population recovery. An increase in koala numbers subsequent to control was unlikely to be due to *in situ* breeding, but instead immigration from surrounding uncontrolled areas of habitat (or areas where only sterilisation was undertaken and population densities remained high).

6 Comparative Use of Preferred and Non-preferred Habitat

6.1 Introduction

This chapter reports on a radio-tracking study aimed at determining how koalas on Kangaroo Island use vegetation communities that do not contain regionally preferred tree species. Regionally preferred species are considered those species of trees which are used preferentially by koalas in areas of habitat which support high densities of koalas (i.e. *E. viminalis cygnetensis*). The specific aims of this part of the study were to find out whether koalas live permanently in areas that consist of non-preferred tree species, hereto referred to as non-preferred habitat, and if so, whether they establish stable home ranges within these areas.

Koalas have the reputation of being extremely fussy eaters. The general conclusion from studies of habitat preferences has been that koalas preferentially browse on only one or a few of a range of eucalypt species available to them in any given region (Cork *et al.* 2000; Table 6-1). Access to preferred tree species is often considered essential for the long-term survival of individuals and the establishment and persistence of breeding populations (Eberhard 1972; Sharp and Phillips 1997). The suitability of vegetation communities as potential koala habitat is therefore usually classified and ranked according to whether regionally preferred browse species are present or absent (e.g. Bryan 1996; Bryan 1997; Lunney *et al.* 1997; StJohn 1997; Mitchell 1998; Lunney *et al.* 1998; Phillips *et al.* 2000).

By necessity, most studies on koala habitat preferences have been conducted in areas that support relatively high densities of koalas (Melzer and Lamb 1994; Cork *et al.* 2000). Consequently, identification and assessment of koala habitat has tended to reflect the tree preferences of high density populations. It has often been assumed that tree communities infrequently used, or sparsely populated by koalas, are poor quality habitats that are only occupied temporarily by subordinate males or dispersing koalas seeking new home ranges (Eberhard 1972; StJohn and Ball 1995; StJohn 1997; Cork and Braithwaite 1990; Gordon *et al.* 1990).

Table 6-1: Regionally preferred food tree species throughout Australia

Author	Locality	Preferred Tree Species
Eberhard 1972	Kangaroo Island, SA	<i>E. viminalis cygnetensis</i>
Gall 1980	Tucki Tucki NR, NSW	<i>E. tereticornis</i>
Gordon <i>et al.</i> 1988	Mungalalla Ck, Qld	<i>E. camaldulensis</i>
Gordon <i>et al.</i> 1990	Inverness, Qld	<i>E. tereticornis</i> <i>E. populnea</i>
Hindell and Lee 1987, 1988	Brisbane Ranges NP, Vic	<i>E. viminalis</i> <i>E. ovata</i>
Jurkis and Potter 1997	Eden, NSW	<i>E. cypellocarpa</i> <i>E. longifolia</i>
Martin 1985a	Walkerville, Vic	<i>E. ovata</i>
Melzer and Lamb 1996	Springsure, Qld	<i>E. tereticornis</i> <i>E. crebra</i>
Pahl 1990	Logan City, Qld	<i>E. microcorys</i> <i>E. propinqua</i>
Pieters and Woodall 1996	Gold Coast, Qld	<i>E. tereticornis</i>
Phillips <i>et al.</i> 2000	Port Stephens, NSW	<i>E. robusta</i> <i>E. parramattensis</i>
White 1999	SE Qld	<i>E. tereticornis</i>

Phillips *et al.* (2000) stated that vegetation communities that are comprised solely of non-preferred tree species are only of marginal importance as koala habitat, except where they occur immediately adjacent to those communities and/or areas where regionally preferred tree species occur. Some authors have also suggested that koalas that only have access to non-preferred tree species suffer malnutrition, loss of condition and have a greater susceptibility to disease (Eberhard 1972; Bryan 1997; Gordon *et al.* 1988; Hume 1990). However, there is some evidence which indicates that koalas may establish resident populations in moderate to low quality habitat where non-preferred tree species dominate, albeit at low densities (Melzer and Lamb 1994, 1996; Munks *et al.* 1996; Ellis *et al.* 1997; Kavanagh 1999; Phillips and Callaghan 2000).

A radio-tracking study of a population of koalas at Springsure in Queensland found that koalas not only frequented vegetation communities which contained the regionally preferred tree species *E. tereticornis*, but also commonly (approx. 30% of sightings) used other tree communities in which this species was absent (Melzer and Lamb 1996). Surveys in nearby brigalow woodland found low density populations of koalas (one koala per 67-210 ha of woodland) in tree communities which did not contain any regionally preferred browse species (Melzer and Lamb 1994). Similarly, Munks *et al.* (1996) conducted a survey of koala faecal pellets in the semi-arid woodlands of the Desert Uplands in northern Queensland and found that low density populations of koalas were associated with a broad range of vegetation associations including those which did not contain regionally preferred browse species. On the basis of their findings Munks *et al.* (1996) concluded that sub-optimal habitats were likely to be important areas of useable habitat. Occasional

reports of koala sightings, and the capture of a koala near Wilcannia in western New South Wales, also led Ellis *et al.* (1997) to conclude that a sparse, permanent population of koalas may exist in habitat previously thought to be unsuitable for koalas in western New South Wales.

Eucalyptus viminalis cygnetensis is the preferred browse species of koalas in highly populated riverine areas on Kangaroo Island (Philpott 1965; Eberhard 1972; StJohn 1997; Horgan 1998). Both *E. leucoxydon* and *E. camaldulensis* are also classified as important browse species; though secondary to *E. viminalis cygnetensis* (StJohn and Ball 1995; StJohn 1997). Areas of non-preferred tree species, such as *E. baxteri*, *E. obliqua* and *E. cosmophylla*, are considered to be non-preferred habitat for koalas on Kangaroo Island (StJohn 1997). Nonetheless, koalas on Kangaroo Island have often been sighted in areas where regionally preferred tree species are absent. These koalas are usually assumed to be vagrants that spend short periods in unsuitable habitat while dispersing from one area of preferred habitat to another (St John and Ball 1995). The frequency of these sightings and their distance from known areas of preferred habitat suggests that koalas may actually be spending considerable amounts of time in non-preferred vegetation communities and possibly residing in these areas permanently.

Although there has been some preliminary research conducted on koala populations in areas consisting of non-preferred tree species (Melzer and Lamb 1994; Jurkis and Potter 1997; Phillips and Callaghan 2000), little is known about the ecology or conservation and management significance of these populations. The management significance of koala populations in non-preferred habitat is a particularly relevant issue on Kangaroo Island, where high density koala populations in

E. viminalis cygnetensis habitat have been subject to an intense management program aimed at reducing the overall koala population on the Island. The existence of a resident population of koalas in vegetation associations comprised of non-preferred tree species would alter the hereto known distribution and estimated population size of koalas on Kangaroo Island considerably, particularly given that non-preferred trees species occupy a much larger area of the island than preferred trees species which are largely confined to riverine areas.

If koalas do reside in areas of non-preferred habitat then a comparative study of koalas in preferred and non-preferred habitat would also provide a valuable opportunity to explore the influence that the environment has on spatial use of habitat, particularly home range size. There are numerous examples of studies that have found home range size to vary depending on habitat quality. This has been demonstrated for several species including the brush-tailed phascogale (*Phascogale tapoatafa*; van der Ree *et al.* 2001), Eurasian red squirrel (*Sciurus vulgaris*, Wauters *et al.* 2001), bobcat (*Felis rufous*; Gompper and Gittleman 1991), coyote (*Canus latrans*; Gompper and Gittleman 1991), black bear (*Urus americanus*, McLoughlin *et al.* 2001; Gompper and Gittleman 1991), rufous hummingbird (*Selasphorus rufus*; Kodric-Brown and Brown 1978; Gass *et al.* 1976) and golden-winged sunbird (*Nectarinia reichenowi*, Gill and Wolf 1975). A review of home range estimates for koalas from various studies shows that there is also considerable variation in home range size for koalas in differing habitat types throughout Australia (Table 6-2). In some cases there is almost two orders of magnitude difference in the home range sizes which have been reported (e.g. Mitchell 1990*b* vs. Jurkis and Potter 1997). The general

trend is for home range size to be smaller in habitat containing *E. viminalis cygnetensis* and larger in habitat where *E. viminalis cygnetensis* is absent.

Table 6-2: Comparison of reported koala home range sizes from various studies throughout Australia. FK: fixed kernel; HM: harmonic mean

Location	Preferred Tree Species	Home Range Estimator	Home Range Size (ha)		Author
			Male (n)	Female (n)	
French Island, Vic	<i>E. viminalis</i>	90% HM	2 (13)	1 (18)	Mitchell, 1990 ^b
Brisbane Ranges, Vic	<i>E. viminalis</i>	90% HM	3 (5)	2 (5)	Hindell and Lee, 1988
Kangaroo Island, SA	<i>E. viminalis cygnetensis</i>	75% FK	14 (6)	5 (8)	Horgan, 1998
Kangaroo Island, SA	<i>E. viminalis cygnetensis</i>	70% HM	9 (10)	4 (9)	Clark, 1998
South-east Qld	<i>E. tereticornis</i>	95% FK	34 (8)	15 (16)	White, 1999
Springsure, Qld	<i>E. tereticornis</i>	95%HM	87 (10)	39 (9)	Melzer, 1995
Eden, NSW	<i>E. cypellocarpa</i>	90% HM	184 (5)	265 (2)	Jurskis and Potter, 1997

Utilisation of habitat by koalas in preferred and non-preferred tree associations on Kangaroo Island was investigated using radio-telemetry. Preferred areas of habitat comprised of vegetation associations containing *E. viminalis cygnetensis* and non-preferred habitat typically consisted of an *E. baxteri*, *E. obliqua*, *E. cosmophylla* tree association. The aims of the radio-tracking study were to:

- investigate the use of areas of regionally preferred tree associations by koalas
- determine if koalas in vegetation associations which consist of only non-preferred tree species establish long-term, stable home ranges
- examine tree species use in areas where preferred tree species are absent

- undertake a preliminary assessment of population densities of koalas in non-preferred habitat
- compare home ranges of koalas in areas of non-preferred habitat with those of koalas in areas of preferred habitat
- determine if koalas breed in areas of non-preferred habitat.

6.2 Methods

Two groups of koalas were radio-tracked: one group in preferred habitat which contained *E. viminalis cygnetensis*; and one group in non-preferred habitat which comprised of vegetation associations containing *E. baxteri*, *E. obliqua* and *E. cosmophylla*. Study sites containing non-preferred tree species were located on Ella Matta and on properties surrounding Parndana (Figure 2-1). Sites containing preferred habitat were located at Mine Creek and Deep Creek (Figure 2-1).

