

The ecological effects of sealed roads in arid ecosystems

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The ecological effects of sealed roads in arid ecosystems



Enhua Lee

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The effects of roads on landscapes and wildlife and their ecological processes are substantial and represent a major anthropogenic disruption to the natural environment. Current understanding of the impacts of roads for their strategic management is hampered by a lack of information on 1) the influence of the ecosystems on road effects, 2) the effects of roads on higher-order ecosystem responses (populations and communities), and 3) the overall impacts of roads on ecosystems and their wildlife (on both abiotic and biotic ecosystem components).

This study used the Silver City Highway in arid New South Wales, Australia, as a model for a typical road in an arid ecosystem to investigate the ecological effects of arid-zone roads and their management. The study examined the spatial variation of soil, vegetation, kangaroo and small mammal variables in relation to the road, explored the factors contributing to these respective spatial variations, investigated the effects of arid-zone road management on vegetation, assessed the fragmentation effect of the arid-zone road on small mammals, and determined the patterns, causes and effects of kangaroo-vehicle collisions.

The study revealed that the arid-zone road influenced most of the variables measured, skewed the population demographics of two kangaroo species, and altered the community composition of small mammals, with two small mammal species listed as threatened in NSW and of national significance (*Sminthopsis macroura* and *Leggadina forresti*) negatively impacted by the road. Increases in the amount of water along the road edge drove many of the subsequent effects of the arid-zone road as arid-zone flora and fauna are adapted to exploiting limited and patchily distributed resources. However, current arid-zone road management also influenced vegetation quality, microclimates around the road influenced kangaroo densities and small mammal communities, and kangaroo flight behaviour and temporal variations in traffic volume affected roadkill frequency.

Together, these results suggest that roads have a high overall ecological impact in arid ecosystems. Conservation managers need to first rank the impacts of arid-zone roads in order of their conservation importance and need for mitigation, and from there, devise relevant informed management frameworks to target these impacts.

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Abstract

The effects of roads on landscapes and wildlife and their ecological processes are substantial and represent a major anthropogenic disruption to the natural environment. Current understanding of the impacts of roads for their strategic management is hampered by a lack of information on 1) the influence of ecosystems on road effects, 2) the effects of roads on higher-order ecosystem responses (populations and communities), and 3) the overall impacts of roads on ecosystems and their wildlife (on both abiotic and biotic ecosystem components).

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Chapter 1

General Introduction

The effects of roads on landscapes and wildlife and their ecological processes are substantial and represent a major anthropogenic disruption to the natural environment (Trombulak and Frissell, 2000; Spellerberg, 2002; Forman *et al.*, 2003). The ecological effects of roads are so considerable and distinct from the effects of other linear features and anthropogenic disturbances that a name describing the study of the ecological effects of roads has evolved in recent times in recognition of these significant and unique effects (Forman *et al.*, 2003). The study of road ecology, as it is now known, has drawn a growing amount of international attention since its inception (in about the 1970s when global road networks expanded and scientists became aware of the magnitude of the effects of roads on the natural environment, Serrano *et al.*, 2002; Sherwood *et al.*, 2002; Spellerberg, 2002; Forman *et al.*, 2003). Many studies investigating the multitude of effects of roads have now been conducted (reviews by Andrews, 1990; Bennett, 1991; Forman and Alexander, 1998; Spellerberg, 1998, 2002; Trombulak and Frissell, 2000; Underhill and Angold, 2000; Forman *et al.*, 2003).

Roads, which are open ways for the passage of vehicles that range from dirt tracks through to sealed multilane highways (Forman *et al.*, 2003), affect surrounding landscapes and wildlife in several ways. They impact microclimates around them through changes in wind flows (Forman *et al.*, 2003), water flows (Montgomery, 1994), temperatures (Whitford, 1985; Rosen and Lowe, 1994), light levels (Goosem, 2000, 2001; Haskell, 2000), and soil densities (Iveson *et al.*, 1981). Microclimates are also altered through additions of particles and pollutants (Lagerwerff and Specht, 1970; Quarles *et al.*, 1974; Van Bohemen and Janssen Van De Laak, 2003), salts (McBean and Al-Nassri, 1987), gases (Spencer *et al.*, 1988; Angold, 1997), and noise (Reijnen *et al.*, 1995). As a result of these changes in microclimates, roads impact vegetation, altering their structure and health (Spencer and Port, 1988, Spencer *et al.*, 1988; Angold, 1997; Norton and Stafford-Smith, 1999), and community compositions at areas near roads relative to areas further away from roads (Angold, 1997; Greenberg *et al.*, 1997). The combined impacts of microclimate and

vegetation changes, including loss of vegetation, growth of different types of vegetation, and increases in edge habitat (Angold, 1997; Greenberg *et al.*, 1997; Goosem, 2000) at roadsides then affect fauna. Roads and their modified microclimates and vegetation can act as barriers to faunal movement (Barnett *et al.*, 1978; Mader, 1984), fragmenting populations on either side of roads. Fauna can additionally alter their movements away from roads (Gerlach and Musolf, 2000; Dyer *et al.*, 2002; Keller and Largiader, 2002; Shine *et al.*, 2004; Steen and Gibbs, 2004) and avoid crossing roads (Mader, 1984; Garland and Bradley, 1984; Richardson *et al.*, 1997; Goosem, 2001; Rondinini and Doncaster, 2002) such that the barrier effects of roads are further augmented. Fauna can also be attracted to roads (Rosen and Lowe, 1994; Lee *et al.*, 2004; Aresco, 2005) and this attraction can result in increases in wildlife mortality on roads (Mumme *et al.*, 2000; Hels and Buchwald, 2001; Aresco, 2005; Ramp *et al.*, 2005; Seiler, 2005). Moreover, reproductive output and success (Fernandez, 1993; Ortega and Capen, 1999) and physiological states (MacArthur *et al.*, 1979; Wasser *et al.*, 1997) of fauna can be negatively impacted by roads. These impacts of roads may have population and community effects for vegetation and fauna, and such effects, plus effects on the physical and chemical environments, raise serious concerns about the stability and sustainability of wildlife populations adjacent to roads, as well as the diversity and integrity of wildlife communities and ecosystems.

Despite the broad range of research on the impacts of roads and vehicular traffic on the natural environment, current understanding of the impacts of roads for their strategic management is hampered by a lack of information on 1) the influence of the ecosystems traversed by roads on road effects, 2) the effects of roads on higher-order ecosystem responses (populations and communities), and 3) the overall impacts of roads on ecosystems and their wildlife (ie. impacts on both abiotic and biotic components of ecosystems). The effects of roads are influenced by the ecosystems traversed by roads since roads interact with the ecological processes of ecosystems in different ways, affecting the magnitude or expression of effects (Gutzwiller and Barrow 2003; Brooks and Lair 2005). For example, disturbances of soil profiles adjacent to roads during road construction are likely to have greater impacts on soil profiles in arid ecosystems than in other, more mesic ecosystems as soil profiles recover more slowly in arid areas than in mesic areas (Charley and Cowling, 1968; Lovich and Bainbridge, 1999). In addition, water running off from road

surfaces in arid ecosystems is likely to have a greater effect on plant growth than similar amounts of water running off road surfaces in more mesic environments as water is more limiting to primary productivity in arid ecosystems than mesic ecosystems (Westoby, 1980; Stafford Smith and Morton, 1990). Effects of enhanced plant growth along road edges in arid ecosystems could subsequently affect faunal distributions and abundance more so than in mesic environments due to the patchier distribution and more limited amounts of food resources in arid ecosystems (Stafford Smith and Morton, 1990). Studies to date have not specifically addressed the influence of ecosystems in affecting the expression of road effects (but see Garland and Bradley, 1984), and only brief mention of differences in road effects in ecosystems has been made by Boarman *et al.* (1997), Goosem (2001) and Forman *et al.* (2003). Indeed, studies of roads in some ecosystems, such as arid ecosystems (Brooks and Lair, 2005), are so few that we have little knowledge of their effects in these ecosystems at all. This could hinder the management of roads as management strategies addressing particular road effects in one ecosystem may not be appropriate in another ecosystem.

The lack of information on the effects of roads on higher-order ecosystem responses (Spellerberg, 2002; Forman *et al.*, 2003) also obstructs the development of strategic management. To date, a large number of studies have concentrated on documenting the effects of roads on species and identifying potential causes for such effects. For example, many studies of the effects of roads on faunal species have recorded the incidence of their mortality on roads (Coulson, 1982; Drews, 1995; Groot Bruinderink and Hazebroek, 1996; Caro *et al.*, 2000; Hubbard *et al.*, 2000), which have been related to causal factors. Only a handful of these studies have subsequently investigated effects of road mortality on populations and communities (Jones, 2000; Mumme *et al.*, 2000; Lee *et al.*, 2004; Aresco, 2005). Information on the effects of roads at higher-order ecosystem levels is essential for conservation management. This is because such information can lead to the identification of vulnerable populations and communities that can be targeted for management (Burgman and Lindenmayer, 1998).

A final major impediment to the development of strategic management frameworks for roads is the lack of information on the overall impacts of roads on ecosystems and their wildlife. Studies of road effects have not attempted to investigate effects on both the abiotic

and biotic components of ecosystems, integrating multiple combinations of these components. Instead, studies have been relatively specific and have concentrated on separate road effects (exceptions are studies that have looked at the different effects of roads on a variety of faunal groups, Jaeger *et al.*, 2005; Ramp *et al.*, 2005). This disjointed approach to understanding the effects of roads constrains conservation management as management cannot be prioritised in order of conservation importance for mitigation.

Clearly, the influence of ecosystems on road effects, the effects of roads on higher-order ecosystem responses, and the overall effects of roads on ecosystems and their wildlife must be addressed before we can comprehensively understand the ecological effects of roads for strategic conservation management (management could involve implementing various mitigation measures targeting factors identified as influencing road effects, or could involve employing ecological compensation measures if mitigation is not effective; Cuperus *et al.*, 1999). However, a study that attempts to investigate all of these issues at once is likely to be a huge undertaking. The best approach for tackling these issues is to examine the effects of roads on higher-order ecosystem responses and the overall effects of roads in one ecosystem (while identifying which factors influence these effects for future mitigation). Follow-up studies of these issues in other ecosystems can then be conducted.

This study examines the effects of roads in the context of an Australian arid ecosystem and explores the causal factors for these effects. An arid ecosystem was chosen as studies conducted in arid ecosystems are few (Brooks and Lair, 2005) and arid ecosystems cover up to one third of the earth's land surface (Kinlaw, 1999), so are ecosystems in which the effects of roads should be studied. Informed management of arid-zone roads is of major importance in Australia and is relevant for conservation biology in the Australian environment. This is because the majority of the continent is arid (approximately 70 %, Stafford Smith and Morton, 1990) and many roads run through arid areas that support fragile vegetation communities and unique wildlife. In addition, many of Australia's arid-zone small mammals have become extinct or threatened since European settlement (Dickman *et al.*, 1993). Any anthropogenic disturbance that could threaten the integrity of the arid ecosystem or further threaten the status of small mammals needs to be appropriately managed. The study is by necessity local in scale so the generality of findings of arid-zone road effects can only be tested by further study. Even so, local-scale studies

provide details of road effects that may not be detected in regional-scale studies (Serrano *et al.*, 2002) and are thus important in the understanding of the effects of arid-zone roads. In addition, general principles emerge from the study that have applicability across arid ecosystems.

Chapters in this thesis are intended for future publication. Consequently, repetition of material is inevitable and unavoidable. Efforts are made to avoid repetition where possible through cross-referencing. In addition, Chapter 2 is dedicated to outlining details of the study site and conditions through the study so that this information is only given once. Four data chapters are included in the thesis. Chapter 3 examines spatial variations in the cover, structure and quality of vegetation relative to an arid-zone road, examines spatial variations in some physical and chemical properties of soil relative to the road, discusses factors influencing these variables, and explores the effects of current roadside management on vegetation quality and diversity. Chapter 4 describes temporal and spatial variations in densities of four kangaroo species relative to the arid-zone road, examines temporal variations in kangaroo movements across the road, and discusses factors influencing these densities and movements. Chapter 5 explores the patterns of kangaroo mortality on the arid-zone road, determines the spatial, temporal and biological causes of kangaroo mortality, and examines the population and community effects of kangaroo mortality. Chapter 6 investigates spatial variations in small mammal communities, richness and biomass relative to the arid-zone road, discusses factors influencing these variables, examines sex ratios of common small mammal populations in relation to the road, and assesses the barrier effect of the road on small mammal movements. The final chapter, Chapter 7, considers the results of the data chapters and discusses future directions for the strategic management of arid-zone roads.

Chapter 2

Study area

2.1 Fowlers Gap Arid Zone Research Station

This study was conducted at the University of New South Wales Arid Zone Research Station, Fowlers Gap, ($31^{\circ} 05' S$, $141^{\circ} 43' E$) in north-western NSW, Australia (Figure 2.1). Fowlers Gap is located approximately 110 km north of Broken Hill at the northern end of the Barrier Ranges and covers an area of 38,888 hectares. The station is typical of Australia's southern sheep rangelands, and is held by the University as a working sheep station, as well as a centre for research, teaching, and tourism (Croft, 2004).



Figure 2.1: Location of Fowlers Gap Arid Zone Research Station in New South Wales.

2.1.1 Geology and geomorphology

Fowlers Gap Station is comprised of three physiographic sections which trend north and south with the regional strike (Mabbutt, 1973). The western section is made up of undulating lowland with low ridges (between 180 and 240 m above sea level), the central section is a belt of ranges and foothills (part of the Barrier Ranges, reaching up to 294 m above sea level in the north), and the eastern section consists of alluvial plains descending

eastward (from about 170 and 140 m above sea level) that flanks the lower course of Fowlers Creek (Mabbutt, 1973; Figure 2.2). As the central ranges were formed by the contact of the Willyama Block (part of the ancient continental Basement) with the Bancannia Trough (a structural depression filled with at least 2000 m of Devonian, Cretaceous and later deposits), upper Devonian rocks are exposed. Thus, the western part of the station, including both the western and central physiographic sections, lie on Upper Precambrian and Devonian sedimentary rocks, while the eastern section of alluvial plains lie on Quaternary deposits (Ward and Sullivan, 1973).