6.2.1 Capture and Radio-Tracking

Systematic searches for koalas initially commenced in late 1997 and focussed on locating koalas in non-preferred habitat where densities of koalas were low. Due to the relative ease of locating koalas in highly populated areas of preferred habitat, searches did not commence in this habitat type until sufficient numbers of animals were located in non-preferred habitat (approx. August 1998). This progression of searching for and capturing koalas resulted in some differences in the timing and duration of periods of radio-tracking for different koalas, however all radio-tracking periods did overlap (Figure 6-1).

Once located, koalas were captured by South Australian National Parks and Wildlife Service staff and fitted with an ear tag and a radio-collar in the 150-151 MHz

frequency range (Titley Electronics Pty Ltd, Ballina, NSW; Transceiver Services, Adelaide, SA). The individually coloured and numbered ear tags allowed for easy identification of research animals, particularly when radio-collars were not visible. Tagging males and females in different ears (males left; females right) also assisted in determining the sex of koalas during population census counts. The weight of captured koalas was recorded before they were released back into the tree in which they were captured.

A Regal 2000 receiver and a directional three element Yagi antenna (Titley Electronics Pty Ltd, Ballina, NSW) were used to relocate radio-collared koalas once a day, for up to ten days a month, between September 1997 and February 2000. Radio-tracking periods for individual koalas ranged from eight months to two years (for those koalas included in final home range analyses) (Figure 6-1). Once located, the species of tree which the koala occupied was recorded as well as its activity when first sighted, presence or absence of other koalas, time of day, tree health (as per Martin 1985*a*) and location on a 1:10,000 aerial photograph. Trees occupied by radio-collared koalas were tagged with either stainless steel or galvanised iron tags to ensure that revisited trees could be identified and assigned the same coordinates within a dataset.

Most koalas were caught and re-collared at least once during the sampling period as radio-tracking periods for individual koalas usually exceeded the twelve-month battery life of the radio transmitters. Unfortunately, some radio-collars failed soon after being fitted in August 1998 and this necessitated the relocation and recapture of six koalas. Although a substantial period of time was spent searching home range areas for these koalas, three could not be re-located (M010, M012, and F012). As a

consequence, sampling periods for each of these koalas were shorter than initially intended.

It was not possible to avoid using sterilised koalas in this study, particularly in areas of preferred habitat where an intense sterilisation program had been under way for a substantial period of time and almost 75% of koalas were sterilised. A study by Horgan (1998) investigated the effect of sterilisation on the home range behaviour of koalas in the Cygnet River and found that there was no apparent difference in the short-term ranging behaviour of sterilised and intact koalas. Furthermore, surgical sterilisation techniques (tubal ligation for females and vasectomy for males) leave reproductive hormone regulation intact and as such it is not expected that there would be any effect of sterilisation on home range behaviour and movements related to breeding (Chambers *et al.* 1999). Based on Horgan's (1998) results and the difficulty of finding sufficient numbers of intact koalas at preferred habitat sites it was decided that sterilised animals would be included in this study.

6.2.2 Health and Age Assessments

All animals were taken to the Koala Rescue Program vet clinic for age and health assessments prior to removal of radio-collars and final release.

All animals were assigned one of seven age classes based on tooth wear, head length and body weight as described by Martin (1981). Animals were assigned to age class 1-3 based on tooth wear, head length and body weight; older animals were assigned to age classes on the basis of tooth wear alone. The relationship between tooth wear, head length and body weight is shown in Table 6-3.

Table 6-3: Criteria used in age assessment of koalas (modified from Martin 1983)

NOTE:
This table is included on page 104 of the print copy of the thesis held in the University of Adelaide Library.

Weight, age class, body condition, coat condition, muscle score and presence or absence of external parasites was recorded by a veterinarian assistant at the clinic. Weights were monitored prior to and during the radio-tracking period for some koalas.

6.2.3 Home Range Analysis

Home range areas, cumulative area curves and daily movements of koalas were analysed with the RANGES V software package (Kenward and Hodder 1995).

Two non-parametric models were used to estimate home range area from the radio-tracking data: (1) the Harmonic Mean Measure (Dixon and Chapman 1980); and (2)

the Fixed Kernel Density Estimator (Worton 1989). Both of these techniques are ideal for estimating the size and shape of home ranges when useable habitat occurs in discrete, fragmented patches, as is the case on Kangaroo Island (White 1994). This is because neither method imposes shape criteria on estimated home ranges, nor do they require an assumption of a bivariate normal distribution of animal locations. Parametric methods such as the Minimum Convex Polygon (Mohr 1947) and Ellipse (Jenrich and Turner 1969) models on the other hand, only provide ellipse or polygon shaped home ranges and give no indication of how intensively an animal uses different parts of its home range (Kenward and Hodder 1995). Many parametric techniques are also strongly influenced by peripheral fixes and may contain large areas that were never visited by the animals that were studied (Kenward and Hodder 1995; Kenward 1987). This is a particular problem for species, such as the koala, which make occasional excursions well outside of their normal foraging range.

Of all the available techniques, both the Harmonic Mean and Fixed Kernel Density have been found to be the least biased and variable home range estimators (Boulanger and White 1990; Seaman and Powell 1996; Seaman *et al.* 1999). However, in order to perform well, both techniques require larger sample sizes than is necessary with parametric home range estimators. In particular, Kernel-based estimates from small samples identify home range structure poorly and tend to over estimate home range size (Seaman 1997). The collection of at least 30 and preferably upwards of 50 observations per home range is recommended (Seaman *et al.* 1999).

Koala ID	1997				1998								1999								2000														
	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar				
M003																		*																CR	
M004																		*																	CF
M005																		*																	CR
M006																		*																	CR
M007																																			CR
M008				CR														*																	Dead
M009																CF		*																	CR
M010											*				CF																				
M011												Dead																							
M012															CF																				
M014											*		CF					*																	CR
F003																		*																	CR
F004																																			CR
F005																		*																	CR
F006																									*										CR
F007																									*										CR
F008																																			CR
F009																		*																	CR
F010											*	J														J	CR								
F011											*		CF					*							*										CR
F012					J											CF																			
F013																									*	J									CR
F014											*																CR								
F015											J							*							J										CR
F016																											CF								

Figure 6-1: Period of radio-tracking for each radio-collared koala. M: Male F: Female CF: collar failed * koala re-collared J: joey emerged CR: collar removed

In this study, the effect of sample size was assessed by plotting cumulative home range area against the number of radio-tracking locations available for each radio-collared koala (Kenward and Hodder 1995; Comport *et al.* 1996). The minimum required data set was then defined as the point after which additional locations resulted in minimal increase and/or variation in home range size thereby assisting in determining how many fixes are needed to accurately define home range (Harris *et al.* 1990; Kenward and Hodder 1995).

Isopleths of 50% and 90% were chosen to estimate koala home range areas and core areas respectively. Although commonly used, 95% isopleths were not selected to estimate home range areas, as this probability level tended to provide home ranges that included large areas that koalas never occupied. Prior to analysis, data sets were also manually checked to ensure that locations associated with dispersal or disturbance events, such as capture and release, were not included in the home range analysis. The use of probability levels and the subjective evaluation of the researcher are both accepted criteria for selection of movements that are normal (White and Garrott 1990). A home range is not all the area that an animal traverses during its lifetime, but rather the normal area that it uses over some specified period of time to carry out the activities of securing food, mating and caring for young (Burt 1943).

Comparisons of home range data were made using the Student's t-test where data were distributed normally and the Wilcoxon Rank Sum test where data were not normal. Normality of data was tested using the Shapiro-Wilk W test and where possible log 10 transformations were used to adjust non-normal data.

6.2.4 Daily Movement

Determination of the distance travelled by an individual over time can be as relevant as estimating home range size, particularly when considering ecological variables such as habitat use and habitat quality (Koeppel *et al.* 1977; White and Garrott 1990; Connor and Leopold 2001).

Distances of daily movements were calculated using the RANGES V interfix measurement option. Only fixes that corresponded to activity associated with normal home range movements were used in the analysis; fixes associated with dispersal or short sojourns outside of the home range were not included in analyses.

Comparisons of distance data were made using the Student's t-test where data were distributed normally and the Wilcoxon Rank Sum test where data were not normal. Normality of data was tested using the Shapiro-Wilk W test and where possible log 10 transformations were used to adjust non-normal data.

6.2.5 Tree Species Preferences

Tree species preferences were determined by comparing the observed proportion of sightings of koalas in a tree species with the expected proportion of sightings based on the availability of tree species within a given home range area (Neu *et al.* 1974; White and Garrott 1990; Comport *et al.* 1996). The availability of tree species was estimated from vegetation surveys that were conducted within each koala home range in February 1998.

At least four 0.25 ha (50 m × 50 m) sample plots were completed in each home range, with the number of sample plots varying (i.e. increasing) depending on the area

occupied by each koala. As all the trees at Mine Creek were already tagged for monitoring purposes (Chapter 5), tree species availability was based on an absolute count of the number of trees of each species for that site. Expected values were calculated by multiplying the proportion of a tree species in a home range by the total number of times a koala was recorded in that tree species during the radio-tracking study. Chi-squared analysis was used to test for the goodness-of-fit of the observed use of trees to the expected use of trees based on availability (Neu *et al.* 1974; White and Garrott 1990). If there was no preference for a particular species of tree, then usage occurred in proportion to availability.

6.2.6 Population Census

Population censuses were conducted in preferred and non-preferred habitat areas to gauge the relative density of koalas in each habitat type. Census sites were located in the same areas that koalas were radio-tracked.

Population censuses were conducted at sites containing non-preferred habitat in December 1998 and March 1999. A population census was conducted at the Deep Creek site in March 2000. Mine Creek population counts were conducted at least quarterly between December 1997 and March 2000, as part of a tree health and koala population monitoring study conducted at this site (Chapter 5).

A two-count method, as described by Caughley and Sinclair (1994), was used to estimate population size. This method involved two observers (or two groups of observers) searching a specified census area independently and recording the number of koalas seen. The second observer (or group of observers) also recorded whether the koalas they observed were sighted by the first observer; as indicated by an

inconspicuous chalk mark at the base of trees in which koalas were found. The total size of the population (Y) was then estimated using the following formula:

$$Y = \frac{(B + S_1 + 1)(B + S_2 + 1)}{(B + 1)} - 1$$

Where:

S_1 is the number of koalas seen by the first observer, but not the second observer;

S_2 is the number of koalas seen by the second observer, but not the first observer;

and

B is the number of koalas that were observed by both observers one and two.