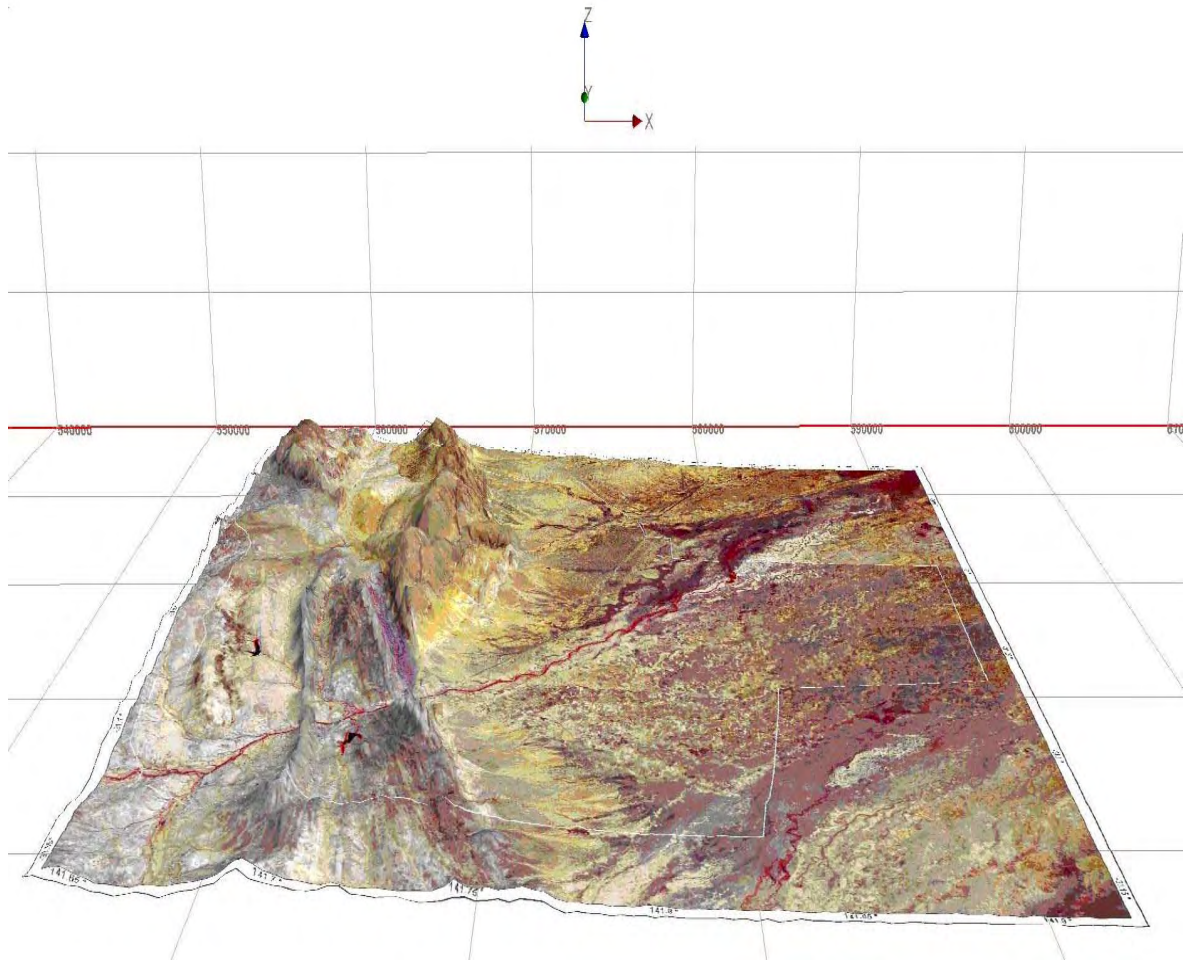


Figure 2.2: Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) image draped over a digital elevation model (DEM) of Fowlers Gap Arid Zone Research Station. The image is at 10x vertical exaggeration as viewed from the south and trees are shown in red. Image created by Dr. Ian Roach (Department of Earth and Marine Sciences, Australian National University).

2.1.2 Soils

The soils of Fowlers Gap are typical of those of the Australian arid zone in general. Upland soils are generally shallow, while many of the alluvial soils are quite deep. Most soils are mainly reddish in colour due to the thin coat of iron oxide pigment surrounding sand grains, although concentrations of lime or other salts can mask the red colour in some soils. Organic matter is relatively unimportant as a colour pigment in the soils and only a few topsoils are naturally browner than their subsoils. There are four main soil types on Fowlers Gap: upland soils, alluvial soils, soils of patterned ground, and brown solonized soils. Variations in soil appear to correspond to factors of time (expressed in surface stability), although variations in relief, parent material and vegetation also influence soil properties. Soils are varied, and include loamy, sandy, light and heavy textured, and texture-contrast soils (Corbett, 1973).

2.1.3 Flora

Vegetation of Fowlers Gap is low, woody and open and represents southern arid Australia's shrub-steppe. The four main categories of plant communities on the station are low shrubland, tussock grassland, tall open-shrubland and low open-woodland. Of these plant communities, low shrublands comprising of woody perennial shrubs (< 1 m; chiefly of the Chenopodiaceae family) dominate in the western parts. The main genera are *Atriplex* (saltbushes), *Maireana* (bluebushes) and *Sclerolaena* (copperburrs). In contrast, tussock grasslands (approximately 50 cm, mainly *Astrebla* species) dominate the eastern alluvial plains. Tall open-shrublands, mainly *Acacia victoriae* (prickly wattle), *Acacia aneura* (mulga) and *Casuarina* species, form a smaller component of Fowlers Gap compared to the low shrubland and tussock grassland communities. Low open-woodlands comprise the smallest of the vegetation communities. River red gum (*Eucalyptus camaldulensis*) woodlands are the most common of the low open-woodland communities; however woodlands made up of *Casuarina* species and Curly mallee (*Eucalyptus gillii*) are also present on the station (Burrell, 1973).

Arid zone vegetation is heavily influenced by rainfall (Noy-Meir, 1974; Westoby, 1980; Stafford Smith and Morton, 1990; Moss and Croft, 1999) so after wet periods, vegetation in the plant communities of Fowlers Gap (in inter-shrub areas, inter-tussock

areas, and in the lower canopy) change with the germination and growth of ephemeral plants. The quantity of ephemeral growth depends on the amount of rain falling in a wet period and the accompanying evaporative conditions, with the result that ephemeral cover may be relatively high after only small amounts of rain during the cooler months of the year and relatively low after high amounts of rain during the hotter months of the year. As germination of ephemeral plants is dependent on temperature (Stafford Smith and Morton, 1990; Jurado and Westoby, 1992), the composition of plants also varies throughout the year. Grasses (for example *Enneapogon* and *Eragrostis* species) are most abundant among the ephemerals during summer, while forbs (small herbaceous dicotyledons, for example *Helipterum* and *Helichrysum* species) are the most abundant of the ephemerals during winter (Moss and Croft, 1999; Witte, 2002).

Plant communities of Fowlers Gap are additionally influenced by landforms and soils, exercised largely through the control of runoff, infiltration and the water storage capacity of soils (Harrington *et al.*, 1984, Tongway and Ludwig, 1990, Stafford Smith and Morton, 1990; Dunkerley and Brown, 1995; Ludwig and Tongway, 1995). Thus tall open-shrublands occur along rocky outcrop zones where crevices allow deep water storage and root penetration and on lower hillslopes receiving run-on (mostly along minor drainage tracts and channels, and in the ranges and slopes of the western section of the station); low shrublands and tussock grasslands are broken up into a mosaic of areas with and without perennial vegetation reflecting control of run-on and run-off by microtopography and the associated spatial variation in soil structure and chemistry; and low open-woodlands are restricted to the margins of large river channels.

2.1.4 Land systems

Land systems are areas or groups of areas throughout which there is a recurring pattern of topography, lithology, soil and vegetation (Mabbutt *et al.*, 1973). Fourteen land systems are recognised on Fowlers Gap (Mabbutt *et al.*, 1973; Figure 2.3). These land systems are divided primarily by topography and predominant lithology, then by soils and vegetation, and are subdivided further into smaller land units which give more details of landforms, soils and vegetation.

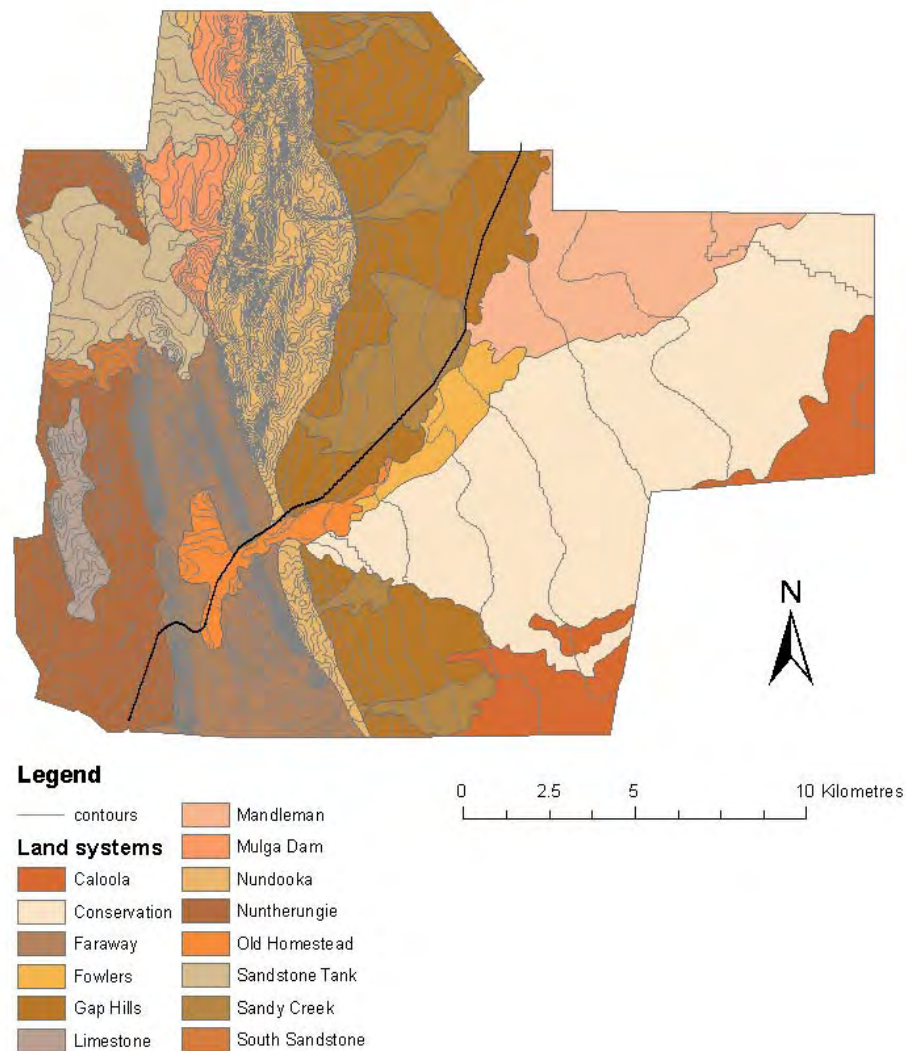


Figure 2.3: Land systems of Fowlers Gap Arid Zone Research Station. The Silver City Highway (black line) is also shown.

2.1.5 Fauna

Fowlers Gap supports a diverse range of fauna from many taxonomic groups. Large mammals include four kangaroo species: red kangaroos (*Macropus rufus*), euros (*Macropus robustus erubescens*), western grey kangaroos (*Macropus fuliginosus*) and eastern grey kangaroos (*Macropus giganteus*). Large but variable populations of red kangaroos (estimated as ranging from 10 to 20 kangaroos km⁻² between 1985 and 1987; Edwards *et al.*, 1996) are mostly found on the open plains in the eastern sections of the station (Croft, 1991a), whereas large populations of euros (estimated as ranging from 3 to 20 kangaroos km⁻² in 1984 to 1986; Clancy and Croft, 1992) are found in the rocky

outcrops and hills around the western sections of the station (Croft, 1991b). Smaller populations of grey kangaroos (estimated as ranging from 0.5 to 6.5 kangaroos km⁻² between 1985 to 2005 in north-west New South Wales encompassing Fowlers Gap; NSW National Parks and Wildlife Service, Kangaroo Management Program) are found in association with cover, with western grey kangaroos mainly associated with low open-woodland and tall open-shrubland communities and eastern grey kangaroos mainly associated with low open-woodland communities (Dawson, 1998).

Smaller mammal species are well represented and include fat-tailed dunnarts (*Sminthopsis crassicaudata*), stripe-faced dunnarts (*Sminthopsis macroura*), narrow-nosed planigales (*Planigale tenuirostris*), Giles' planigales (*Planigale gilesi*), Forrest's mice (*Leggadina forresti*), sandy inland mice (*Pseudomys hermannsburgensis*), short-beaked echidnas (*Trachyglossus aculeatus*), and several microchiropteran bat species belonging to the Molossidae and Vespertilionidae families (2 and 7 species respectively) (checklist of small mammals, Fowlers Gap; <http://www.bios.unsw.edu.au/fgap/guide.htm>). Five species (stripe-faced dunnarts, Forrest's mice, sandy inland mice, little pied bats, *Chalinolobus picatus*, and inland forest bats, *Vespadelus baverstocki*) are listed as vulnerable in Schedule 2 of the NSW Threatened Species Conservation Act (1995, No. 101).

A diverse and abundant array of herpetofauna and avifauna are also present on Fowlers Gap (checklist of reptiles, frogs, and birds, Fowlers Gap; <http://www.bios.unsw.edu.au/fgap/guide.htm>). Thirty-nine species of lizards (from 5 families), 12 species of snakes (3 families), and 8 species of frogs (2 families) have been identified on the station. Four species of herpetofauna are listed as vulnerable in Schedule 2 of the NSW Threatened Species Conservation Act (1995, No. 101): crowned geckos (*Diplodactylus stenodactylus*), yellow-tailed plain-sliders (*Lerista xanthura*), Stimson's python (*Liasis stimsoni*) and narrow-banded snakes (*Simoselaps fasciolatus*). Of the avifauna, over 130 species from 49 families have been sighted on Fowlers Gap, six of which are listed as vulnerable in Schedule 2 of the NSW Threatened Species Conservation Act (1995, No. 101) (blue-billed ducks, *Oxyura australis*; freckled ducks, *Stictonetta naevosa*; black-breasted buzzards, *Hamirostra melanosternon*; square-tailed kites, *Lophoictinia isura*; scarlot-chested parrots, *Neophema splendida*; and pied honeyeaters, *Certionyx variegatus*) and one of which is listed as endangered (Australian bustards,

Ardeotis australis) in Schedule 1 of the NSW Threatened Species Conservation Act (1995, No. 101).