Observers also recorded the tree species that koalas were observed in, the sex of sighted koalas and presence or absence of young.

6.3 Results

6.3.1 Health Assessments

A total of 25 (11 male: 14 female) koalas were radio-collared in areas of preferred and non-preferred habitat (Table 6-4).

Health data for radio-collared koalas are presented in Table 6-4. Generally, koalas in both preferred and non-preferred habitat types were found to be in good condition and of comparable weights.

Table 6-4: Health and weight data for koalas included in final home range analysis. Data were not complete for M010 and F012 as collars on each of these koalas failed, and koalas could not be relocated before they could be scheduled for assessment at the Vet Clinic. Measurements for M010 and F012 are based on assessment in the field during capture and collaring. * Weights sourced from the South Australian Department for Environment and Heritage koala database and recorded at time of sterilization

Koala ID	Age Class	Status	Weight (kg)				Body Condition	Coat Condition	Muscle Score	External Parasites
			6/97*	3/99	8/99	2/00				
Preferred Habitat										
M003	2	D	4.52	9.76	-	10.12	Good	Good	Good	None
M004	2	D	5.03	9.11	-	-	Good	Good	Good	None
M005	4	D	13.8	13.57	-	12.15	Good	Good	Good	None
M006	4	E	-	10.5	-	10.4	Good	Good	Good	None
M007	4	E	-	8.79	-	9.12	Good	Good	Good	None
F003	4	D	6.68	8.31	-	8.6	Good	Good	Good	None
F005	4	E	-	9.43	-	8.7	Good	Good	Good	None
F007	5	D	8.53		8.7	8.05	Good	Good	Good	None
F008	3	D	2.51	6.14		6.96	Good	Good	Good	None
Non-preferred Habitat										
M008	-	E	-	-	-	Dead	-	-	-	-
M009	5	E	-	-	-	11.07	Good	Good	Good	None
M010	4	E	-	-	-	-	Good	Good	Good	None
M014	4	E	-	-	-	10.8	Good	Good	Good	None
F009	5	D	9.96	-	-	9.37	Good	Good	Good	None
F010	3	D	7.96	-	8.0	-	Good	Good	Good	None
F011	2	D	6.74	-	8.9	8.42	Good	Good	Good	None
F012	-	E	-	-	-	-	Good	Good	Good	None
F014	3	D	6.36	-	6.75	-	Average	Good	Average	None
F015	4	E	-	8.14	-	7.47	Good	Good	Good	None

6.3.2 Home Range Analysis

Number of Fixes Required for Home Range Estimates

The sample size required to reliably estimate home range area, in either preferred or non-preferred habitat, depended on the home range estimation technique used. In the case of the fixed kernel technique (90% isopleth) home range area estimates began to asymptote after approximately 50-60 fixes, whereas in many cases the harmonic mean method (90% isopleth) showed no clear asymptote even after 80-90 fixes had been collected (Figure 6-2 to Figure 6-5). This suggests that analysis of datasets with fewer than 80-90 fixes with the harmonic mean method may result in variable and/or inaccurate home range estimates (i.e. an underestimate of home range area (Kenward and Hodder 1995)).

Given that most individual datasets had fewer than 80-90 fixes, it was assumed that results using the harmonic mean method are likely to be less reliable than estimates based on the fixed kernel method.

Home Range Area

Home range and core area estimates were calculated for 19 individual koalas (9 koalas in preferred habitat and 10 koalas in non-preferred habitat). Home range and core area estimates are given in Table 6-5. Individual 50% and 90% home range areas for each koala are provided in Appendix B.

Home range estimates could not be determined for six koalas as these individuals were continually dispersing throughout the study period and did not establish stable home ranges. Dispersing animals occurred in both preferred and non-preferred habitat types (Table 6-5). However, there were twice as many dispersing koalas in

non-preferred habitat (4) compared with preferred habitat (2). More females than males were dispersing.

Both of the dispersing koalas in preferred habitat were adult (age class 4) females that had been sterilised, whereas three (1 female: 2 males) of the four dispersing koalas in non-preferred habitat were entire sub-adults (age class 2 to early 3). The only desexed female that was dispersing in non-preferred habitat was an adult (age class 6) that was originally from an area of preferred habitat on the Cygnet River.

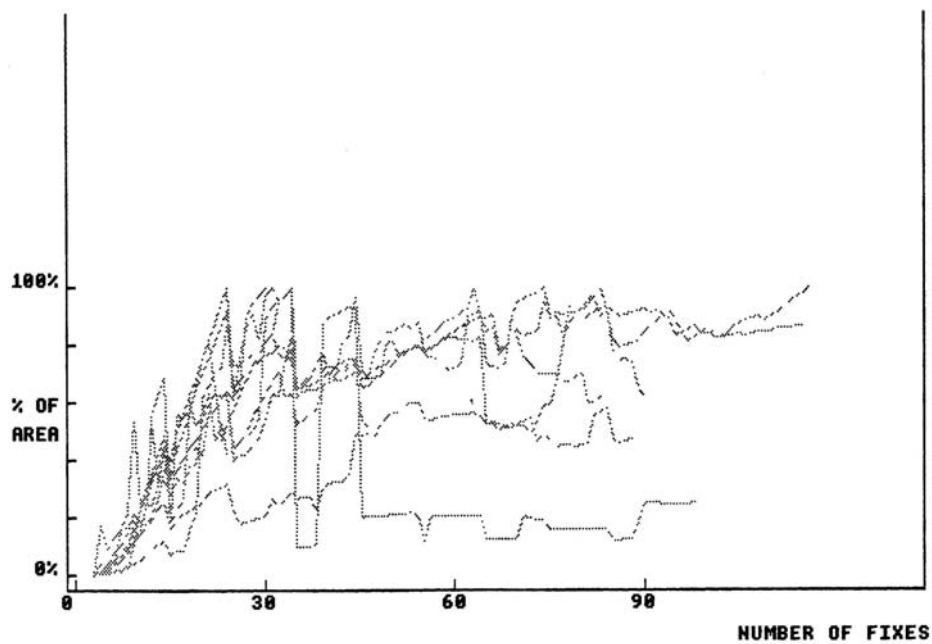


Figure 6-2: Influence of sample size on harmonic mean estimates (90% isopleth) for koalas in preferred habitat (5 male: 4 female)

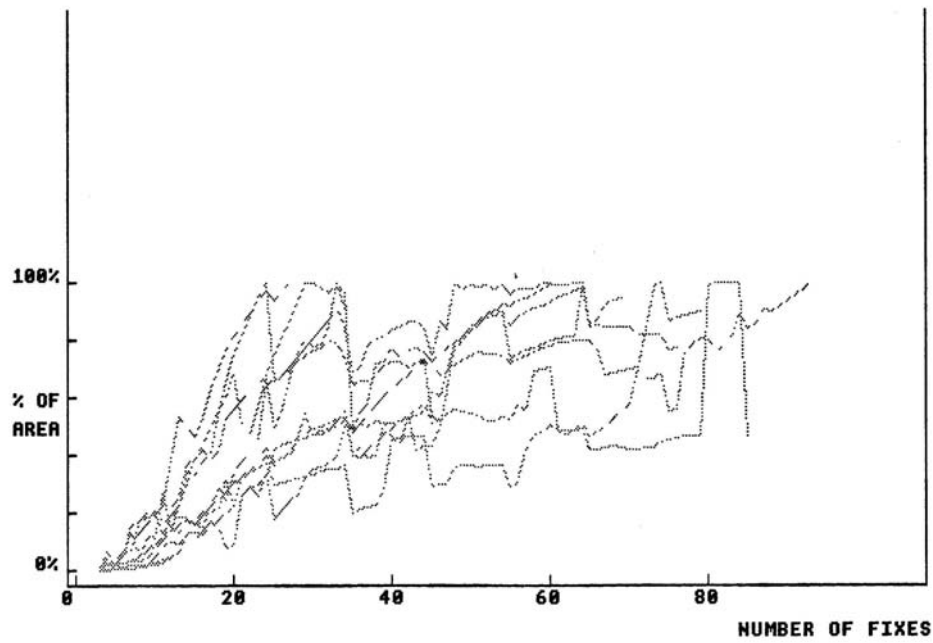


Figure 6-3: Influence of sample size on harmonic mean estimates (90% isopleth) for koalas in non-preferred habitat (4 male: 6 female)

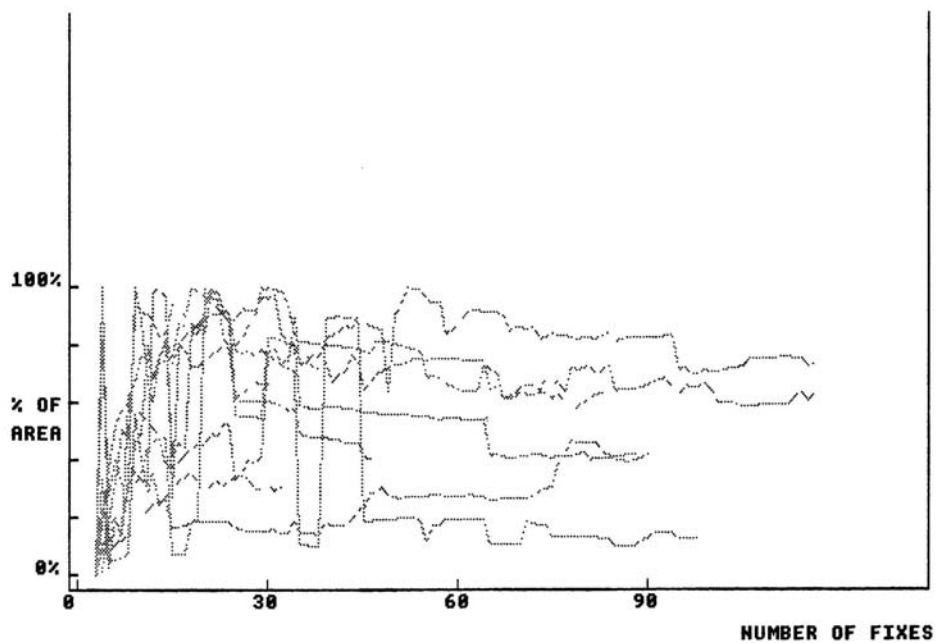


Figure 6-4: Influence of sample size on fixed kernel estimates (90% isopleth) for koalas in preferred habitat (5 male: 4 female)