There are several introduced species on the station (checklist of small mammals, Fowlers Gap; <http://www.bios.unsw.edu.au/fgap/guide.htm>). These include pigs (*Sus scrofa*), goats (*Capra hircus*), wild dogs (*Canis lupus familiaris*), red foxes (*Vulpes vulpes*), cats (*Felis catus*), house mice (*Mus domesticus*) and rabbits (*Oryctolagus cuniculus*). Control programs are employed to reduce the numbers of some introduced species; namely, trapping and shooting of pigs, regularly mustering and removal of goats, 1080 baiting of wild dogs and foxes, and endemic infection of rabbits with calicivirus. These programs have had some success in reducing the numbers of introduced species, but due to the difficulty of completely removing animals, particularly in the hilly areas of the station (Witte, 2002), control programs must occur regularly. Domestic merino sheep (*Ovis aries*) and domestic cattle (*Bos taurus*) are also stocked on the station for commercial uses, with sheep usually stocked in large numbers (over 6000 in 2004) and cattle kept at lower numbers (50 in 2004; Croft, 2004).

2.1.6 Climate

The climate at Fowlers Gap is described in general terms by Bell (1973) as dry, mildly arid, with hot summers and mild winters. The major climatic characteristics result from the location of the station, which is near the centre of the zone of migrating subtropical high pressure systems (unfavourable for precipitation) and is remote from the moisture-bearing airstreams of the ocean. Detailed climatic records have been kept at Fowlers Gap station for approximately 40 years (since 1966), and as records have been correlated with corresponding data from neighbouring stations with longer climatic records, records at Fowlers Gap are reliable estimates of climatological trends (Bell, 1973).

2.1.6.1 Rainfall

The mean annual rainfall on Fowlers Gap of 238.5 mm (average over 39 years from 1966 to 2004; median = 235.8 mm) is extremely variable (coefficient of variation between 1966 and 2004 = 46.1 %) and patchy in occurrence. Generally, more rain falls during summer, although winter rainfall is more reliable and has a greater impact on vegetation growth (Figure 2.4; Bell, 1973). Rainfall tends to occur in wet spells ranging between one

to six days in duration, and these wet spells are often highly intense. Short bursts of high intensity rain can result in strong run-off; thus water may not infiltrate into soils and become available to plants. Wet spells are interspersed with much longer dry spells ranging between a few weeks to three months. Dry spells may sometimes last for more extended time periods and it is during such times that droughts may occur.

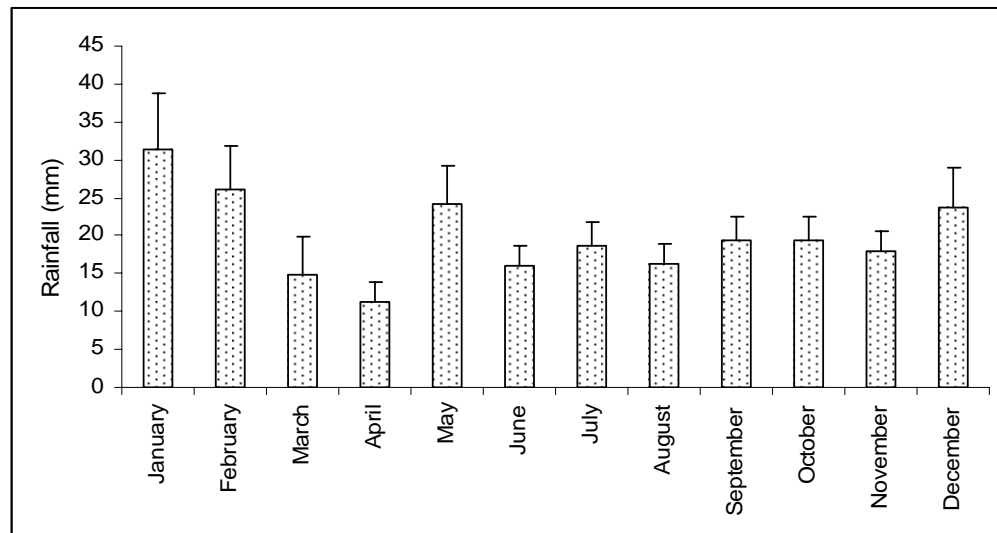


Figure 2.4: Mean monthly rainfall (+ 1 SE) of Fowlers Gap Arid Zone Research Station (January 1967 to September 2005).

2.1.6.2 Temperature

Temperatures at Fowlers Gap are very consistent (Figure 2.5). Daytime temperatures in summer generally exceed 30°C and can reach extremes of over 45°C. Night time temperatures in summer are mild with a mean of approximately 20°C. During winter, daytime conditions are mild to warm, reaching a mean of approximately 18°C, while night time conditions are relatively cool, averaging around 5°C. Cold snaps are sometimes experienced during winter, where temperatures can drop to below freezing. Throughout the year, large diurnal ranges are evident and are typical of the diurnal ranges in most inland areas of Australia (Bell, 1973).

2.1.6.3 Humidity and evaporation

Lower relative humidity prevails in summer (38-42 % at 9 am and 24-27 % at 3 pm) as compared to winter (60-74 % at 9 am and 39-54 % at 3 pm) on Fowlers Gap (Bell, 1973). Annual evaporation is high (2300 mm; McLeod, 1996) and therefore exceeds the mean

annual rainfall by a magnitude of approximately 10 times. Bell (1973) found that even under very wet conditions, monthly rainfall is never likely to exceed monthly evaporation.

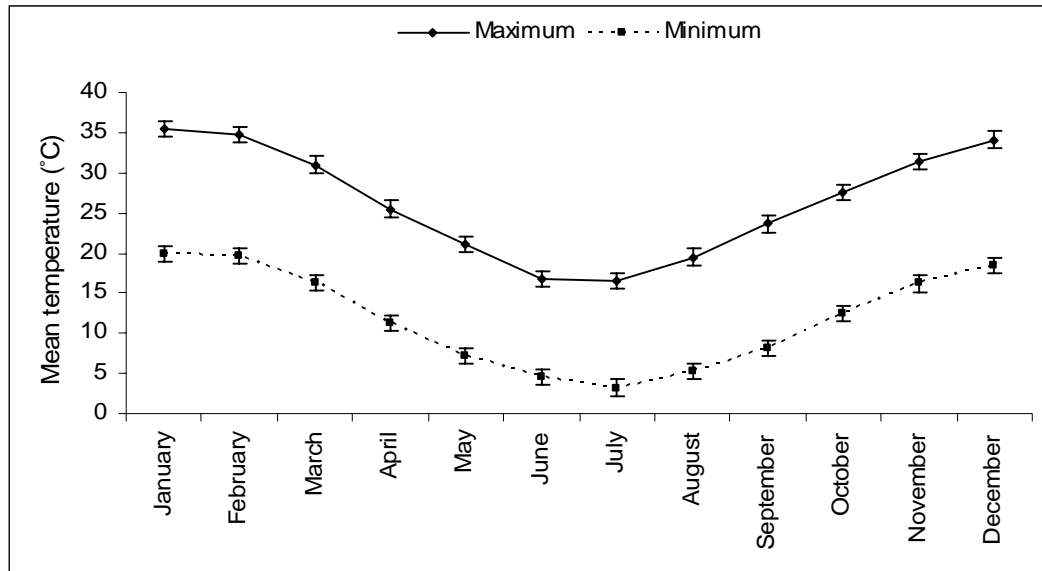


Figure 2.5: Mean daily maximum and minimum temperatures at Fowlers Gap Arid Zone Research Station and their standard deviations (from Bell, 1973).

2.2 Study area

2.2.1 The Silver City Highway

The study centered on the Silver City Highway as it runs from the southern boundary of Fowlers Gap through the undulating lowlands, ranges and foothills (hereafter referred to as the hills landscape type), to its northern boundary through the alluvial floodplains (hereafter referred to as the floodplains landscape type). The portion of the Silver City Highway running through Fowlers Gap is 21.2 km in length (Figure 2.6). The highway was sealed with bitumen approximately 10 years ago and is a dual carriageway around 6.5 m wide. Prior to the road being paved with bitumen, the Silver City Highway was an unsealed, irregularly graded dirt track, estimated to have existed from as early as 1869 when gold was discovered in Tibooburra (Mabbutt, 1973). While the dirt track no doubt had ecological effects, affecting surrounding vegetation via increased levels of dust that may have suppressed plant growth through the blocking of plant stomates (Farmer, 1993), and possibly also affecting faunal movements (dirt roads also affect faunal

movements, Van Dyke *et al.*, 1986; Haskell, 2000; Goosem, 2001; Dyer *et al.*, 2002), its effects on the soil profile and on water re-distribution most likely differed from those of the sealed road due to its position cut into the land surface and simple method of construction (surface compacted and occasionally graded; see Figure 2.7 and section 2.2.1.1 for details of the construction of sealed roads in the arid zone). This study is concerned with the design of sealed roads and the resulting nature of their ecological effects in the arid zone (in conjunction with vehicular traffic that are able to travel faster on a sealed surface). Sealed roads are raised and dome-shaped, and are designed to shed excess water along their length (Austroads, 2000). In addition, sealed roads often have associated structures designed to cope with water flow and erosion (see the following section 2.2.1.1 for more details). Thus, as the effects of sealed roads are not likely be the same as those of dirt tracks, it is likely that any effects measured are not those of past effects, but are due to the road being sealed.

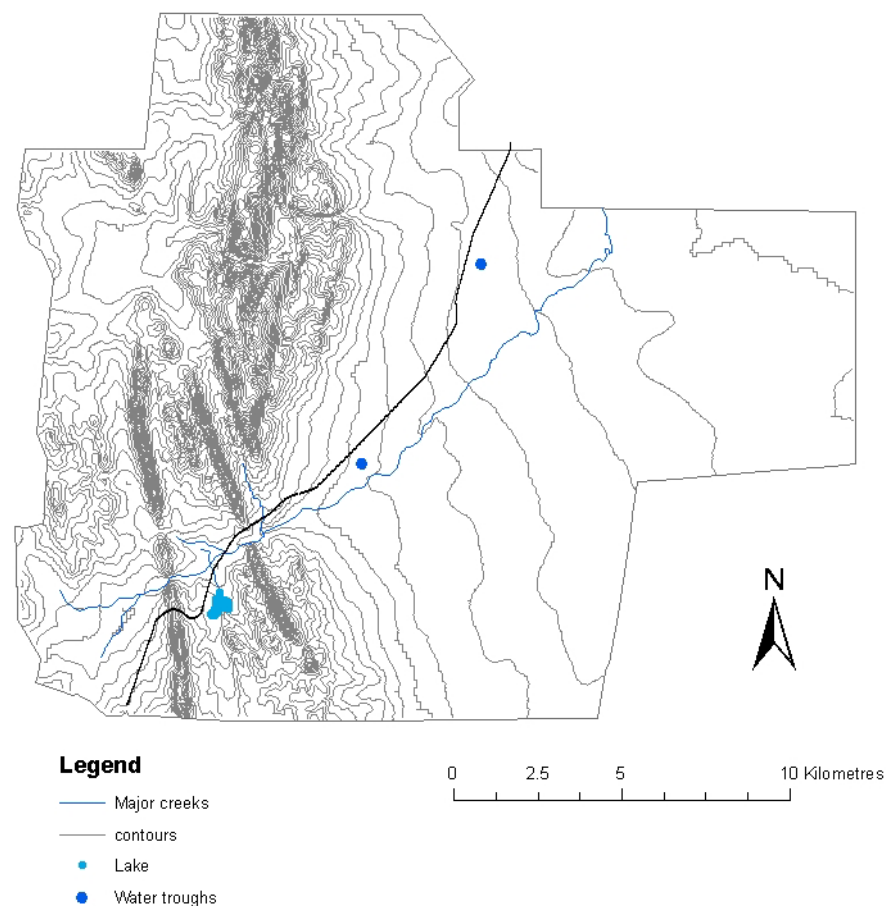


Figure 2.6: Topographic map of Fowlers Gap Arid Zone Research Station showing the Silver City Highway (black line) and major water sources.

a)



b)



Figure 2.7: Pictures of an unsealed section of the Silver City highway a) versus a sealed section b).

2.2.1.1 Construction and design

The Silver City Highway was constructed in a manner typical of other roads in semi-arid Australia. Roads in this area are generally built low to the natural surface level (road centerline approximately 300 mm above the natural surface level), as this area is characterised by wet spells that can result in high surface runoff (Austroads, 2000). Construction is basic, low-cost, and designed to handle low volumes of rural traffic that may include heavy vehicles. During construction, earthworks are first raised using soil from the side of the road (disrupting existing soil profiles) and compacted. Earthworks are then

overlaid with a layer of gravel and sealed with bitumen (most basic), or sealed initially with bitumen, overlaid with a paving fabric (designed to waterproof and to prevent reflective cracking) and further sealed with bitumen. Floodways at main creek channels across roads are usually fortified with rocks (on both sides of the road) to prevent erosion during large rain events, culverts are implemented at smaller drainage areas to allow for water movement across roads, and table drains running parallel to the direction of roads are typical road features (table drains collect water that has run off from the road surface and are usually provided with discharge points that disperse water to surrounding areas and prevent excess water-ponding in table drains; Austroads, 2000). The section of the Silver City Highway running through Fowlers Gap has all these features of arid-zone roads. However, the section running from the southern boundary of Fowlers Gap through the hills and onto the floodplains was built based on the most basic method of arid-zone road construction, with a layer of gravel and bitumen overlying the earthworks. No gravel layer was laid on the last 5 km of the road from the northern boundary of Fowlers Gap. Instead, this section of road had paving fabric overlaying the earthworks which was spray-sealed with bitumen (G. Baker, NSW Roads and Traffic Authority, Western Division, pers comm.).

2.2.1.2 Land systems

The Silver City Highway runs predominantly through four land systems: the Nuntherungie, Old Homestead, Gap Hills, and Sandy Creek land systems (the highway also runs through the Faraway land system, but only for a short distance, Figure 2.3). The Nuntherungie land system lies in the hills at the southern end of the highway and has shale as the underlying lithology. The predominant soils are loamy, and vegetation is mostly contour bands of saltbush. The Old Homestead land system is similar to the Nuntherungie land system in having shale the underlying lithology, but gravel is also present. Soils are calcareous loamy sands and vegetation is characterised by sparse shrubs. As the road passes through the foothills of the central belt (on the eastern side), it passes through the Gap Hills land system. The main land unit making up this section of the Gap Hills land system lies on sandstone/gravel, and soils and vegetation in this land unit are loamy sands/textured soils and saltbush, respectively. The road passes through another land unit making up the Gap Hills land system at its northern end. This land unit contrasts with the land unit just

described and is distinguished by lying on sandstone overlaid with alluvial gravel. Soils in this land unit are sandy loams/textured soils and vegetation is dominated by Mitchell grass. The section of the highway which runs between the two Gap Hills land units in the floodplains lies on the Sandy Creek land system. This land system rests on alluvium, soils are mainly sandy loams (sometimes textured or texture-contrast soils), and vegetation is characterised by Mitchell grass (Corbett, 1973; Mabbutt *et al.*, 1973).

2.2.1.3 Water sources

Four creeks and several smaller channels cross the Silver City Highway (Figure 2.6 shows major creeks only). While these creeks and channels only carry water for a short time after large rain events, with water in creeks flowing over the road surface and water in smaller channels flowing underneath the road via culverts, creeks can retain water in depressions (waterholes) for several weeks after significant rainfall. More permanent water sources near the road (within 200 m) are found in a dammed up body of water lying in a natural catchment area (in the hills near Fowlers Gap homestead), and in two troughs set aside for stock (in the eastern floodplains) (Figure 2.6).

2.2.1.4 Other features

The section of the highway running through the hills (Nuntherungie, Old Homestead and Gap Hills land systems) passes through several road cuttings. These road cuttings are mostly low (less than 2 m above the road surface) apart from one which is approximately 4 m above the road surface (located in the main central belt of ranges). A number of borrow pits, which are holes where soil has been removed to build the road's earthworks, are also present along the highway. These are mostly located along the section of the highway running through the floodplains in the Sandy Creek and Gap Hills land systems, and often have dense stands of vegetation growing inside due to the accumulation of water. Other areas of dense vegetation along the highway (that do not make up the predominant low shrubland and tussock grassland plant communities of the hills and floodplains respectively) include a short strip of shrubs of mostly *Senna* species (stretching for approximately 500 m) in the Sandy Creek land system, and areas of tall open-shrubland and low open-woodland along channels and creeks (scattered through all three of the land systems of the highway). A fence located approximately 50 m from the highway runs the

length of the highway (eastern side of road in the hills and western side of the road in the floodplains). In addition, two stockraces, which are comprised of 50-m long mesh fences positioned 1 m from both sides of the road, are present along the highway at paddock boundaries (one in the hills and one in the floodplains). Stockraces are designed to turn sheep from walking on the road at areas where paddock boundaries meet the road.

2.2.1.5 Management and road use

Little road-maintenance is conducted on the Silver City Highway. Occasionally, holes in the road surface are patched with bitumen by the New South Wales Roads and Traffic Authority (RTA). The RTA also carries out periodic mowing of vegetation along the immediate road edge (strip of mown vegetation extends out to approximately 2 metres from the road edge), where the aim is to increase road safety through improving driver visibility in the road vicinity. Average traffic volume (calculated in the current study for the period during which a traffic monitor was functional: between February 2003 and November 2004) is low, 58.7 ± 1.7 vehicles per day, with light vehicles comprising 86 % of all traffic, and medium and heavy vehicles comprising smaller proportions (7 % each). Average traffic volume during night-time hours only is 14.6 ± 1.7 vehicles per night (comprising of 81 % light vehicles, 6 % medium vehicles and 13 % heavy vehicles). Average vehicle speed is 98.6 ± 0.1 km h⁻¹ and average vehicle speed of night-time traffic only is 96.0 ± 0.3 km h⁻¹.

2.3 Study period and conditions during study

The study was conducted over two years from February 2003 to April 2005 and followed a severe drought in 2002. More specific details of the when fieldwork was conducted are provided in each chapter. During the study, both mean daily maximum temperatures and mean daily minimum temperatures per month were higher than the mean long-term maximum and minimum values per month, with the exception of four of the months (Figure 2.8). Rainfall was relatively low and erratically distributed throughout the study period (Figure 2.9) such that drought conditions (conditions where rainfall over 3 months previous to the period in question is below the 10th percentile; Australian Bureau of Meteorology) were experienced for the majority of the study (18 months altogether; Table

2.1). Nine of the months during the study period had rainfall in the previous 3 months that was less than the 5th percentile of the 39 year record for Fowlers Gap. These months were classified as being in severe drought (as defined by the Australian Bureau of Meteorology).

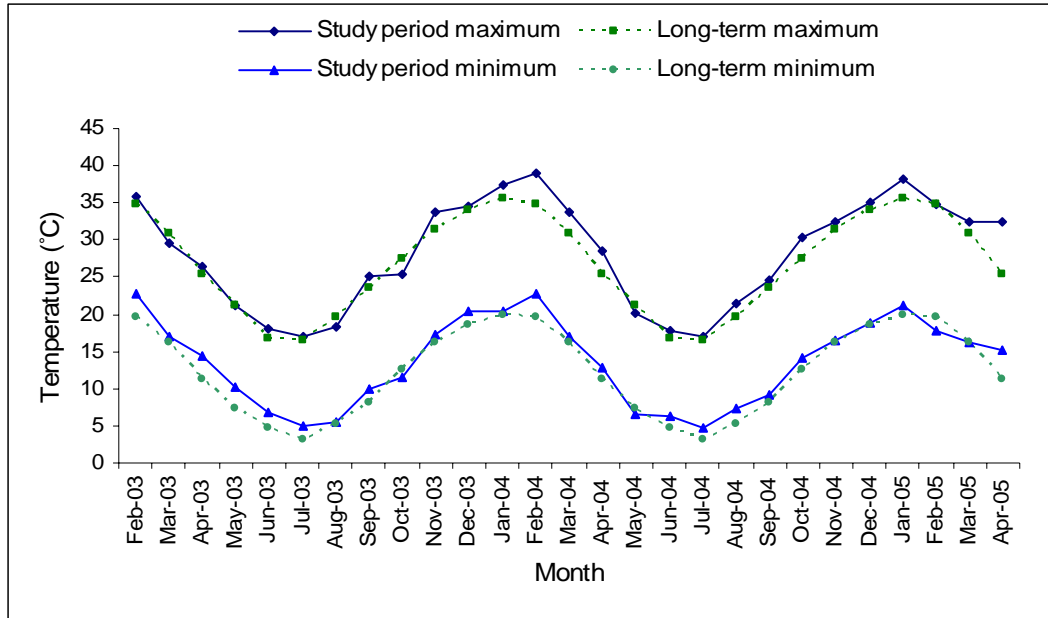


Figure 2.8: Mean daily maximum and minimum temperatures per month during the study. Long-term values for mean daily maximum and minimum temperatures per month are also shown.

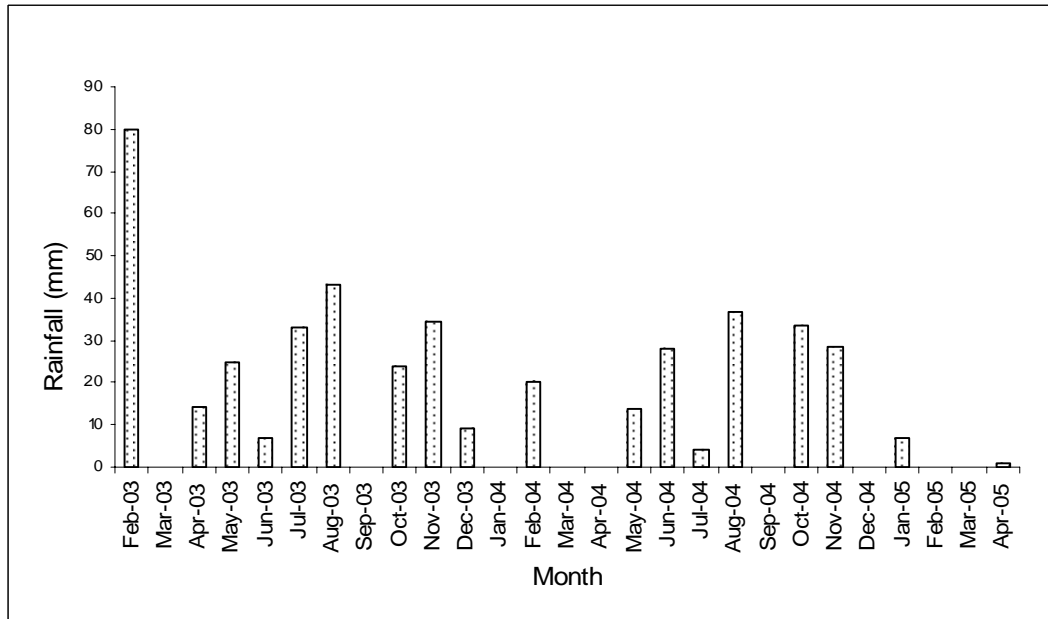


Figure 2.9: Monthly rainfall over the study period.

Table 2.1: Months during study period that were defined as ‘normal’, in drought and with serious rainfall deficiencies. See text for definitions.

Year	Month	Condition
2003	February	Normal
	March	Drought (serious)
	April	Drought
	May	Drought
	June	Drought
	July	Normal
	August	Normal
	September	Drought (serious)
	October	Drought
	November	Normal
	December	Normal
2004	January	Drought (serious)
	February	Drought
	March	Drought (serious)
	April	Drought (serious)
	May	Drought
	June	Drought
	July	Drought
	August	Normal
	September	Drought (serious)
	October	Normal
	November	Normal
	December	Drought (serious)
2005	January	Normal
	February	Drought
	March	Drought (serious)
	April	Drought (serious)

Chapter 3

Effects of the road and road management practices on vegetation and soil

3.1 Introduction

One of the major impacts of roads on landscapes is habitat modification of roadsides (the areas directly adjacent to road surfaces; Spellerberg, 2002), where changes to habitats around roads occur via alterations in plant species composition (Angold, 1997; Greenberg *et al.*, 1997) or plant structure and health (Spencer and Port, 1988, Spencer *et al.*, 1988; Angold, 1997; Norton and Stafford Smith, 1999). Habitat modification of roadsides is a concern to wildlife managers aiming to conserve natural habitats and maintain biodiversity around roads (Angold, 1997; Brooks and Lair, 2005). There are many reasons for this concern, but some of the reasons are that modified habitats around roads can influence the distributions, behaviour and population dynamics of fauna (Spellerberg, 2002), and affect the integrity of natural ecosystem functions (Iverson *et al.*, 1981; Forman and Alexander, 1998). Effects of habitat modification around roads are by no means local. Road networks now permeate ecosystems worldwide; thus mitigating the negative impacts of habitat modification around roads must occur on regional or landscape scales.

Research into the extent and nature of the changes caused by roads to natural habitats is only a recent phenomenon (Spellerberg, 1988, 2002; Trombulak and Frissell, 2000; Forman *et al.*, 2003). Thus, while it is known that habitat modification of roadsides occurs as a result of changes imposed by roads on the surrounding physical and chemical environments (Trombulak and Frissell, 2000), specific effects of roads on surrounding landscapes within different ecosystems have not often been examined, at least not in great depth (but see Garland and Bradley, 1984; Goosem, 2000; Williams *et al.*, 2001; Forman *et al.*, 2003). Some of the patterns and effects of habitat modification around roads may be similar across landscape types and ecosystems (Forman *et al.*, 2003); however, interactions between roads and the characteristics of different landscapes and ecosystems will influence the magnitude of particular road effects (Gutzwiller and Barrow, 2003; Brooks and Lair,

2005). Clearly, deciphering the nature of the effects of roads on roadside habitats among different ecosystems, as well as across landscape types, is essential. Without this knowledge, shaping road management frameworks and designating the best locations for roads to conserve natural habitats around roads and maintain biodiversity is not possible.

Limited studies have investigated the effects of roads on habitat modification in arid ecosystems (Lightfoot and Whitford, 1991; Norton and Stafford Smith, 1999; Brooks and Lair, 2005). Roads in arid ecosystems may not be high in density, but arid ecosystems cover up to one third of the earth's land surface (Kinlaw, 1999), so are ecosystems in which the effects of roads should be studied. Arid-zone roads have the potential to impact heavily on the physical, chemical and biological environments that surround them. This is because water and nutrient resources are highly limited in the arid-zone, patterned over space and time, and are influenced by factors such as soil type and soil density (Westoby, 1980; Stafford Smith and Morton, 1990; Friedel *et al.*, 1993; James *et al.*, 1995; Ludwig and Tongway, 1995). Arid-zone vegetation are adapted to exploiting the heterogeneous distribution of these limited resources, so shifts in resource distribution and availability are accompanied by shifts in vegetation distribution, structure and quality (Tongway and Ludwig, 1994; Dunkerley and Brown, 1995; Cross and Schlesinger, 1999; Lechmere-Oertel *et al.*, 2005). The tendency of roads to change patterns of water flow, nutrient distribution, and soil structure at their edges (Forman *et al.*, 2003) could change the natural heterogeneous distribution of resources typical of the arid-zone, influencing vegetation present in areas adjacent to roads as a result (Norton and Stafford Smith, 1999). Moreover, management of arid-zone roads through the mowing of roadside vegetation could influence vegetation at roadsides by further changing the soil structure adjacent to roads (soil structure could be altered by heavy mowing machinery) and interfering with nutrient recycling. For the latter, arid-zone plants usually withdraw nutrients from their senescing parts before they are excised. Mowing would prevent this withdrawal of nutrients prior to plant parts being removed and nutrients could then become limiting to plants unless nitrogen-fixing micro-organisms were active in the soil (Friedel, 1981).