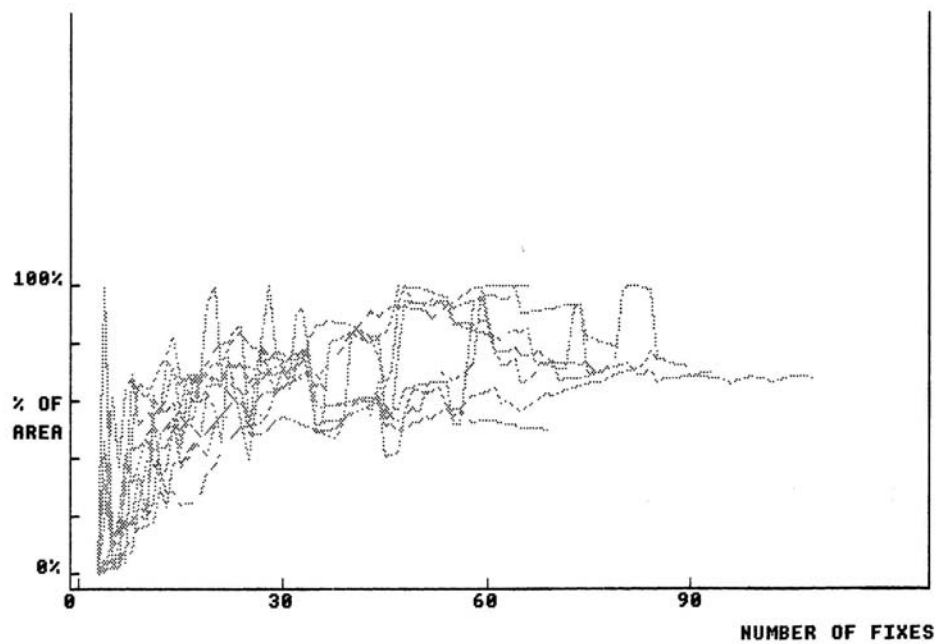


Figure 6-5: Influence of sample size on fixed kernel estimates (90% isopleth) for koalas in non-preferred habitat (4 male: 6 female)

The mean home range area for male koalas in preferred habitat was 8.1 ha for the harmonic mean method (90% isopleths) and 8.2 ha for the fixed kernel method (90% isopleths). Mean female home ranges in preferred habitat varied from 1.9 ha for the harmonic mean method (90% isopleths) to 2.7 ha for the fixed kernel method (90% isopleths). The mean male core ranges (50% isopleth) in preferred habitat were 1.5 ha and 1.3 ha for kernel and harmonic mean methods respectively. Mean core ranges for female koalas in preferred habitat were 0.3 ha for the harmonic mean method and 0.4 ha using the fixed kernel method. Male koalas had a significantly larger mean home range area than females in preferred habitat based on both estimators, however core ranges did not differ significantly between the sexes (Table 6-6).

Mean home range area for male koalas in non-preferred habitat was 40.5ha for the harmonic mean method (90% isopleths) and 53.8ha for the fixed kernel method (90% isopleths). Mean female home ranges in non-preferred habitat varied from 10.1ha for the harmonic method (90% isopleth) to 9.2ha for the fixed kernel method (90% isopleth). The mean male core ranges (50% isopleth) in non-preferred habitat were 10.2 ha and 6.0ha for kernel and harmonic mean methods respectively. Mean core ranges for female koalas in preferred habitat were 2.8ha for the harmonic mean method and 2.7ha using the fixed kernel method. Male koalas in non-preferred habitat had significantly larger mean home range areas than females, but core ranges did not differ significantly for male and female koalas (Table 6-7).

A comparison of estimated home range areas between koalas in preferred and non-preferred habitat shows that koalas in non-preferred habitat had significantly larger home ranges than koalas in preferred habitat (Table 6-8). This was also the case within sexes with male koalas in non-preferred habitat having significantly larger home ranges than males in preferred habitat and females in non-preferred habitat having significantly larger home ranges than female koalas in preferred habitat (Table 6-8).

Core ranges for females differed significantly between the habitat types, but despite substantially different mean values for core ranges no significant difference was found between core ranges for males in preferred and non-preferred habitat (Table 6-8). This latter result is likely to be due to the high level of variability in core home range estimates for male koalas in non-preferred habitat (Table 6-5).

Table 6-5: Home range estimates for koalas in preferred and non-preferred habitat types. n1 is the total number of fixes obtained for an individual koala over the entire tracking period; n2 is the final number of fixes used in home range analysis. D: dispersing koalas

Koala ID	n1	n2	Area (ha)			
			50%HM	90%HM	50%K	90%K
Preferred Habitat						
M003	127	115	1.8	8.2	0.8	4.1
M004	94	89	1.0	6.7	1.4	8.0
M005	125	115	2.7	12.0	3.1	10.6
M006	98	87	0.7	7.9	0.8	9.6
M007	42	29	0.2	5.9	1.5	8.5
F003	96	82	0.2	1.2	0.3	1.8
F004	26	-	D	D	D	D
F005	101	97	0.2	0.5	0.1	0.3
F006	80	-	D	D	D	D
F007	72	31	0.1	1.2	0.6	2.1
F008	45	45	0.8	4.7	0.5	6.6
Non-preferred Habitat						
M008	26	26	0.8	9.2	1.3	10.5
M009	78	78	10.6	69.0	11.8	109.5
M010	59	59	2.3	15.6	3.1	14.1
M011	27	-	D	D	D	D
M012	19	-	D	D	D	D
M014	92	92	10.1	68.0	24.7	81.2
F009	107	107	1.6	6.9	2.0	7.3
F010	92	68	1.2	7.2	1.1	5.1
F011	95	65	1.2	9.0	1.8	9.0
F012	51	32	7.6	21.0	8.2	19.2
F013	39	-	D	D	D	D
F014	107	75	1.9	8.3	1.5	6.8
F015	88	84	2.8	8.1	2.4	7.5
F016	38	-	D	D	D	D

Table 6-6: Comparison of home range area and core area estimates for male and female koalas in preferred habitat (5 male: 4 female)

	Sex	Area (ha)			T ¹	z ²	p
		Mean	s.d.	Range			
Fixed Kernel							
90%	Male	8.2	2.5	4.1 - 10.6	-3.15		0.016
	Female	2.7	2.7	0.3 - 6.6			
50%	Male	1.5	0.9	0.8 - 3.1	-2.35		0.051
	Female	0.4	0.2	0.1 - 0.6			
Harmonic Mean							
90%	Male	8.1	2.3	5.9 - 8.2	-4.30		0.003
	Female	1.9	1.9	0.5 - 4.7			
50%	Male	1.3	1.0	0.2 - 1.8	-1.62		0.105
	Female	0.3	0.3	0.1 - 0.8			

¹ Two-tailed t-test² Wilcoxon ranked sums**Table 6-7: Comparison of home range area and core area estimates for male and female koalas in non-preferred habitat (4 male: 6 female)**

	Sex	Area (ha)			z ¹	P
		Mean	s.d.	Range		
Fixed Kernel						
90%	Male	53.8	49.3	10.5 – 109.5	2.03	0.042
	Female	9.2	5.1	5.1 - 19.2		
50%	Male	10.2	10.7	1.3 - 24.7	1.17	0.241
	Female	2.8	2.7	1.1 - 8.2		
Harmonic Mean						
90%	Male	40.5	32.5	9.2 - 69	2.03	0.042
	Female	10.1	5.4	6.9 - 21		
50%	Male	6.0	5.1	0.8 - 10.6	0.75	0.454
	Female	2.7	2.5	1.2 - 7.6		

¹ Wilcoxon ranked sums

Table 6-8: Comparison of home range areas and core area estimates for male and female koalas in preferred and non-preferred habitat (9 male: 10 female)

	Habitat Type	Area (ha)			z ¹	P
		Mean	s.d.	Range		
Female						
90% Kernel	Preferred	2.7	2.7	0.3 - 6.6	-2.23	0.025
	Non-preferred	9.2	5.1	5.1 - 19.2		
50% Kernel	Preferred	0.4	0.2	0.1 - 0.6	-2.45	0.014
	Non-preferred	2.8	2.7	1.1 - 8.2		
90% Harmonic Mean	Preferred	1.9	1.9	0.5 - 4.7	-2.45	0.013
	Non-preferred	10.1	5.4	6.9 - 21		
50% Harmonic Mean	Preferred	0.3	0.3	0.1 - 0.8	-2.46	0.013
	Non-preferred	2.7	2.5	1.2 - 7.6		
Male						
90% Kernel	Preferred	8.2	2.5	4.1 - 10.6	2.08	0.037
	Non-preferred	53.8	49.3	10.5 - 109.5		
50% Kernel	Preferred	1.5	0.9	0.8 - 3.1	1.48	0.138
	Non-preferred	10.2	10.7	1.3 - 24.7		
90% Harmonic Mean	Preferred	8.1	2.3	5.9 - 12	2.08	0.037
	Non-preferred	40.5	32.5	9.2 - 69		
50% Harmonic Mean	Preferred	1.3	1.0	0.2 - 2.7	1.35	0.177
	Non-preferred	6.0	5.1	0.8 - 10.6		
Pooled Data (within habitat type)						
90% Kernel	Preferred	5.7	3.8	1.8 - 10.6	-2.00	0.045
	Non-preferred	27	36.9	5.1 - 109.5		
50% Kernel	Preferred	1.0	0.9	0.1 - 3.1	-2.74	0.006
	Non-preferred	5.8	7.5	1.1 - 24.7		
90% Harmonic Mean	Preferred	5.4	3.9	0.5 - 12	-2.74	0.006
	Non-preferred	22	24.8	6.9 - 69		
50% Harmonic Mean	Preferred	0.9	0.9	0.1 - 2.7	-2.70	0.007
	Non-preferred	4	3.9	1.2 - 10.6		

¹ Wilcoxon ranked sums

Daily Movements

Average daily movements for all koalas are presented in Table 6-9. Frequency distribution of distance travelled by koalas from one day to the next in preferred and non-preferred habitat is presented in Figure 6-6 and Figure 6-7.

Male koalas in preferred habitat moved a mean distance of 132 m/day (median 105 m/day) and females in preferred habitat a mean distance of 52 m/day (median 25 m/day). Mean distance travelled by male koalas in non-preferred habitat was 181 m/day (median 150 m/day) and mean distance travelled for females in non-preferred habitat was 88 m/day (median 60 m/day). Dispersing females moved a mean distance of 180 m/day (median 78 m/day) whereas dispersing males moved a mean distance of 189 m/day (median 108 m/day). Frequency distributions of daily movements show that most koalas move relatively short distances (i.e. <50 m) from one day to the next.

Statistical comparison of mean distance travelled per day shows that although non-dispersing male koalas moved significantly further from day-to-day than non-dispersing females in both preferred and non-preferred habitat, dispersing males did not move significantly further than dispersing females (Table 6-10).