This study was designed to empirically quantify the effects of an arid-zone road on roadside vegetation and soil, and to relate roadside vegetation cover, structure and quality with spatio-temporal factors. In addition, the study set out to quantify the effects of mowing

on the quality and diversity of arid-zone roadside vegetation across two landscape types in arid Australia. It was not intended to be a large-scale study on the wider effects of an arid-zone road on a regional scale, which might include such alterations as changes to the flow of ephemeral creeks across landscapes. Rather, changes at the road edge in comparison to nearby areas in the arid hinterland were the focus of the study. Specific aims were: 1) to determine the effects of an arid-zone road on roadside vegetation cover, structure and quality, 2) to assess whether soil chemistry, moisture and compaction in roadside areas differed from soil chemistry, moisture and compaction sampled locally in the arid hinterland, 3) to describe the relationships between attributes of arid-zone vegetation and spatio-temporal factors including soil variables, proximity to the road and climate, 4) to determine whether vegetation quality in mown roadside areas differed from vegetation quality in unmown roadside areas along an arid-zone road, and 5) to investigate the effect of mowing along an arid-zone road on arid-zone plant diversity. The first aim was examined at two scales. At the fine-scale, vegetation at incremental distances from the road edge was examined to determine whether the road created differences in vegetation attributes at its immediate edge. On a larger scale, the cover, structure and quality of roadside vegetation was compared with vegetation in the hinterland that was located well beyond the construction and management zone of the road.

3.2 Methods

3.2.1 Effects of the road on vegetation and soil

3.2.1.1 Monitoring sites

Because vegetation in the Australian arid zone is typically patchy on a heterogeneous landscape which includes extensive scalds and gilgais (depressions; Tongway and Ludwig, 1994; Dunkerley and Brown, 1995), temporal variation is best measured from changes in vegetation at fixed sites across a range of seasonal conditions rather than a set of randomly selected sites at each sampling period (Green, 1993). Thus, ten permanent sites (5 per landscape type) were established along the road for vegetation and soil measurements (Figure 3.1; see section 2.2 for details of study road). The sites were initially selected by randomly choosing from 547 previously logged points along the

road. These points were collected every 10 seconds while driving at a constant speed of 25 km/h with a GPS data logger (DGPS-XM-XE, R.I. Keskull) attached to a GPS receiver (Garmin II Plus).

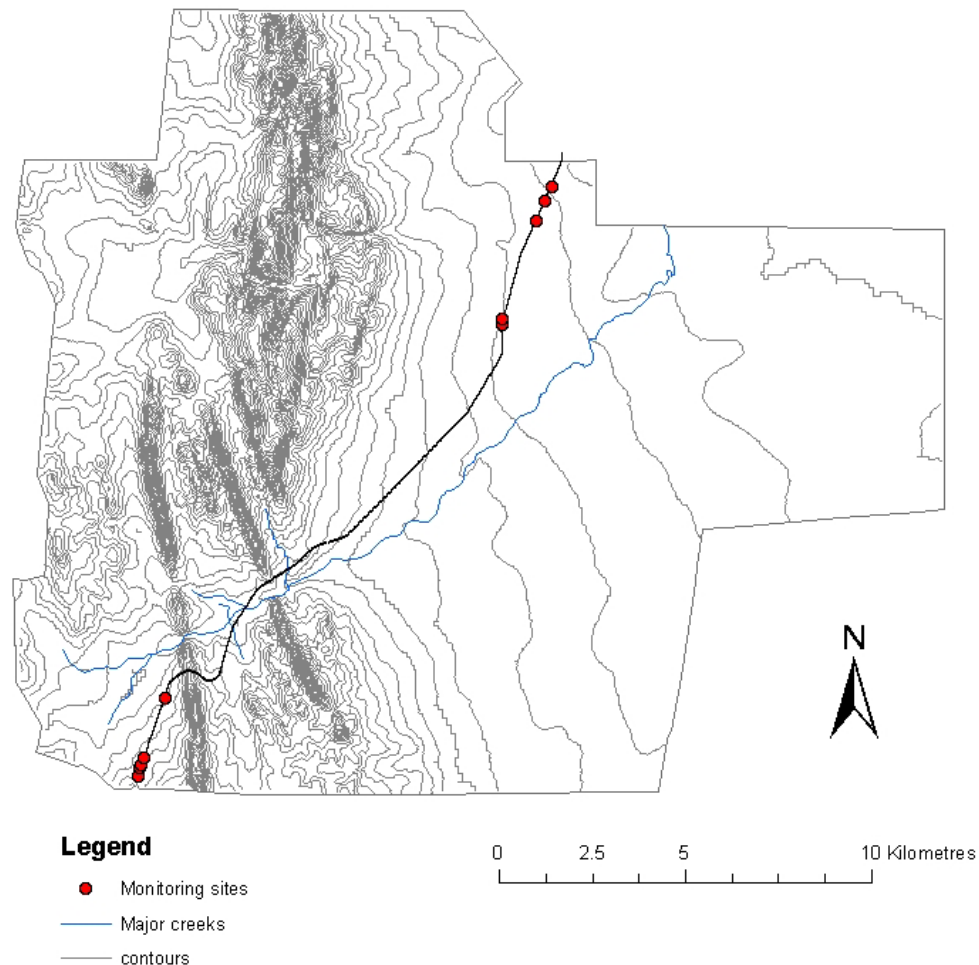


Figure 3.1: Topographic map of Fowlers Gap Arid Zone Research Station showing site locations along the Silver City Highway (black line).

Each site was comprised of three monitoring areas based on distance from the road. These were the road edge, the fence (located approximately 50 m from the road edge and running parallel to the road), and the hinterland (located 250 m from the road edge) (Figure 3.2). Monitoring areas were chosen at these distances as roads have been shown to influence soil and vegetation both in the immediate areas adjacent to the road and areas up to 250 m away from the road (250 m in Lagerwerff and Specht, 1970; 80 m

in Quarles *et al.*, 1974; 200 m in Angold, 1997, 2002). Unfortunately, due to logistic constraints, it was not possible to achieve a greater number of spatial replicates through the monitoring of additional roads. This is a potential limitation of the study, but many authors such as Oksanen (2001, 2004) argue that reasonable predictions can nevertheless be made from large-scale studies lacking replication.

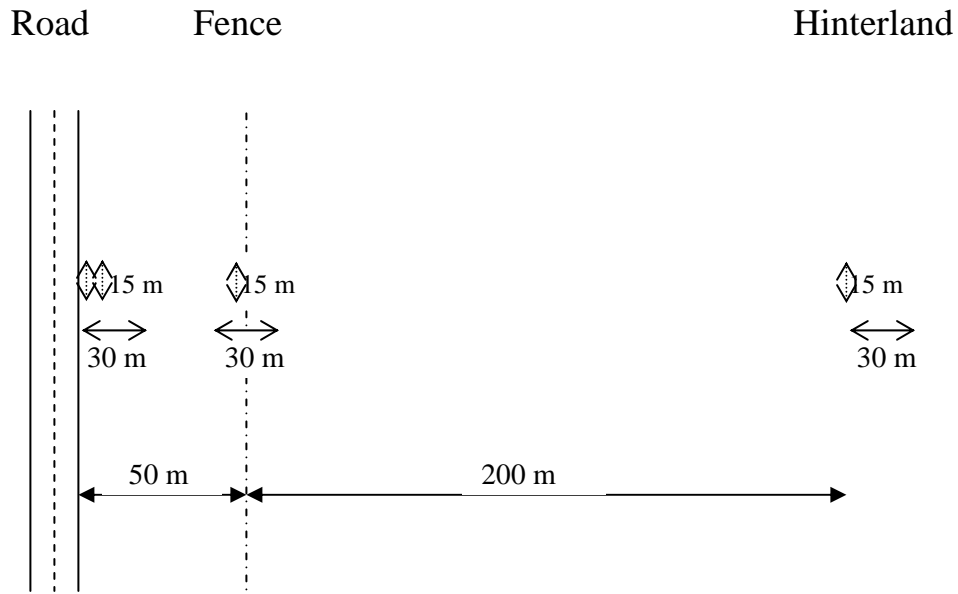


Figure 3.2: Layout of monitoring areas within a site. Transects for measuring vegetation, soil moisture and soil compaction (\longleftrightarrow) and soil chemistry (\diamond) are shown.

3.2.1.2 Vegetation data

Vegetation measurements were conducted seasonally over two years from April 2003 to January 2005 (eight surveys in total). Plants were classified as grasses, forbs, copperburrs, round-leafed chenopods (bluebushes), or flat-leafed chenopods (saltbushes) (Table 3.1) as these groups generally represent the variety of life forms present in rangeland plant communities adapted to arid conditions (Harrington *et al.*, 1984, Dawson and Ellis, 1995).

At each of the monitoring areas, the cover, height (a measure of structure) and greenness (a measure of quality) of each plant group were estimated per meter along 30-m transects orientated perpendicular to the direction of the road (Figure 3.2). This was achieved by laying a 30-m tape across the vegetation and estimating the % cover

(proportion of the tape intersected by the plant), height to the nearest 5 cm, and greenness in five categories (0%, 1-20%, 21-40%, 41-60%, 61-80% or 81-100%) in each meter interval for each plant group. If more than one stand of a plant group was measured within a metre then a mean height and greenness weighted by the cover of each stand was calculated for the relevant plant group using a custom designed *Microsoft Visual Basic 6.0* application.

Table 3.1: General characteristics and descriptions of plants groups used in vegetation surveys.

Plant group	Description and main genera
Grasses	Monocotyledons. Includes both annual and perennial members of the family Poaceae, eg. <i>Astrebla</i> spp., <i>Enneapogon</i> spp., <i>Eragrostis</i> spp., and <i>Digitaria</i> spp.
Forbs	Diverse category of small herbaceous dicotyledons which are mostly ephemeral, eg. <i>Helipterum</i> spp. and <i>Helichrysum</i> spp., although perennial forms also belong to this group, eg. <i>Brachycome</i> spp. and <i>Solanum</i> spp.
Copperburrs	Generally short-lived perennial sub-shrubs with thorny fruits and succulent leaves, eg. <i>Sclerolaena</i> spp.
Round-leafed chenopods	Perennial shrubs with round fleshy leaves, known as bluebushes, eg. <i>Maireana</i> spp.
Flat-leafed chenopods	Perennial shrubs with flat leaves onto which salts are often excreted, eg. <i>Atriplex</i> spp., <i>Rhagodia</i> spp. and <i>Chenopodium</i> spp.

3.2.1.3 Soil data

3.2.1.3.1 Soil moisture

Measurements of soil moisture were conducted in parallel with the eight vegetation surveys. However, the final data set included seven surveys for soil moisture as the data for the summer of 2004 were excluded due to equipment failure.

Soil moisture was measured using a theta probe (ML2 theta probe) which works by measuring the standing wave ratio (the ratio between the amount of signal that is transmitted from the centre rod into the soil, and the amount that is reflected within the area enclosed by the outer rods), which is then converted directly into measures of soil moisture content. This device was used as reliable, accurate, repeatable and quick measurements could be made due to the theta probe using only one frequency confined to the area of soil

enclosed by the outer electrodes, with electrodes that could be inserted directly into the soil. Measurements (in $\text{mm}^3.\text{mm}^{-3}$) were made every metre along the same 30-m transects used for surveying vegetation.

3.2.1.3.2 Soil chemistry

Soil samples were taken once during a dry period in mid-March 2004 (rainfall in the last six months totalled only 63.3 mm, and no rain fell prior to the sampling time for 28 days). Sampling was chosen to coincide with a dry period as nutrient levels are known to be influenced by rain (Charley and Cowling, 1968; Friedel, 1981; Friedel *et al.*, 1993). In this study, it was assumed that the overall and general patterns of soil chemistry at the monitoring sites and areas did not vary significantly over the study period as no rain event was exceedingly high. Indeed, a study of three range types in central arid Australia conducted by Friedel (1981) indicated that temporal differences in nutrient levels varied around relatively stable levels on all range types. Peaks in incubated nitrogen and extractable phosphorus levels were measured after a large rain event (measuring over 150 mm) but afterwards returned to average levels experienced during periods of lower/little rainfall (of around 10 mm). In addition, previous studies on spatial and temporal variations in soil chemistry conducted in arid Australia have indicated that while temporal variations occur in soil nutrient levels, wide generalizations about spatial patterns in soil nutrient levels can be made, both at landscape and microhabitat levels over time (Tongway and Ludwig, 1994; Dunkerley and Brown, 1995).

Soil samples were collected at each of the sites and monitoring areas along 15-m transects (Figure 3.2). Unlike the vegetation transects, the soil sampling transects were orientated parallel to the direction of the road. This was done to obtain maximum information for soil chemistry at the monitoring areas while minimizing costs. Besides the three monitoring areas at the road edge, fence and hinterland, an additional area was monitored. This area was located at the side of the road in a low-lying area (table drain) approximately 10 m from the road edge, although actual distances varied at each replicate site. It ran the length of the road in a parallel direction to the road and was of interest because nutrients may have accumulated there (see section 2.2.1.1).

Because the monitoring areas at the road edge and table drain were run-on areas, transects at the fence and hinterland were also placed in run-on areas. This removed any experimental biases as it is known that run-on areas differ from run-off areas (the former are higher in soil nutrients and moisture) (Tongway and Ludwig, 1994; Dunkerley and Brown, 1995). Along the transects, six sub-samples of soil were taken every 2.5 m. Only the top 5 cm soil layers were sampled. These sub-samples were air dried at room temperature (approximately 20°C) for one week and then combined to make one composite sample per transect. In preparation for laboratory analysis, the composite samples were divided randomly into four groups to reduce any biases in selecting final samples for analysis (random division ensures an even distribution of soil particle sizes). One of these groups was used for final analyses. Final soil samples were passed through 2 mm and 1 mm sieves, with soil ground between each sieving stage.

Soils were analysed for pH, electrical conductivity (EC), exchangeable cations (potassium, K^+ , calcium, Ca^{2+} , sodium, Na^+ , and magnesium, Mg^{2+}), active carbon, nitrate, and available phosphorus as these are known to affect plant growth. The techniques used to analyse the soil samples followed standard procedures, with the most appropriate procedures selected when necessary (Table 3.2). For example, there are a number of methods available for determining levels of exchangeable cations; thus a procedure appropriate for the soil typical of arid areas (calcareous soils dominated by permanent charge with low organic content) was used for this study.

Table 3.2: Procedures used for each soil chemistry test and source.

Test	Procedure	Source
pH and EC	1:5 water extraction	Rayment and Higginson, 1992
Exchangeable cations	Water soluble cations first determined using 1:5 water extraction. NH_4Cl extracted cations then determined using 1:20 1M NH_4Cl at pH8.5. Exchangeable cations determined as the difference between NH_4Cl extracted and water soluble cations	Rayment and Higginson, 1992
Active C	2M $KMnO_4$ in 1M $CaCl_2$	Weil <i>et al.</i> , 2003
Nitrate	Sodium salicylate procedure	Yang <i>et al.</i> , 1998
Available P	Bray 1-P	Rayment and Higginson, 1992

3.2.1.3.3 Soil compaction

Soil compaction measurements were taken once in early February 2005 during a dry period (no rain fell for over 3 months prior to compaction measurements). As with soil chemistry, it was assumed that soil compaction did not vary significantly through the study period. A dial penetrometer (Pocket Geostester, Zoli Maurizo, Italy) affixed with a 10 mm diameter plunger was used for all measurements as appropriate for use on mixtures of sandy and clayey soils. Measurements of penetration force (in kg cm⁻²) were taken every metre along the 30-m transects used for surveying vegetation and soil moisture.

3.2.2 Effects of mowing on vegetation

3.2.2.1 Monitoring sites

As there were limited areas along the road where the immediate road verge was not mown (around road marker poles), selection of sites for monitoring unmown areas could not be randomised. Instead, 30 sites were selected on the basis of their intact stands of unmown vegetation around road marker poles (15 sites in the hills and 15 in the floodplains), and within these sites, unmown areas were paired with mown areas in order to assess differences in vegetation. Each mown area was selected by throwing a tent peg over the shoulder to a distance within 5 to 10 m while standing at an unmown area.

3.2.2.2 Vegetation data

Vegetation in mown and unmown areas were monitored in 1-m² plots over three months after mowing of the roadside vegetation occurred. There were three surveys altogether, conducted at one month, two months and three months after mowing, and these were performed between late January and early April 2004. In each plot, plants were identified to species (nomenclature follows Cunningham *et al.*, 1981), and their percentage cover, and greenness in five categories (0%, 1-20%, 21-40%, 41-60%, 61-80% or 81-100%) were estimated.

3.2.3 Weather data

Weather data (temperature, humidity, barometric pressure, wind speed, wind direction, rainfall) were collected on an hourly and daily basis via an automatic weather

station (WM-918) located at the Fowlers Gap Homestead. Temporal variables of interest included average maximum temperatures, total rainfall, days since last rain, and the last rainfall amounts as temperature and rainfall influence plant growth in the arid zone (Harrington *et al.*, 1984; Stafford Smith and Morton, 1990). Average maximum temperatures and total rainfall were calculated for 1 week, 2 weeks, 1 month, 2 months and 3 months before vegetation and soil moisture surveys were conducted, while days since last rain and last rainfall amounts were determined with reference to the dates on which vegetation and soil moisture surveys were conducted.

3.2.3 Data analysis

3.2.3.1 Comparisons of vegetation variables between metre intervals within monitoring transects

Vegetation data were analysed for differences in cover, height and greenness between metre intervals at each monitoring area using Friedman's tests, followed by Dunn's tests to determine where significant differences lay (significant when $p < 0.05$; Siegel and Castellan, 1988). The mean ranks for each metre interval were graphed and used as additional visual assessments of possible trends along transects (Friedman's tests work on the principle of ranking data and then analysing ranks; Field, 2000). As such, ranks give indications of higher or lower values, and viewing plots of ranks immediately show patterns for where higher or lower values lie). Both entire datasets and split datasets (by landscape type) were examined. Plant groups used for analysis included grasses, forbs and copperburrs since these groups were well represented at all of the sites and monitoring areas. An additional group, pasture (calculated as the sum of grasses, forbs and copperburrs for cover values and the mean of grasses, forbs and copperburrs for height and greenness values), was also used in analysis to determine variation in vegetation that might attract and be utilised by mammalian herbivores as this was of interest in later chapters examining the effects of the road on kangaroos. Analyses were conducted with the mean values calculated over all samples to smooth out temporal variations displayed by arid-zone vegetation and to obtain general patterns of vegetation growth at the monitoring areas. Season has some effect on vegetation composition (winter forbs versus summer grasses) but is not a predictor of cover, height or greenness because of unpredictable rainfall (see Chapter 2).

3.2.3.2 Comparisons of vegetation and soil variables between monitoring areas

Comparisons of vegetation were made using both univariate and multivariate methods, with analyses of variance (Anova) used for comparisons of pasture cover, height and greenness, and multivariate analyses of variance (Manova) used for simultaneous comparisons of the cover, height and greenness of grasses, forbs and copperburrs. The two analyses were performed to explain variation in both the general patterns of vegetation and the patterns for individual plant groups, and to determine which plant group was most responsible for the observed patterns. Anova and Manova were two-factor in design (landscape type and position). Landscape type was examined as a potential factor influencing vegetation, however as the aim of the study was to determine the effects of the road on vegetation, landscape type was only of interest if it interacted with position. Results will therefore focus on positions and landscape-type x position interactions. Four positions were examined by dividing the roadside transect into the immediate road edge and the table drain, and comparing these to each other and the fence and the hinterland transects. This was because the road may have had more of an effect on the immediate area adjacent to it and on areas in the table drain than on metre intervals further from the road edge, so using average values calculated over the entire roadside transect may not have detected real effects of the road on vegetation. Representative values of vegetation cover, height and greenness for the road edge, fence and hinterland positions were calculated by taking the values in the first metre of the roadside transects as representative of the road edge, and the mean values of all the metre intervals in the fence and hinterland transects as representative of the fence and hinterland. As the position of the table drain varied for each site, metre intervals covering the table drain area were first visually identified per site, and mean values of the identified metre intervals were calculated per site to represent the table drain.

Comparisons of soil variables between monitoring areas were made using two-factor Manova (landscape type and position). Again, landscape type was not of primary interest in the study and was only considered important as part of landscape-type x position interactions. The soil dataset comprised of soil chemistry variables, plus soil moisture and compaction variables. Mean values of soil moisture and compaction were first calculated for the same four positions as for vegetation (road edge, table drain, fence and hinterland), with additional calculations made for soil moisture to obtain mean values over all samples

before being added to the soil chemistry dataset. In addition, estimations of missing soil moisture values were made by regression estimation, with adjustments added to values using random error components based on residuals, as the presence of stones in the soil prevented soil moisture measurements at the fence and hinterland transects in the hills.

Assumptions of statistical methods were tested prior to analyses for comparisons of vegetation and soil variables. Firstly, the residuals of the dependent variables were checked for normality and homogeneity by examining frequency histograms of standardised residuals with normal curves fitted, normal P-P plots of standardised residuals, and scatterplots of standardised residuals against the predicted standardised values of the dependent variables. These were done in preference to formal tests of normality and homogeneity (eg. Shapiro-Wilk and Kolmogorov-Smirnov tests for normality and Levene's test for homogeneity) as these tests often reject null hypotheses of normality in situations when subsequent tests may be accurate (Quinn and Keough, 2002). If assumptions of normality and homogeneity were violated, data were transformed (usually square-root or natural-log transformed) and the residuals re-examined. Transformations that best met the assumptions of normality and homogeneity of residuals were used in subsequent analyses.

Secondly, in order to ensure that tests performed were valid, and that any differences which were found between landscape types or positions were real (rather than reflections of the spatial heterogeneity typical of the arid-zone), examinations of variability were performed for the ten replicate sites for both vegetation and soil variables. Thus, coefficients of variation (CV) were calculated (standard deviation of sites divided by the mean of sites x 100) for each landscape type and position to determine whether spatial variation was high (high values over 50 %). In addition, two-factor Anova was performed for vegetation variables (seasons used as replicates) to determine whether landscape types or positions showed more variation in vegetation than others.

Results from Anova, Manova, and post-hoc tests were considered significant if $p < 0.05$. If significant differences were found between positions by Anova, Ryan-Einot-Gabriel-Welsch Q range (REGWQ) post hoc tests were used to determine where differences lay (the REGWQ procedure has good power and tight control of the Type 1 error rate when group sizes are equal, Field, 2000). If significant interaction effects were detected, data were retested for differences between landscape types at each position

separately (one-factor Anova). The nature of significant differences detected by Manova was examined in two ways: using separate two-factor Anova for dependent variables followed by REGWQ range post hoc tests, and with discriminant analyses. Where significant interaction effects existed, one-factor Anova were run for each position separately. All Manova used Pillai's trace statistic as this statistic is the most robust of the test statistics for Manova (Field, 2000; Quinn and Keough, 2002). All data manipulation and analyses were carried out using SPSS for Windows V13.0 (SPSS Inc., Chicago).

The multivariate analytical methods used to compare vegetation and soil between monitoring areas were appropriate for use in this study. However, it is known that the power of these tests to detect significant differences decreases when the ratio of the number of dependent variables to the number of observations is high (Anderson, 2001). This may have been the case for the analysis of soil where 11 dependent variables were considered in a dataset of 40 observations. Thus, an additional multivariate test that is also able to partition variance and generate a multivariate analogue to Fisher's F-ratio, but uses permutations to calculate p-values (permutational manova or permanova, Anderson, 2001; McArdle and Anderson, 2001), was used to complement and check the results of the original soil analysis (test performed in PERMANOVA 1.6; Anderson, 2005). This was followed by a permutational test of multivariate dispersion (permdisp) (program used: PERMDISP; Anderson, 2004a), performed to determine whether differences found were due to differences in location or differences in dispersion among the groups (results were considered significant if $p < 0.05$).

Prior to analysis by Permanova and Permdisp, soil data were transformed as appropriate for normality and standardised by dividing values by the square root of their within group variances (or error mean square values) (standardisations when using Permanova and Permdisp were necessary as measurement units were different amongst variables, Anderson, 2001). This standardisation method was used so that any existing variations between groups would be preserved (compared to when values are simply divided by their standard deviations) (D. Warton, Dept. Statistics UNSW, pers comm.). In the analysis, Euclidean distance measures were chosen and 9999 permutations (large numbers of permutations increase precision, Anderson, 2001) were performed for generating p-values for multivariate and post-hoc tests.

3.2.3.3 Relationship between vegetation and soil variables

The influences of soil variables on vegetation cover, height and greenness were modelled using stepwise multiple regression. Models were constructed from vegetation datasets that had mean values for the vegetation variables calculated over samples (to remove temporal variation in vegetation). Soil data used in the models were reduced components as determined prior to analysis from a principal component analysis (PCA). This approach of using components rather than the original soil variables was taken to reduce the number of soil variables and to reduce collinearity (soil variables were highly correlated). In the PCA, the number of principal components was selected according to the number of components on the steep slope of the scree plot. The Kaiser Criterion (eigenvalue > 1) was not used as the resulting communalities (after extraction) for components with eigenvalues > 1 were not greater than 0.7 and Kaiser's guideline is only accurate when communalities are greater than 0.7 (Field, 2000). In addition, an orthogonal varimax rotation was performed to reduce the number of variables contributing strongly to each component and increase the differentiation between components. The 11 soil variables were reduced to three components and accounted for 79.63 % of total variance. There were strong extraction communalities for all soil variables (majority of variables above 0.8) indicating that high amounts of variability were accounted for and that the extracted components represented the variables well. Component 1 was positively correlated with pH, exchangeable Mg, and exchangeable Na and negatively correlated with compaction; Component 2 was positively correlated with EC, exchangeable Ca and soil moisture; and Component 3 was positively correlated with nitrate, Active C, available P and exchangeable K (see Table A3.9 in Appendix 3 for correlations between soil variables and extracted components).

Checks of model accuracy and assumptions were made after running regressions. Two measures were used to assess model accuracy and identify influential cases: Cook's distance, and leverage measures (values greater than 1 for Cook's distance, and values twice the average leverage values are a concern). Checks of collinearity were made using three methods: scanning a correlation matrix of predictor variables (values above 0.6 are a concern); looking at variance inflation factors (VIF) (values should be below 10, and the average should not be substantially greater than 1); and looking at tolerance statistics

(values below 0.1 indicate a serious problem) (Field, 2000). Checks of normality of errors and homoscedasticity were performed as outlined in section 3.2.3.2. If the accuracy or assumptions of the models were compromised, steps were taken to amend them as necessary (influential cases removed, intercorrelated variables removed leaving in variables that best correlated to the dependent variable, and data transformed, with tests then re-run). Variables included in final models were those which were individually significant at $p < 0.05$. All regressions and the PCA were run in SPSS for Windows V13.0 (SPSS Inc., Chicago).

3.2.3.4 Relative importance of spatio-temporal factors influencing vegetation variables

To determine the relative importance of spatial factors (landscape type or positions) compared to temporal variables, the influences of landscape type, position, landscape-type x position interactions, total rainfall, average maximum temperature, number of days since last rain and last rain amounts on vegetation variables were modelled using univariate general linear models (GLM, conducted in SPSS for Windows V13.0; landscape type was only of interest if it interacted with position). Soil variables could not be included in these models along with landscape type and position as all soil variables were strongly correlated to these larger-scale spatial predictors. For total rainfall and average maximum temperature, the strongest relationships with the dependent variables were first determined for a number of time-frames (one week, two weeks, one month, two months and three months prior to vegetation surveys), and those that best correlated were entered into models. Models were constructed from vegetation datasets that had mean values for the vegetation variables calculated over replicate sites to remove the extra spatial variation in vegetation present at the replicate sites.

Model terms were added into GLM using a stepwise technique, with all terms and interactions initially entered into the model and dropped if not significant at $p < 0.05$. The final model was that which included terms for which elimination would have reduced the explanatory power of the model (that is, the model which accounted for the most variation; Adjusted R^2 used, Quinn and Keough, 2002). Only landscape-type x position interactions were investigated. The nature of significant differences was assessed with Bonferroni corrected post hoc comparisons for factors and the sign of β calculated using regression analysis for variables. If significant interaction effects were detected, differences between habitats were tested for each position separately (one-factor Anova).