Table 6-9: Daily distance travelled for each radio-collared koala

Habitat Type	Koala ID	N	% Days Koala Moved	Range (m)	Mean (m)	Median (m)
Preferred	M003	86	90	0 – 393	126	109
	M004	65	74	0 – 343	64	36
	M005	85	94	0 – 640	207	201
	M006	59	86	0 – 524	158	115
	M007	19	100	20 – 306	103	80
	F003	62	68	0 – 110	25	17
	F005	70	84	0 – 398	45	22
	F007	21	67	0 – 250	87	46
	F008	35	77	0 – 185	52	42
Non-preferred	M008	16	69	0 – 404	97	57
	M009	62	90	0 – 746	252	208
	M010	44	93	0 – 609	184	151
	M014	68	97	0 – 629	193	149
	F009	83	92	0 – 344	66	55
	F010	54	93	0 – 434	103	66
	F011	52	90	0 – 294	56	43
	F012	24	96	0 – 335	122	118
	F014	59	73	0 – 465	71	50
	F015	64	95	0 – 810	111	73
Dispersing Animals	M011	20	100	14 – 740	302	298
	M012	11	91	0 – 174	75	75
	F004	18	72	0 – 491	99	61
	F006	50	96	0 – 377	96	65
	F013	26	92	0 – 1444	318	109
	F016	27	89	0 – 675	189	147

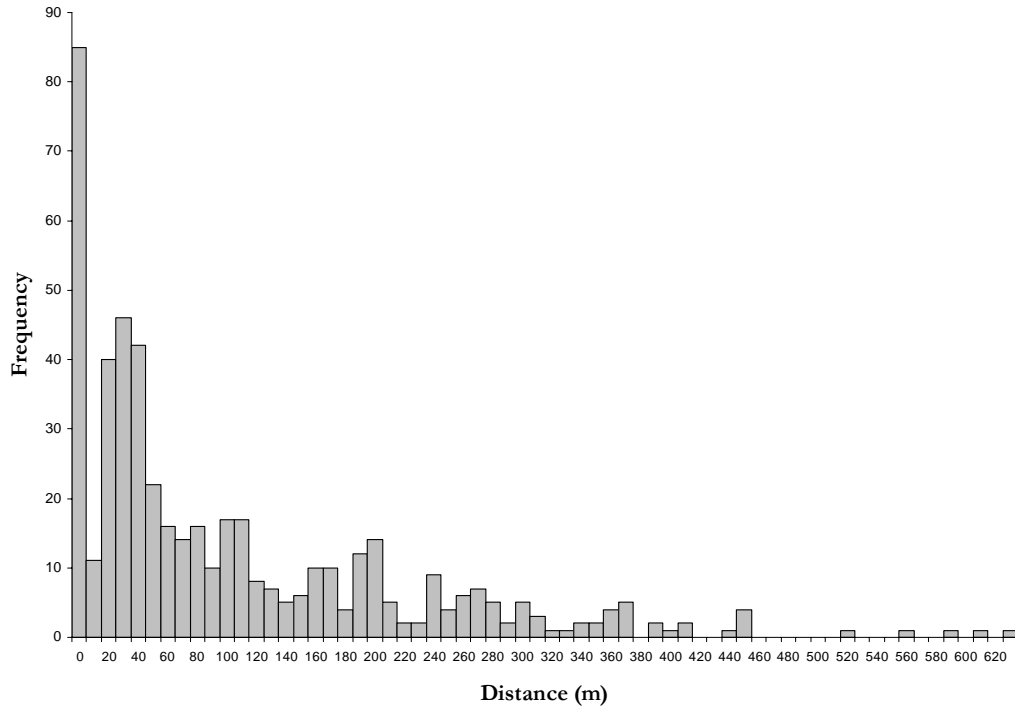


Figure 6-6: Frequency distribution of distance travelled by koalas in preferred habitat (4 male: 5 female)

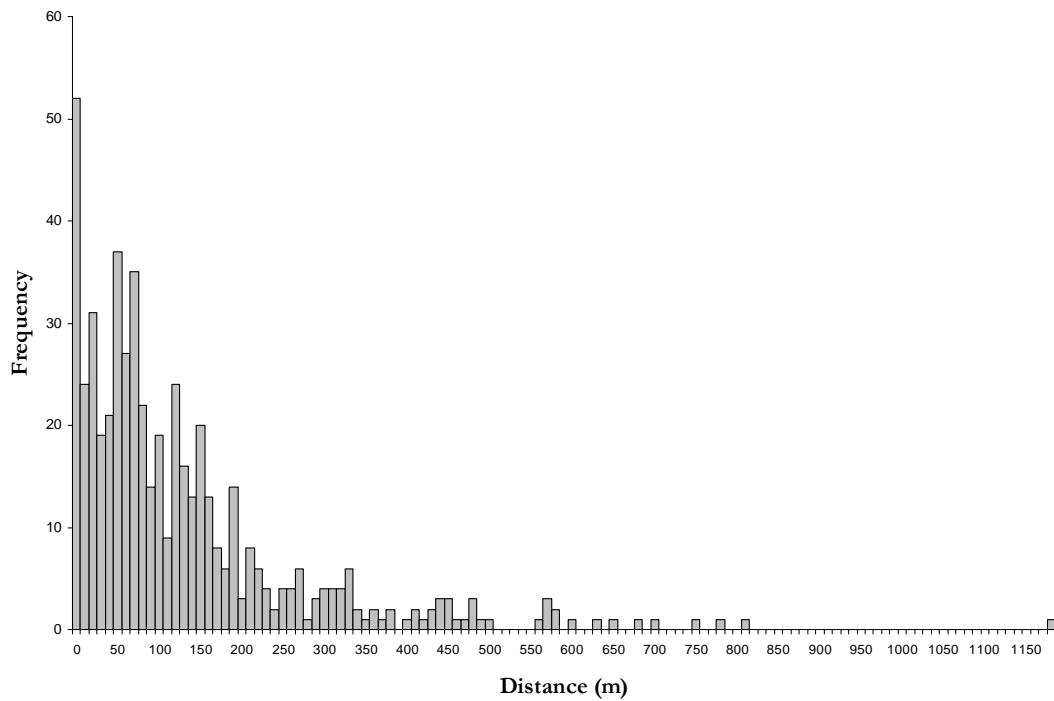


Figure 6-7: Frequency distribution of distance travelled by koalas in non-preferred habitat (4 male: 6 female)

Table 6-10: Statistical comparison of daily distance travelled by radio-collared koalas

	Sex/Habitat Type	Mean (m/day)	n	s.d.	t ¹	P
Preferred						
	Male	132	5	54.1	-2.67	0.032
	Female	52	4	25.8		
Non-preferred						
	Male	181	4	64.1	-3.18	0.013
	Female	89	6	27.7		
Dispersing Koalas						
	Male	188	2	161.1	-0.12	0.907
	Female	175	4	104.5		
Male Koalas						
	Preferred	132	5	54.1	-1.27	0.245
	Non-preferred	181	4	64.1		
	Non-preferred	181	4	64.1	0.08	0.938
	Dispersing	188	2	161.1		
	Preferred	132	5	54.1	0.78	0.469
	Dispersing	188	2	161.1		
Female Koalas						
	Preferred	52	4	25.8	-2.08	0.071
	Non-preferred	89	6	27.7		
	Non-preferred	89	6	27.7	-1.99	0.082
	Dispersing	175	4	104.5		
	Preferred	52	4	25.8	-2.29	0.062
	Dispersing	175	4	104.5		

¹ Two-tailed t-test

Comparison of daily movement for dispersing male koalas in preferred habitat and non-preferred habitat found no significant differences (Table 6-10). Similarly, there was no significant difference in daily distance travelled between any of the groups of female koalas.

6.3.3 Tree Species Preferences

Radio-collared koalas were observed in the following ten eucalypt and five non-eucalypt tree species during the study period:

E. baxteri

E. obliqua

E. cladocalyx

E. viminalis cygnetensis

E. cneorifolia

Acacia retinoides

E. cosmophylla

Callistemon rugulosus

E. diversifolia

Exocarpus cupressiformis

E. fasciculosa

Hakea rostrata

E. globulus

Pinus radiata

E. leucoxydon

Koalas were sighted in eucalypt species in 95% of cases, with only 5% of the 1376 home range recordings being attributed to non-eucalypt tree species. Non-eucalypt tree species were excluded from assessment of tree preference as there were too few data points to meet the requirements of analysis (i.e. too many expected values below five to allow for reliable chi-squared analysis). Similarly, *E. cladocalyx*, *E. cneorifolia*, *E. diversifolia* and *E. globulus* were excluded from analysis as koalas were recorded in these eucalypt species rarely (6, 1, 1 and 10 times respectively).

Observed frequencies of use of tree species were found to differ significantly from availability of tree species when data for koalas in each habitat type were analysed

separately. Koalas in preferred habitat selectively used *E. viminalis cygnetensis* and *E. leucoxylon*, but tended to avoid *E. baxteri*, *E. obliqua*, *E. fasciculosa* and *E. cosmophylla*. ($\chi^2 = 233$, df 5, $P < 0.001$; Figure 6-8). In contrast, koalas favoured *E. obliqua* and *E. leucoxylon* in non-preferred habitat and avoided *E. baxteri*, *E. cosmophylla* and *E. fasciculosa*. ($\chi^2 = 284$, df 4, $P < 0.001$; Figure 6-9).

Analysis of tree use data for individual koalas shows that there is considerable variability in individual preference for tree species within habitat types (Table 6-11). Statistical analysis of tree preference for each individual koala is presented in Appendix C.

Although most koalas in preferred habitat selectively used *E. viminalis cygnetensis*, as expected based on results of analysis of pooled data, one koala (F005) was found to avoid *E. viminalis cygnetensis* in preference for *E. leucoxylon* and two koalas (M007; F007) showed no significant preference for any of the eucalypt species available (i.e. these koalas used each tree species in proportion to availability). There was greater individual variability in preference for tree species in non-preferred habitat with two koalas (M008; F014) showing a preference for *E. leucoxylon*, five koalas (M009; M010; M014; F010; F015) preferentially using *E. obliqua* and one female koala (F009) preferring *E. cosmophylla*.

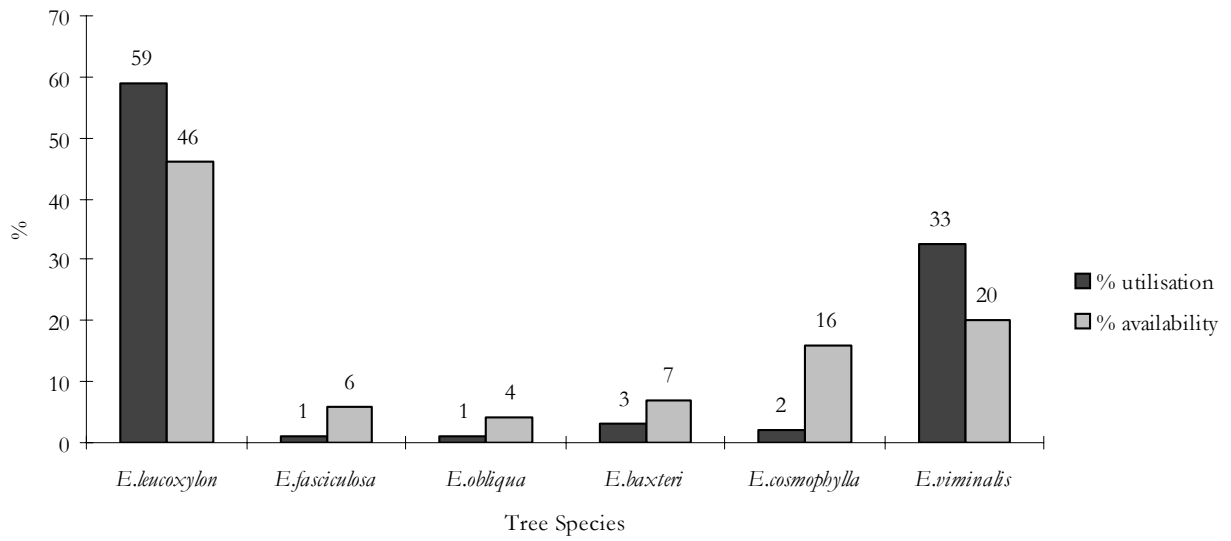


Figure 6-8: Observed use by koalas and availability of eucalypt tree species in preferred habitat based on 710 observations (5 male: 4 female)

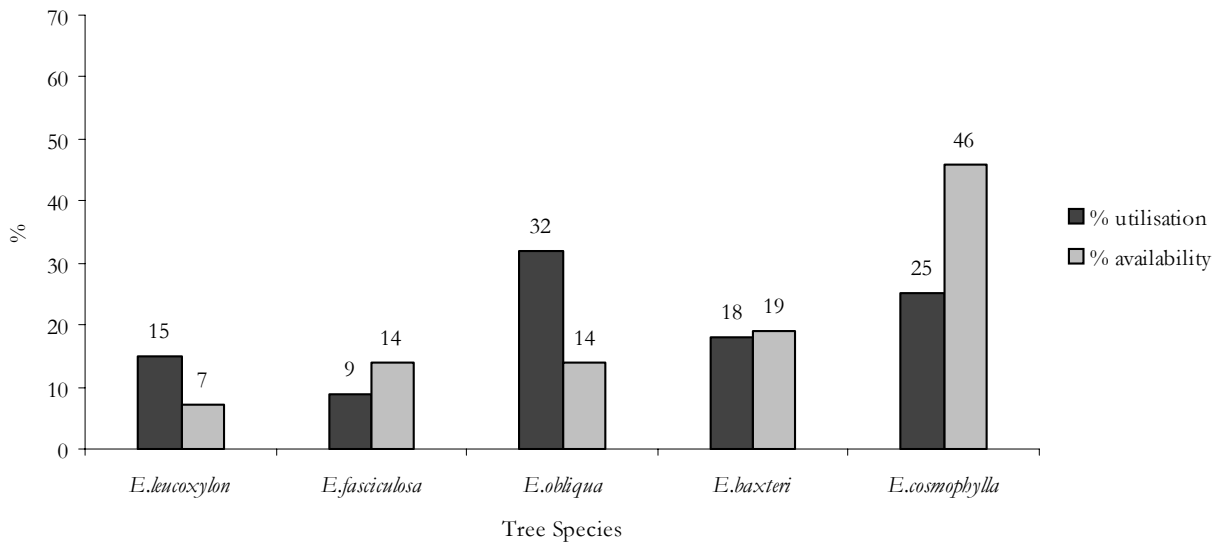


Figure 6-9: Observed use by koalas and availability of eucalypt tree species in non-preferred habitat based on 634 observations (4 male: 6 female)

Table 6-11: Tree preference for individual koalas in preferred and non-preferred habitat types. Tree species used greater than expected are shown as preferred. Preferred species in bold indicate most preferred species available. Blank cells indicate that tree species did not occur within individual koalas home range. Statistical analysis of tree preference for each individual koala is presented in Appendix C

Koala	χ^2	Df	P	Tree Species					
				E.leuc	E.fasc	E.obl	E.baxt	E.cosm	E.vim
Preferred Habitat									
M003	208.51	5	<0.001	Prefer	Avoid	Avoid	Avoid	Avoid	Prefer
M004	34.87	2	<0.001	Avoid	Avoid			Avoid	Prefer
M005	63.64	5	<0.001	Prefer	Avoid	Avoid	Avoid	Avoid	Prefer
M006	9.38	2	0.009	Prefer	Avoid	Avoid			Prefer
M007	2.74	2	0.26	NP	NP			NP	NP
F003	117.80	2	<0.001	Avoid	Avoid			Avoid	Prefer
F005	50.68	2	<0.001	Prefer	Avoid			Avoid	Avoid
F007	2.99	2	0.32	NP	NP			NP	NP
F008	9.93	2	0.015	Avoid	Avoid			Avoid	Prefer
Non-preferred Habitat									
M008	37.93	3	<0.001	Prefer		Prefer	Avoid	Avoid	
M009	38.09	2	<0.001			Prefer	Avoid	Avoid	
M010	25.99	4	<0.001	Prefer	Avoid	Prefer	Prefer	Avoid	
M014	113.90	3	<0.001	Prefer		Prefer	Avoid	Avoid	
F009	8.21	3	0.042		Avoid	Prefer	Avoid	Prefer	
F010	37.44	4	<0.001	Prefer	Avoid	Prefer	Prefer	Avoid	
F011	-	-	-	-	-	-	-	-	-
F012	-	-	-	-	-	-	-	-	-
F014	145.50	4	<0.001	Prefer	Avoid	Prefer	Avoid	Avoid	
F015	46.91	2	<0.001			Prefer	Avoid	Avoid	

6.3.4 Population Census

Overall areas of non-preferred habitat were found to support lower densities of koalas than areas of preferred habitat. A summary of census results is presented in Table 6-12. Mine Creek census results from 1997 to 2000 are presented in Figure 5-2 (Chapter 5).

Table 6-12: Summary of population census results. Censused areas (column five) consisted only of vegetated areas and did not include cleared areas (i.e. pasture) between patches of vegetation

Property/ Census Site	Habitat Type	Census Date	Pop. Est. (Y)	Census Area (ha)	Pop. Density
Ella Matta: Site 1	Non-preferred	12/98	6	7	0.81/ha
Ella Matta: Site 2	"	12/98	3	8	0.38/ha
Pioneer Bend	"	12/98	1	10	0.10/ha
Tremaine's	"	12/98	1	9	0.11/ha
Tremaine's	"	3/99	4	9	0.44/ha
Deep Creek	Preferred	3/00	3	6	0.5/ha
Mine Creek	"	12/97 – 3/00	12 - 43	10	1.20 – 4.27/ha

The low density of koalas recorded at Deep Creek is misleading, as this area has been subject to an intense translocation and sterilisation program that has been conducted since early 1997. Hence, the number of koalas found in Deep Creek during the census in 2000 is considered to be 'artificially' low. The Mine Creek site has also been subject to an intense management effort, both in terms of translocations and sterilisation, and koala numbers at this site are also relatively low when compared to results from censuses conducted before management commenced. Table 6-13

provides estimated koala densities at Mine Creek and Deep Creek, based on Department of Environment and Heritage annual census data, and shows that prior to management both sites supported considerably higher densities of koalas than they did throughout this study. Sterilisation has occurred in some areas of non-preferred habitat since 1997, but no translocations have occurred.

Table 6-13: South Australian Department for Environment and Heritage annual census results for Mine Creek and Deep Creek 1996-1998.
* Translocation and sterilisation of koalas commenced at both sites in early 1997

NOTE:
This table is included on page 129 of the print copy of the thesis held in the University of Adelaide Library.

6.4 Discussion

6.4.1 Use of Non-preferred Habitat

Areas of non-preferred habitat were found to support resident koalas that had well established home ranges. These koalas were also found to be in good condition and of comparable weight to koalas in preferred habitat. Based on these results there is a healthy population of koalas in areas of non-preferred habitat that forms an important part of the ecology of this species on Kangaroo Island.

Whether koalas in non-preferred habitat represent a viable stand-alone population or a sink population that relies on immigration from more productive source

populations (e.g. preferred habitat) for long-term persistence is not known. Anecdotal observations suggest that koalas are successfully breeding in non-preferred habitat. All of the entire females in this habitat type bred at least once during the duration of this study and two of these female koalas bred twice during the two years that they were radio-collared (Figure 6-1). However, without an accurate estimate of the mortality rate it is not possible to determine if within-habitat reproduction is sufficient to balance local mortality in non-preferred habitats on Kangaroo Island.

6.4.2 Home Range Size

Home ranges of koalas in non-preferred habitat were considerably larger than observed home ranges for koalas in preferred habitat. Home range size is primarily determined by an animal's energetic needs and by the distribution of available food within its habitat (McNab 1963; Mace and Harvey 1983). The abundance and predictability of food resources in time and space is an important determinant of home range size because survival and reproduction is often food limited (McLoughlin and Ferguson 2000). McLoughlin *et al.* (2001) developed a conceptual model of spatial organisation for food-maximising, solitary animals, based upon factors that affect variation in home range size such as the abundance and distribution of food resources within an animal's habitat. The model, as depicted in Figure 6-10, predicts that in high quality habitat, where food is abundant and predictable in time and space, populations are characterised by small home ranges, high population densities and high home range overlap. McLoughlin *et al.* (2001) suggest that small home ranges occur where food is abundant or predictable because animals will be able to maximise required energy intake over a small area. Further, the model predicts a shift to larger home ranges, and a decrease in density and home range overlap, as habitat quality

decreases to more moderate or low quality. It is suggested that larger ranges are needed to effectively collect less abundant or more spatially and/or temporally variable food to meet energy demands.

Although this study did not investigate level of home range overlap in preferred and non-preferred habitat, the McLoughlin *et al.* (2001) model is still relevant when considering observed differences in home range sizes between koalas in preferred and non-preferred habitat. As the model predicts home range size was found to be larger in low quality, non-preferred habitat, and smaller in high quality, preferred habitat. The disparity in observed home range size may be a result of there being fewer more widely distributed palatable food trees in non-preferred habitat compared with an abundance of palatable species in preferred habitat. Although koalas in both habitat types are likely to have similar energy needs, individuals may be required to meet these needs in habitats that have quite different available food resources.