Checks were made to ensure that the residuals of the dependent variables were normal and that the variances of the residuals were constant (see section 3.2.3.2 for details on checking assumptions). In addition, the homogeneity of regression slopes was checked by examining interactions between variables and factors separately (p should not be significant for these interactions). Checks of collinearity were made by examining Pearson's correlations (Field, 2000; Quinn and Keough, 2002). If variables were found to be highly correlated, the variable that correlated less strongly to the dependent was removed as a predictor. Reported significance values of interactions were derived from the final models, whereas significance values of terms contained in interactions were derived from models run for these terms without interactions. Statistics for non significant terms were obtained by re-running the final models containing all significant terms with each non-significant term included individually.

3.2.3.5 Relationship between soil moisture and spatio-temporal factors

Soil moisture was the only soil variable with both spatial and temporal data available. Thus, to gain further insights into the relationships between spatio-temporal factors and vegetation variables, the relationship between soil moisture and spatio-temporal factors was also investigated using a univariate GLM. Because the presence of stones in the soil prevented soil moisture measurements at the fence and hinterland transects in the hills, estimations of missing soil moisture values were made by regression estimation (soil chemistry and compaction dataset used). Like the temporal factors influencing vegetation, the strongest relationships between soil moisture and total rainfall and average maximum temperature were first determined over a number of weekly and monthly timeframes and those that best correlated with soil moisture were entered in the model. For the methods used for obtaining the model and the procedures for checking assumptions and correcting violations of assumptions, see section 3.2.3.4.

3.2.3.6 Comparisons of greenness between mown and unmown quadrats

Plant species were grouped into broad plant groups as outlined in Table 3.1. Average greenness values for each plant group were then calculated per mown and unmown plot, with greenness values first weighted by the cover of each plant species if more than one species of plant was present in a plant group per plot. As only plant groups

that could attract and be utilised by mammalian herbivores were of interest (for later chapters), only the average greenness of grasses, forbs, copperburrs, and pasture (calculated as the mean of grasses, forbs and copperburrs) were examined for differences between mown and unmown plots. Both entire datasets and split datasets (by landscape type) were examined using paired t-tests (significant if $p < 0.05$, SPSS for Windows V13.0). Analyses were conducted on average vegetation data (mean over all surveys) to determine the overall effect of mowing on vegetation greenness, but since the study was also interested in determining the effects of mowing on vegetation both immediately after mowing occurred and some time after mowing occurred, separate analyses were additionally conducted on vegetation data from the three vegetation surveys.

3.2.3.7 Comparisons of plant diversity between mown and unmown quadrats

Simpson's diversity indices were calculated using the program *Species Diversity and Richness* (Version 3.02, Pisces Software, UK) and comparisons between indices for mown and unmown quadrats were made using randomisation tests for significant differences between quadrats (significant if $p < 0.05$). These tests work by re-sampling 10,000 times from a distribution of species abundances produced by a summation of the mown and unmown samples. Like the comparisons of greenness between mown and unmown quadrats, both entire datasets and split datasets (by landscape type) were examined, and analyses were conducted on average vegetation data (mean over all surveys) and vegetation data from the three vegetation surveys.

3.3 Results

3.3.1 Comparisons of vegetation variables between metre intervals within monitoring transects

3.3.1.1 Vegetation cover

Plots of mean ranks per metre interval, which illustrate patterns of higher or lower values (see section 3.2.3.1), showed that different patterns of vegetation cover were present along roadside transects between landscape types for all plant groups examined other than copperburrs (Table 3.3). While patterns of vegetation cover were observed, Friedman's tests found that differences were mostly non-significant, with follow-up Dunn's tests revealing that significant differences in vegetation cover were not in relation to metre intervals at the road edge. Nevertheless, higher cover values were seen at the road edge in the hills and lower cover values were seen at the road edge in the floodplains (except for copperburrs) compared to metre intervals distant from the road edge (Table 3.3). Figure 3.3 illustrates these general trends with the composite vegetation group, pasture.

Besides detecting differences in patterns of vegetation cover at the road edge compared to metre intervals further away from the road edge, the graphs of mean ranks per meter also distinguished peaks in cover between approximately 9-15 m from the road edge, and an increase in cover toward the ends of roadside transects. These increases occurred in both landscape types for all plant groups (see Figure 3.3 for patterns in pasture group) although patterns were most obvious for grasses (Figure 3.4).

No differences in vegetation cover were found between metre intervals within the fence and hinterland transects (Table A3.1 in Appendix 3). Plots of mean ranks per metre interval confirmed these results, but also identified an area of slightly higher vegetation cover around the middle of the fence transect along the fence-line which interrupted the transect (Figure A3.1 in Appendix 3).

Table 3.3: Results from Friedman's tests and patterns in vegetation cover (as detected from plots of mean ranks per meter interval) along 30-m roadside transects for the entire road (n = 10), hills (n = 5) and floodplains (n = 5).

Vegetation	Total road		Hills		Floodplains	
Pasture	$F_{(1,29)} = 41.61$ $p = 0.061$	No strong patterns	$F_{(1,29)} = 38.05$ $p = 0.121$	Higher at edge	$F_{(1,29)} = 47.44$ $p = 0.017$	Lower at edge
Grasses	$F_{(1,29)} = 36.89$ $p = 0.149$	No strong patterns	$F_{(1,29)} = 29.06$ $p = 0.462$	Higher at edge	$F_{(1,29)} = 52.13$ $p = 0.005$	Lower at edge
Forbs	$F_{(1,29)} = 42.69$ $p = 0.049$	No strong patterns	$F_{(1,29)} = 29.32$ $p = 0.449$	Higher at edge	$F_{(1,29)} = 40.82$ $p = 0.071$	Lower at edge
Copperburrs	$F_{(1,29)} = 28.74$ $p = 0.479$	No strong patterns	$F_{(1,29)} = 46.12$ $p = 0.023$	Higher at edge	$F_{(1,29)} = 27.88$ $p = 0.524$	No strong patterns

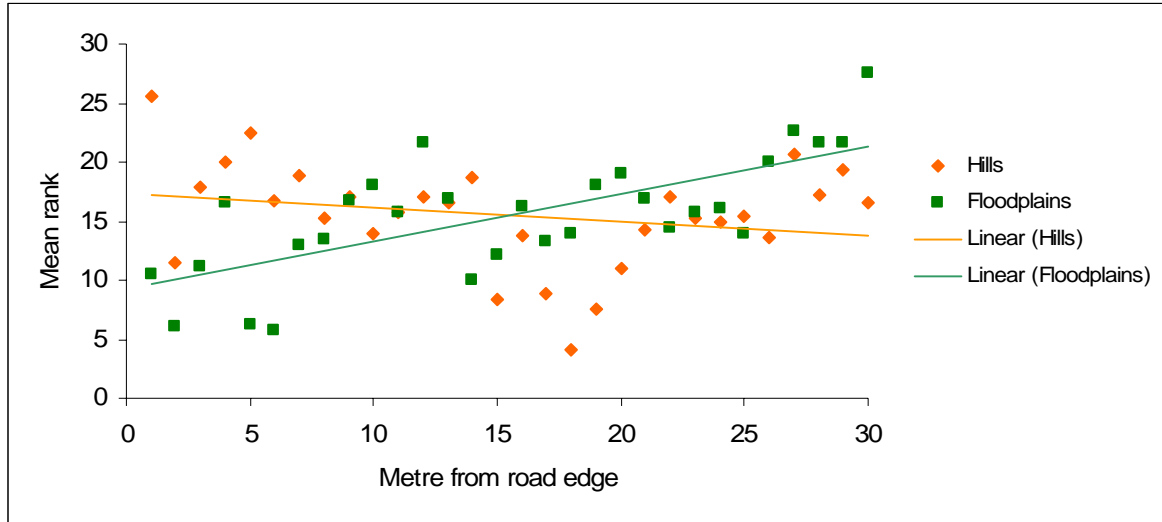


Figure 3.3: Plot of mean ranks per metre interval for pasture cover in the hills and floodplains (n = 5 sites per landscape type). Mean ranks are calculated for landscape types separately and are not comparable between landscape types. Linear trendlines have been added (Hills: $y = -0.11x + 17.28$, $R^2 = 0.05$; Floodplains: $y = 0.40x + 9.27$, $R^2 = 0.49$).

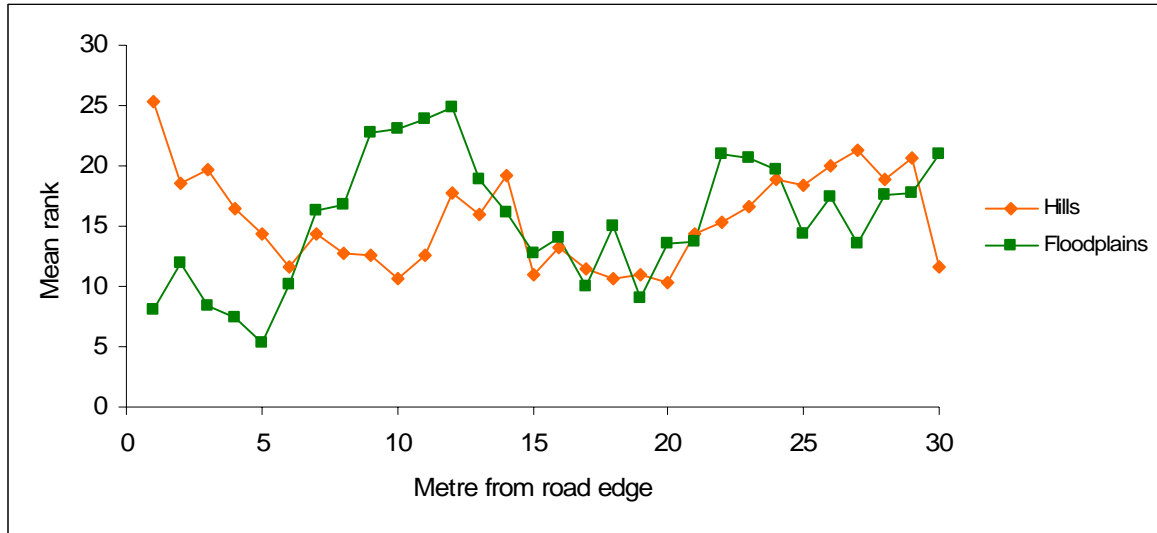


Figure 3.4: Plot of mean ranks per metre interval for grass cover (n = 5 sites per landscape type) showing peaks in cover at approximately 7-15 m and high cover ranks from 22 m. Mean ranks are calculated for landscape types separately and are not comparable between landscape types.

3.3.1.2 Vegetation height

Patterns of vegetation height at the roadside were not as defined as patterns of vegetation cover in either landscape type and significant differences between metre intervals detected by Friedman's tests were not in relation to the first metre at the road edge (Table 3.4). However, plots of mean ranks per metre interval for vegetation height along roadside transects showed some patterns which were similar to vegetation cover for some plant groups: grasses and forbs were taller at the road edge in the hills (see Figure 3.5 for grasses), and grasses were generally shorter at the road edge in the floodplains compared to other metre intervals further from the road edge (Figure 3.5). Overall patterns of vegetation height at the road edge compared to metre intervals further from the road were masked by peaks in height at 9-15 m and increases in height toward the ends of roadside transects which occurred for all plant groups in both landscape types (Figure 3.5). These regions of increased vegetation height were located at the same places as areas of increased vegetation cover.

Table 3.4: Results from Friedman's tests and patterns in vegetation height (as detected from plots of mean ranks per meter interval) along 30-m roadside transects for the entire road (n = 10), hills (n = 5) and floodplains (n = 5).

Vegetation	Total road		Hills		Floodplains	
Pasture	$F_{(1,29)} = 53.04$ $p = 0.004$	No strong patterns	$F_{(1,29)} = 39.30$ $p = 0.096$	No strong patterns	$F_{(1,29)} = 41.17$ $p = 0.067$	No strong patterns
Grasses	$F_{(1,29)} = 34.10$ $p = 0.236$	No strong patterns	$F_{(1,29)} = 26.87$ $p = 0.579$	Higher at edge	$F_{(1,29)} = 41.48$ $p = 0.063$	Lower at edge
Forbs	$F_{(1,29)} = 33.83$ $p = 0.246$	No strong patterns	$F_{(1,29)} = 27.76$ $p = 0.531$	Higher at edge	$F_{(1,29)} = 31.59$ $p = 0.338$	No strong patterns
Copperburrs	$F_{(1,29)} = 31.67$ $p = 0.335$	No strong patterns	$F_{(1,29)} = 43.57$ $p = 0.040$	No strong patterns	$F_{(1,29)} = 28.99$ $p = 0.466$	No strong patterns

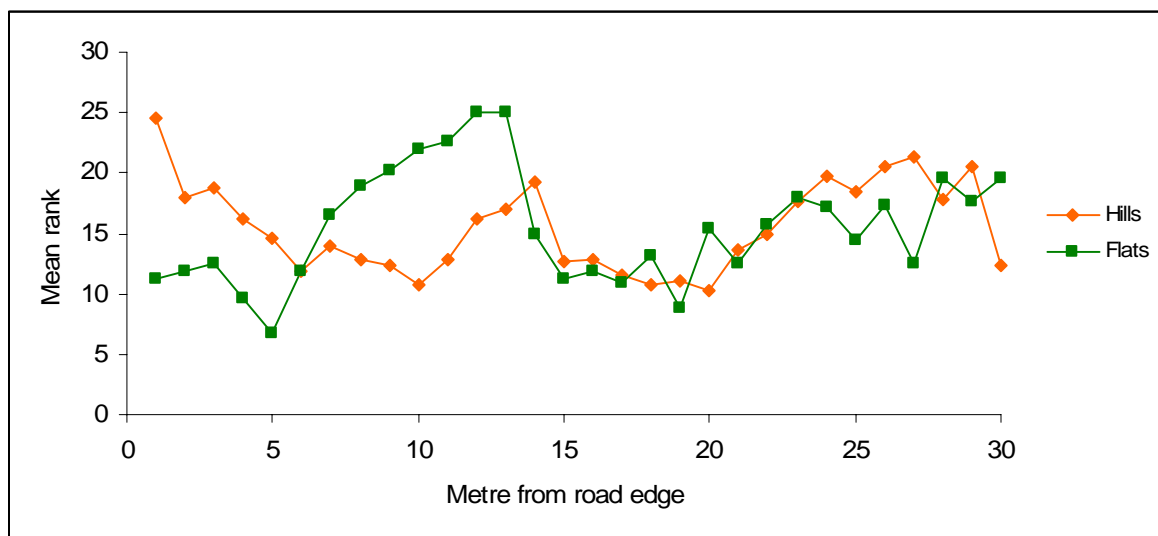


Figure 3.5: Plot of mean ranks per metre interval for height of grasses in the hills and floodplains (n = 5 sites per landscape type). Mean ranks are calculated for landscape types separately and are not comparable between landscape types. Trendlines are not included as differences at the road edge compared to metres further from the road edge are being masked by peaks in height further along the transects.