Herbivores' decisions of whether or not to feed on an individual plant are informed by both by the plant's nutritional value and its defences (Moore *et al.* 2005). The nutritional value and concentration of plant secondary metabolites (PSMs) has been found to limit the food intake of a herbivore, or deter it from feeding altogether, and therefore contributes to habitat heterogeneity (Lawler *et al.* 2000). Recent work by Lawler *et al.* (1998, 2000) has shown that varying concentrations of PSMs in some eucalypts can cause deterrence in herbivores such as koalas and ringtail possums. Likewise, Moore *et al.* (2005) found that while nutritional value of foliage influenced feeding, a group of PSMs known as formylated phloroglucinol compounds accounted for most between-tree variation in the amount that koalas eat of a particular species.

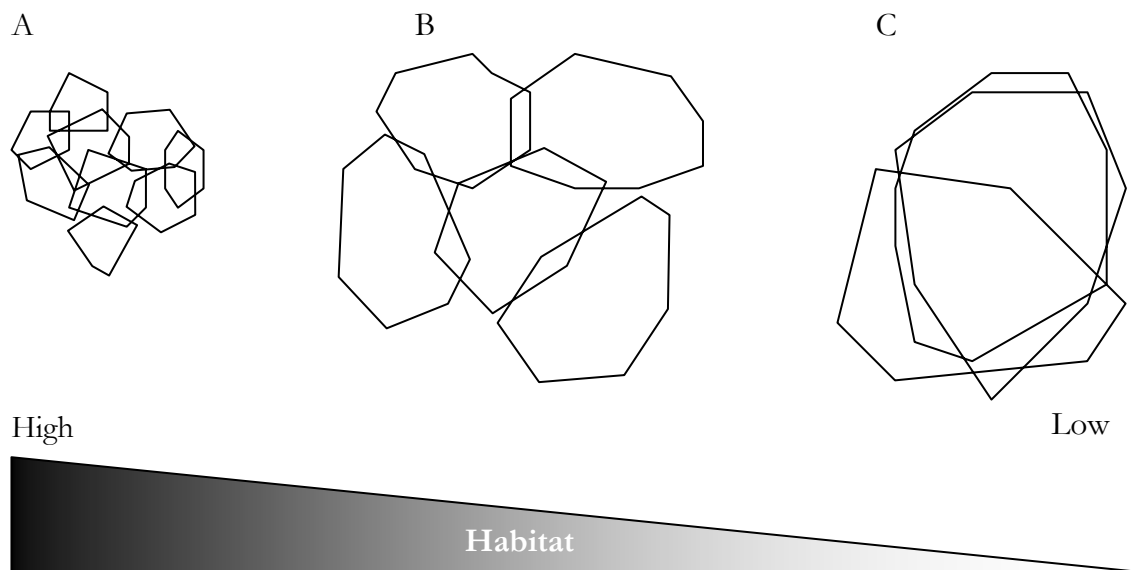


Figure 6-10: **McLoughlin *et al.* (2001) space-use model.** Spatial organisation of individuals varies along a continuum according to habitat quality, which can be defined by the abundance and predictability of food resources. (A) In areas of high quality habitat, populations are characterised by high densities, small home ranges, and high home range overlap. (B) In areas of intermediate quality habitat, populations are characterised by intermediate densities, moderately sized home ranges, and low levels of home range overlap. (C) In areas of low quality habitat, populations are characterised by low densities, large home ranges, and high home range overlap

These results suggest there may be considerable patchiness in the distribution and abundance of palatable food trees within eucalypt communities. This in turn may affect the foraging behaviour of individuals, with potential flow-on effects for spatial use of habitat and home range size. Based on home range estimates, non-preferred habitats in this study had resident koalas with larger home ranges than koalas preferred habitat; consistent with the difference in quality of tree species.

6.4.3 Population Density

Koalas were found to occur at relatively low densities in areas of non-preferred habitat and higher densities in preferred habitat. Non-preferred habitat was considered areas which did not contain the regionally preferred tree species *E. viminalis cygnetensis*. The density of koalas surveyed in areas of non-preferred habitat for this study ranged from 0.1 to 0.81 koalas per hectare. In contrast surveys conducted by the Department for Environment and Heritage along the Cygnet River prior to sterilisation and translocation, recorded koala densities of up to five koalas per hectare. In an island-wide population survey across all habitat types on Kangaroo Island in 2000-01, Masters *et al.* (2004) found low-quality habitat (dominated by *E. obliqua*) supported an average density of 0.35 koalas per hectare; whereas high-quality habitat (dominated by *E. viminalis*) supported an average of 2.16 koalas per hectare. These observations are supported by other studies which have also found koala population densities to be lower in areas where regionally preferred tree species are either absent or sparsely distributed (Melzer and Lamb 1994; Jurkis and Potter 1997; Sullivan 2000; Masters *et al.* 2004, Table 6-14).

Similar results have also been reported for numerous other species including field voles (*Microtus agrestis*; Erlinge *et al.* 1990), Lumholtz's tree-kangaroo (Newell 1999*a,b*), pied flycatchers (*Ficedula hypoleuca*, Silvern 1998) and Eurasian red squirrels (Wauters *et al.* 2001). Silvern (1998), Erlinge *et al.* (1990) and Wauters *et al.* (2001) all found breeding densities of their study animals to increase with improved habitat quality and Newell (1999*a*) found population densities of Lumholtz's tree-kangaroos to be positively correlated with habitat quality on the Atherton Tablelands.

Like home range size, intraspecific variability in population density is also considered to be associated with the distribution and abundance of food resources (Damuth 1981; McLoughlin *et al.* 2001). Species that require large home ranges usually cannot maintain locally dense populations because of the limited amount of energy available within a given area (McNab 1963). Similarly, locally dense populations cannot be maintained when individuals of a population require large home ranges in order to survive within a particular habitat type.

Table 6-14: Koala population densities reported in various studies throughout Australia

Location	Dominant Tree Species	Preferred Tree Species	Population Density (koalas/ha)	Author
French Island, Vic	<i>E. viminalis</i>	<i>E. viminalis</i>	7.5	Mitchell and Martin, 1990
Kangaroo Island, SA	<i>E. viminalis</i> <i>cygnetensis</i>	<i>E. viminalis</i> <i>cygnetensis</i>	5.5	StJohn, 1997
Brisbane Ranges, Vic	<i>E. viminalis</i>	<i>E. viminalis</i>	1.2	Hindell, 1984
Lismore, NSW	<i>E. tereticornis</i>	<i>E. tereticornis</i>	4.0	Gall, 1980
Springsure, Qld	<i>E.tereticornis</i>	<i>E.tereticornis</i>	1.1	Gordon <i>et al.</i> , 1990
Redland Shire, SE Qld	<i>E. fibrosa</i>	<i>E. tereticornis</i>	0.4	White and Kunst 1990
Capella, Qld	<i>E. melanophloia</i>	<i>E. tereticornis</i>	0.005	Melzer and Lamb, 1994
Springsure, Qld	<i>Acacia harpophylla</i>	<i>E. tereticornis</i>	0.015	Melzer and Lamb, 1994
Eden, NSW	<i>E. sieberi</i>	<i>E. cytellocarpa</i>	0.006	Jurskis and Potter 1997
Mulglands, SW Qld	<i>Acacia spp.</i>	<i>E. populnea</i> / <i>E. coolabah</i>	0.0007 – 0.27	Sullivan, 2000
Kangaroo Island, SA	<i>E. viminalis</i> <i>cygnetensis</i>	<i>E. viminalis</i> <i>cygnetensis</i>	2.16	Masters <i>et al.</i> 2004
Kangaroo Island, SA	<i>E. obliqua</i>	<i>E. viminalis</i> <i>cygnetensis</i>	0.35	Masters <i>et al.</i> 2004

6.4.4 Daily Movements

Daily movement figures reported in this study are within the range of estimates from other studies (Table 6-15).

Overall, the mean daily distances travelled by koalas in non-preferred habitat were consistent with estimates reported by Jurkis and Potter (1997), Pieters and Woodall (1996) and Hull (1985). Each of these studies were undertaken in habitat that was considered to be sub-optimal to koalas either because of the absence of preferred tree species or presence of modified landscape characteristics, such as the semi-suburban environment in Pieters and Woodall's (1996) study. Some figures, such as the estimate reported by Jurkis and Potter (1997) for female koalas (210 m/day) were considerably higher than the results reported in this study; however this could be due to differences in habitat characteristics such as level of habitat fragmentation.

Estimated daily movements of koalas in preferred habitat on Kangaroo Island were higher than mean distances reported by Mitchell (1990*b*), but again this discrepancy may be related to differences in tree composition at Mitchell's (1990*b*) study site and areas of preferred habitat in this study. Koalas in Mitchell's (1990*b*) study occupied pure stands of *E. viminalis* whereas *E. viminalis cygnetensis* on average only made up 20% of the tree species composition of preferred habitat in this study. Overall the results from this study and others demonstrate that koalas in non-preferred habitat move further than koalas in preferred habitat.

Table 6-15: Comparison of reported average daily movements of koalas

Location	Male (m)	Female (m)	HabitatType	Author
Eden, NSW	230	210	Sub-optimal/ non-preferred	Jurskis and Potter, 1997
Gold Coast, Qld	274	105	Sub-optimal/ non-preferred	Pieters and Woodall, 1996
Ballarat, Vic	207	71	Sub-optimal/ non-preferred	Hull, 1985 ¹
French Island, Vic	66*	39*	Preferred	Mitchell, 1990 ^b
Kangaroo Island, SA	132	52	Preferred	This study
Kangaroo Island, SA	181	88	Non-preferred	This study

* Means have been calculated from average distances presented by the author for breeding and non-breeding seasons.

¹ Cited by Peters and Woodall (1996)

Koalas were able to traverse large areas of cleared land and were not reliant on vegetation corridors. Koalas used isolated trees in cleared paddocks and routinely visited discrete habitat patches within their home ranges. Similar observations have been made by White (1994, 1999) and Prevett (1991) in studies of koalas in both semi-urban and rural landscapes. Prevett (1991) concludes that success in crossing large tracts of open land suggests that continuous tracts of habitat in the form of vegetation corridors are not essential for koala movement. This ability of koalas to move through fragmented landscapes is also demonstrated in this study by the movement of dispersing animals. Some koalas in this study travelled up to 30 km through highly modified agricultural land in only a few months. These results indicate that koalas may not be as susceptible to habitat fragmentation as has been previously suggested (Hume 1990). Rather, rural landscapes may provide valuable habitat for koalas (White 1999).

6.4.5 Tree Species Preferences

Koalas in non-preferred habitat showed a distinct preference for *E. obliqua* and *E. leucoxylon*. Although koalas in preferred habitat also selected for *E. leucoxylon* they showed strongest preference for *E. viminalis cygnetensis*. A study by Lawler *et al.* (1998) found that selection for *Eucalyptus viminalis* is influenced by the variation in the concentrations PSMs in the foliage of this species. In contrast, little is known about the nutritional quality or palatability of *E. obliqua*, however key secondary compounds that have been identified in *E. viminalis* have not been identified in the subgenus *Monocalyptus* which includes *E. obliqua* (Moore and Foley 2000). This suggests that other unknown factors may influence diet selection in this species. It is worth noting that captive koalas were observed feeding on both *E. viminalis* and *E. obliqua* in feeding trials at Cleland Wildlife Park.

There was considerable intraspecific variation in selection of tree species with a number of koalas showing preferences for tree species other than *E. viminalis cygnetensis*, *E. leucoxylon* and *E. obliqua*. Koalas have been found to forage on a wide variety of eucalypt species despite their reputation for being extremely fussy. Across their range koalas have been observed eating or sitting in 120 different eucalypt species (Moore and Foley 2000). In recent years research on the diet selection of koalas has focussed on the foliar chemistry of trees (Lawler *et al.* 1998; Lawler *et al.* 2000; Moore and Foley 2000). This work has shown that the chemistry of leaves, particularly concentrations of PSMs, can determine food intake by koalas irrespective of other aspects of nutritional quality or taxonomy (Lawler *et al.* 1998). Hence, a koala could be expected to eat any foliage with the appropriate morphology and chemistry to allow it to be recognised as palatable food.

6.4.6 Management Implications

The presence of a resident population of koalas in non-preferred habitat on Kangaroo Island was generally discounted until the commencement of this study. For many years, estimates of koala abundance and distribution on Kangaroo Island, focussed primarily on populations of koalas in preferred habitat in Flinders Chase National Park and along the Cygnet River (StJohn 1997; Duka and Masters 2005). Today, methods of estimating population size on Kangaroo Island incorporate populations of koalas within high-, medium- and low quality habitats according to composition of eucalypt species (Masters *et al.* 2004). Each of these habitat types is characterised as follows:

- high quality habitat comprises vegetation communities which contain *E. viminalis cygnetensis*, *E. ovata*, *E. camaldulensis* and *E. leucoxyton* as primary species
- medium quality habitat comprises vegetation communities which are likely to contain *E. viminalis cygnetensis*, *E. leucoxyton* and *E. camaldulensis* as secondary species
- low quality habitat comprises vegetation communities which contain *E. obliqua*, *E. baxteri* and *E. fasciculosa* as primary species.

The revised koala population estimate based on this more comprehensive stratified sampling approach is ~ 27,000 (Masters *et al.* 2004). This is more than five times greater than the population estimate of 3000-5000 calculated in 1996/7 (StJohn 1997; Possingham *et al.* 1996). This cannot be explained by natural population growth as a high proportion of koalas in many areas have been sterilised and the disparity in population size exceeds the expected doubling time of 2-3 years for disease free populations (Martin 1997).

Not only is the current koala population estimate for Kangaroo Island greater than previous years, but koalas are now known to be far more widely distributed across the Island in habitat types which were previously considered unsuitable habitat. It is estimated that more than half of the current estimated population of koalas on Kangaroo Island occurs within low quality (i.e. non-preferred) habitat consisting mainly of *E. obliqua* and *E. baxteri* (P. Masters, personal communication, 10 July, 2002). Of the 54,365 hectares of koala habitat on Kangaroo Island; 40,706 hectares is now classified as low-quality habitat, 12,909 hectares as medium-quality and 750 hectares as high-quality habitat (Masters *et al.* 2004).

At its commencement the koala management program on Kangaroo Island aimed to sterilise more than 70% (2,500 koalas) of the koala population in order to effectively curb population growth and over-browsing. Unfortunately it appears as though this initial effort to control koala numbers may have fallen well short of its target of 70% of the total population. By 2000, 3396 koalas had been sterilised and 1105 had been translocated (Masters *et al.* 2004). Accurate habitat models are essential when making decisions about the management of a species (Cork *et al.* 2000). This is particularly the case when an accurate population estimate is fundamental to the success of population control programs such as that on Kangaroo Island.

6.5 Summary

Observations indicate that a potentially viable, low density population of koalas occupies non-preferred habitat on Kangaroo Island. Koalas were found to use a wide range of eucalypt species and many individual koalas survived solely on a diet of tree species that were previously considered to be non-preferred by koalas on Kangaroo Island. These non-preferred habitats should be considered to be habitats with low

carrying capacity rather than poor quality or sub-optimal (Melzer and Lamb 1994).

The results of this study indicate that non-preferred areas of habitat have significant conservation and management value, just as areas that sustain high-density populations of koalas do.

7 Conclusion: Managing Over-browsing by Koalas

Over-abundant koala populations and resultant over-browsing of vegetation has presented an ongoing challenge for wildlife managers in many areas of south-eastern Australia for almost a century. Despite this long history the most appropriate method of managing over-abundant koala populations continues to be debated, with no agreement on a single solution that effectively meets wildlife management objectives and community expectations.

In South Australia and Victoria translocation and fertility control, via surgical sterilisation or contraceptive implants, are the key techniques used to reduce koala numbers in over-abundant populations. In 1997 a management program was put in place on Kangaroo Island that aimed to achieve and maintain an infertility rate of 70% (via sterilisation) and immediately reduce the koala population by 30% (via translocation). These targets were developed based on the population estimate for Kangaroo Island of 3000 – 5000 koalas and the understanding that the majority of koalas occurred in the Cygnet River valley and Flinders Chase National Park with vagrant or small established populations reported from elsewhere (Duka and Masters 2005).

The presence of a resident population of koalas in areas outside Flinders Chase National Park and the Cygnet River catchment was generally discounted until the commencement of this study. A radio-tracking study of koalas outside of these areas found a potentially

viable, low density population of koalas which survive on a wide range of eucalypt species that were previously considered to be not palatable or non-preferred by koalas on Kangaroo Island. As a result of these findings, methods of estimating the population size of koalas on Kangaroo Island now incorporate populations of koalas within high-, medium- and low quality habitats according to composition of eucalypt species (Masters *et al.* 2004). The revised koala population estimate based on this more comprehensive stratified sampling approach is ~ 27,000 (Masters *et al.* 2004). It is now estimated that over half the Island's koala population resides in areas of low-quality habitat outside of Flinders Chase National Park and the Cygnet River catchment.

From the commencement of the Koala Rescue Program in 1997 through to 2001 approximately 3, 500 koalas were sterilised, and of these approximately 1,100 translocated to the south-east of South Australia (Duka and Masters 2005). Although some decline in reproductive output was recorded in some areas of Kangaroo Island, this level of control effectively targeted less than 15% of the island's revised population estimate of 27,000 koalas (Duka and Masters 2005).

Although the Koala Rescue Program was intended to reduce the koala population to a sustainable level and trigger recovery of degraded habitat; the decline of habitat condition and localised extinction of the preferred browse species *E. viminalis cygnetensis* has continued (Paton *et al.* 2002; Masters *et al.* 2004). Results from this study show that eucalypts have a high capacity for compensatory growth and recovery if browse pressure is removed. Where over-browsing occurs the imperative for successful restoration of defoliated trees is to substantially reduce the density of koalas in the short-term and

maintain reduced population levels, and associated levels of browsing, in the long-term. Population estimates between 1997 and 2000 demonstrate that koala numbers at Mine Creek did fall in response to control measures. However, the reduction in koala density at Mine Creek was short-term and due largely to translocation rather than the effect of sterilisation. Sterilisation may be usefully applied to maintain low koala densities after an initial population reduction via alternative control methods, but sterilisation alone is unable to affect much change in severely over-browsed habitats in the immediate term.

Although translocation is an option that does immediately reduce koala numbers its capacity is limited by the number of potential release sites that are available and the carrying capacity of receiving habitats. To aid in the rapid reduction in browse pressure the Koala Rescue Program initially aimed to remove approximately 30% of the koala population in Flinders Chase National Park and the Cygnet River Valley. Based on the existing koala population estimate of ~ 27,000 further management using the existing management strategy would need to translocate many thousands of koalas, many of which occur at low densities (0.1 to 0.81 koalas per hectare) throughout large and inaccessible tracts of vegetation to other areas of habitat in order to achieve an immediate and sustained reduction in the koala population. Not only would this be logistically challenging but would also be time consuming and costly.

In 1996 the Koala Management Task Force recommended a once-off cull of koalas on Kangaroo Island followed by sterilisation, limited translocation and habitat rehabilitation. The recommendation of the 11-member committee was unanimous (Possingham 1997, Appendix D). The decision was made using principles of ecological risk assessment with

two objectives in mind: to minimise further damage to ecosystems on Kangaroo Island; and to avert, or minimise, animal suffering. It is arguable that had this occurred, recovery of habitat on Kangaroo Island would have begun by now and the restoration of threatened ecosystems would be underway.

Research in support of koala management has tended to focus on habitat selection (tree species preferences), koala condition and population dynamics with some work done on translocation. However, there has been little investigation of the effects of over-browsing on the vegetation that makes up koala habitat. Neither the National Koala Conservation Strategy (2009) nor the Victorian Koala Management Strategy (2004) objectives include research into trees and other species that rely on vegetation that comprises koala habitat. On Kangaroo Island the local extinction and island-wide degradation of *E. viminalis cygnetensis* is well underway and the condition of other preferred food species is also in decline (Masters *et al.* 2004). Impacts to other species which rely on *E. viminalis cygnetensis* as a resource are also becoming apparent. For example, observations of the foraging behaviour of a number of bird species which use *E. viminalis cygnetensis* show that composition and behaviour of birds using manna gum has changed substantially with the ongoing decline in condition of this tree species (Paton *et al.* 2002). Over-browsing of manna gum in coastal Victoria has reached a level whereby it is considered to be a threat to the conservation of two Ecological Vegetation Classes – Damp Sand Herb-rich Woodland and Stony Rises Woodland (Menkhorst 2004). Research which focuses on the direct impacts of koala over-browsing on trees is valuable because it not only provides greater insight to the viability of habitats post-management but also provides some

assessment of the potential cumulative impacts of over-browsing on other aspects of the ecosystems which koalas live in.

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