No differences in vegetation height were found between metre intervals within the fence and hinterland transects (Table A3.2 in Appendix 3). Plots of mean ranks per metre interval confirmed these results, but, like vegetation cover, identified a slightly higher area of vegetation height around the middle of the fence transect (Figure A3.2 in Appendix 3).

3.3.1.3 Vegetation greenness

Patterns of greenness along roadside transects were generally consistent among all plant groups, with plots of mean ranks against metre intervals showing higher greenness ranks (and thus higher greenness values) at the road edge compared to metre intervals further from the road edge for the majority of vegetation groups in both landscape types (exceptions were grasses and copperburrs in the floodplains; Table 3.5). Significant results from Friedman's tests included differences between the first metre at the road edge and other metre intervals, with the road edge showing higher greenness ranks than the other metre intervals. Thus, pasture greenness at 15 m and 17-20 m from the road edge was significantly lower than at 1 m from the road edge in the hills, with pasture greenness at 12 m and most metre intervals between 15-20 m from the road edge significantly lower than at 1 m from the road edge in the floodplains (Figure 3.6).

Table 3.5: Results from Friedman's tests and patterns in vegetation greenness (as detected from plots of mean ranks per meter interval) along 30-m roadside transects for the entire road (n = 10), hills (n = 5) and floodplains (n = 5).

Vegetation	Total road		Hills		Floodplains	
Pasture	$F_{(1,29)} = 90.32$ $p = 0$	Higher at edge	$F_{(1,29)} = 61.33$ $p < 0.001$	Higher at edge	$F_{(1,29)} = 45.46$ $p = 0.027$	Higher at edge
Grasses	$F_{(1,29)} = 35.52$ $p = 0.188$	Higher at edge	$F_{(1,29)} = 27.82$ $p = 0.528$	Higher at edge	$F_{(1,29)} = 39.65$ $p = 0.090$	Lower at edge
Forbs	$F_{(1,29)} = 40.35$ $p = 0.078$	Higher at edge	$F_{(1,29)} = 25.99$ $p = 0.626$	Higher at edge	$F_{(1,29)} = 36.70$ $p = 0.154$	Higher at edge
Copperburrs	$F_{(1,29)} = 55.98$ $p = 0.002$	Higher at edge	$F_{(1,29)} = 64.10$ $p < 0.001$	Higher at edge	$F_{(1,29)} = 27.76$ $p = 0.531$	No strong patterns

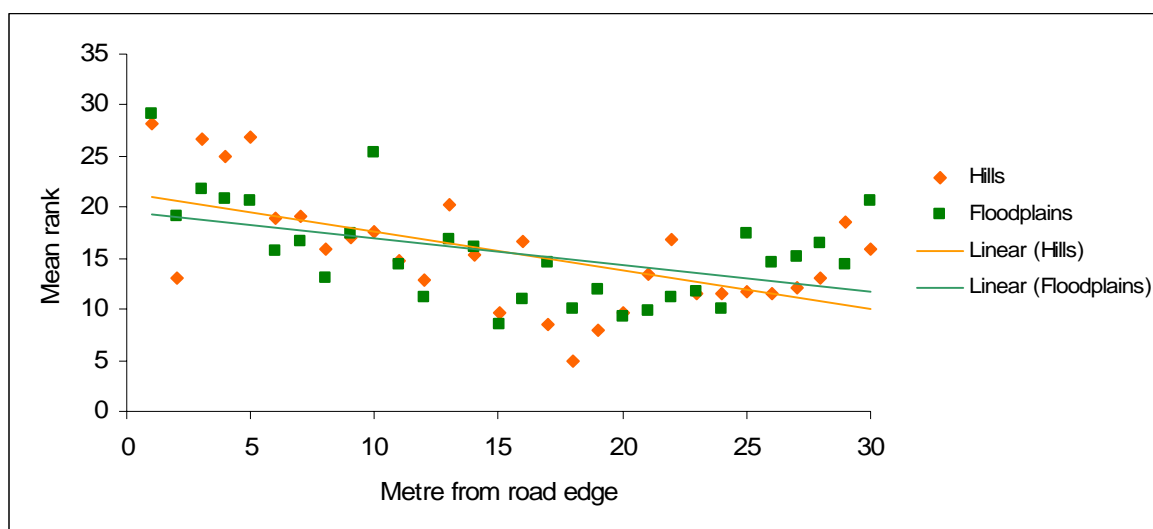


Figure 3.6: Plot of mean ranks per metre interval for pasture greenness in the hills and floodplains ($n = 5$ sites per landscape type). Mean ranks are calculated for landscape types separately and are not comparable between landscape types. Linear trendlines have been added (Hills: $y = -0.38x + 21.39$, $R^2 = 0.34$; Floodplains: $y = -0.27x + 19.62$, $R^2 = 0.23$).

Unlike the peaks in cover and height observed around 9-15 m from the road edge, there were no obvious peaks in greenness in the same area. Increases toward the ends of roadside transects were present for all plant groups in both landscape types (see Figure 3.6 for overall patterns in pasture), however, these increases were slight in comparison to those seen for vegetation cover and height.

Significant differences in vegetation greenness were found between metre intervals within the fence transect for pasture and copperburrs, with higher greenness values occurring along the middle of transects along the fence-line compared to other metre intervals (Table A3.3 in Appendix 3). Plots of mean ranks per metre interval confirmed these differences (Figure A3.3 in Appendix 3) and also identified the same patterns for grasses and forbs. No differences in greenness were found between metre intervals in the hinterland and these patterns were confirmed from plots of mean ranks per metre interval (Table A3.3 in Appendix 3).

3.3.2 Comparisons of vegetation and soil variables between monitoring areas

Analyses of CVs showed significant differences for all pasture variables between positions and landscape type*position interactions (Table A3.4 in Appendix 3), with more

variation at road edge positions for pasture cover, at fence positions for pasture height, and at table drain positions for pasture greenness. Even so overall variation between sites was low (total mean variation for cover = 41.4 ± 2.3 %; height = 41.2 ± 3.3 %; greenness = 29.9 ± 1.8 %). Thus, sites were deemed valid for use as replicates in subsequent analyses. Variation between sites for separate plant groups was not nearly as low as for pasture (total mean variation for plant groups for cover, height and greenness above 50 % except for greenness of forbs). However, apart from a few differences, particularly among grasses (Tables A3.5, A3.6 and A3.7 in Appendix 3), variability was relatively consistent over positions. Soil variables had mostly low CV values but high variability was present at the road edge positions for exchangeable Mg and exchangeable Na (70.9 and 99.1 %), and at table drain positions for EC (60.3 %) (Table A3.8 in Appendix 3).

3.3.2.1 Pasture

Of the pasture variables, only greenness displayed significant differences between positions (Table 3.6) with greenness values highest at the road edge compared to the other positions (Figure 3.7). However, significant interactions for pasture cover, and trends for interactions for pasture height and greenness were found (Table 3.6). Examination of interactions for cover showed significant differences between landscape types at table drain, fence and hinterland positions (table drain: $F_{(1,8)} = 53.76$, $p < 0.001$; fence: $F_{(1,8)} = 12.87$, $p = 0.007$; hinterland: $F_{(1,8)} = 20.78$, $p = 0.002$) with higher values occurring in the floodplains at these positions (Figure 3.8). Trends for landscape type differences for pasture height occurred at the road edge and hinterland positions (higher in floodplains) and at the road edge for pasture greenness (higher in hills).

Table 3.6: Results from 2-factor Anova for pasture cover, height and greenness. Height values were natural-log transformed.

Variable	Landscape type		Position		Landscape type*Position	
Cover	$F_{(1,32)} = 48.04$	$p < 0.001$	$F_{(3,32)} = 0.52$	$p = 0.672$	$F_{(3,32)} = 3.78$	$p = 0.020$
Height	$F_{(1,32)} = 14.66$	$p < 0.001$	$F_{(3,32)} = 1.10$	$p = 0.362$	$F_{(3,32)} = 2.37$	$p = 0.089$
Greenness	$F_{(1,32)} = 3.73$	$p = 0.062$	$F_{(3,32)} = 23.20$	$p < 0.001$	$F_{(3,32)} = 2.34$	$p = 0.092$

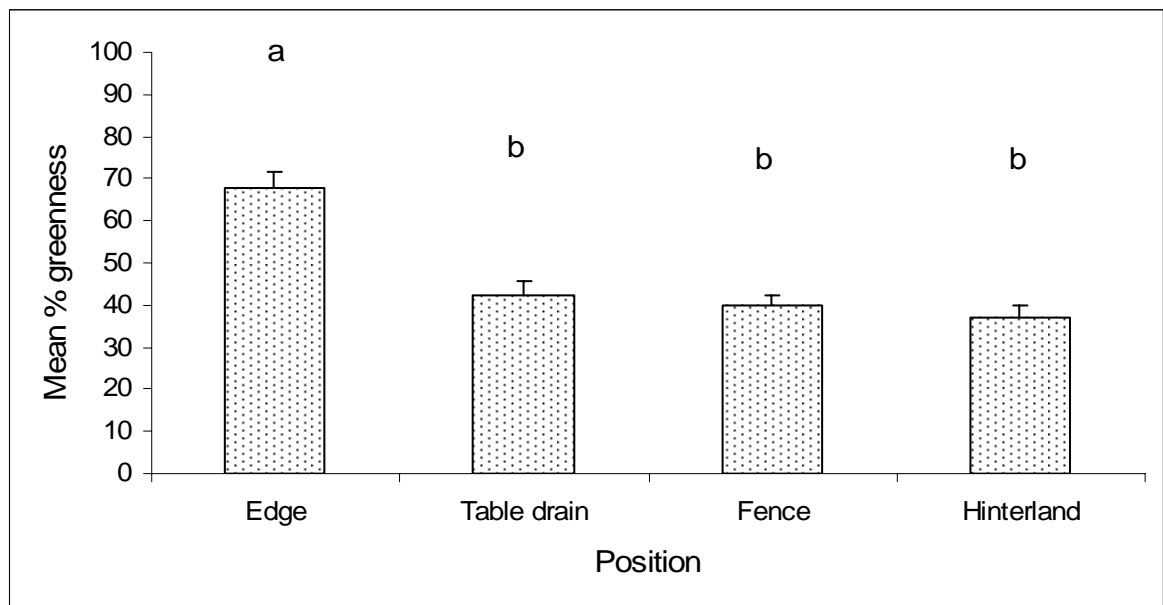


Figure 3.7: Mean % greenness (+ 1 SE) for pasture at different positions relative to the road. Different letters denote significant differences between positions (Ryan-Einot-Gabriel-Welsch range post hoc test).

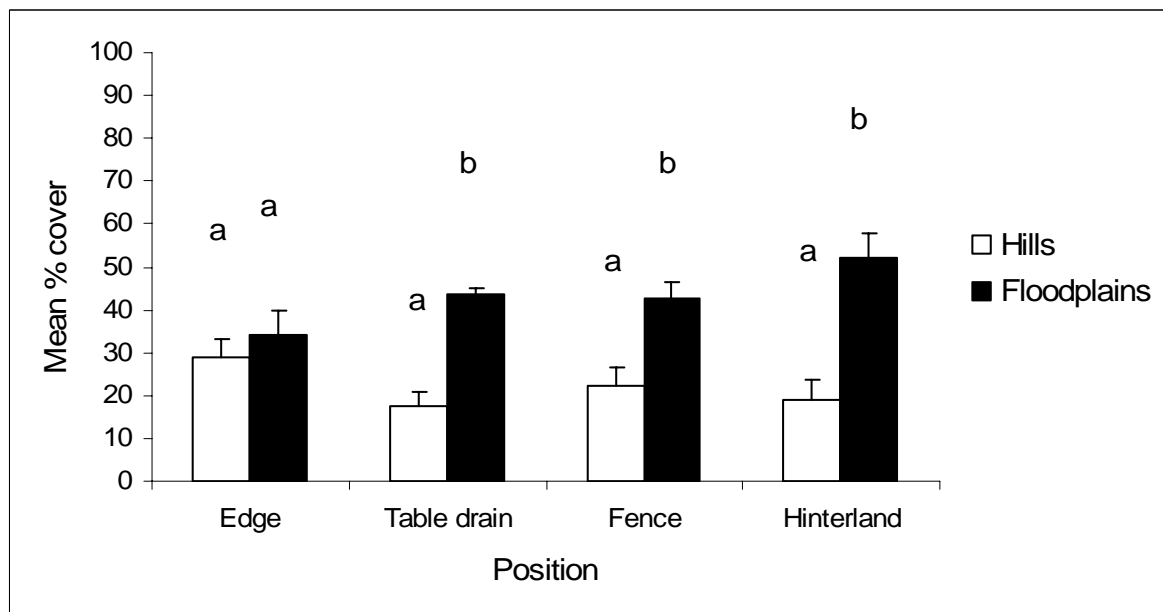


Figure 3.8: Mean % cover (+ 1 SE) for pasture at the positions relative to the road in each landscape type. Different letters denote significant differences between landscape types at each position. Results are from one-factor Anova that followed significant results for interactions.

3.3.2.2 Grasses, forbs and copperburrs

3.3.2.2.1 Cover

Manova found significant differences for vegetation cover between positions ($F_{(9,96)} = 2.25$, $p = 0.025$; Grass and forb values were natural-log transformed and copperburr values were square-root transformed). However, the nature of the differences between positions was difficult to interpret: while results from the separate two-factor Anova for plant groups showed cover differences for copperburrs (lower cover levels found in the table drain compared to at the fence and hinterland positions, with the road edge showing no differences compared to other positions), the result from the discriminant analysis was not significant overall. Even so, the discriminant analysis identified copperburrs as the most responsible plant group for cover differences, followed by forbs and grasses, and separated the road edge and table drain positions from the fence and hinterland positions (different signs of functions at group centroids).

Significant landscape type*position interactions were also present ($F_{(9,96)} = 3.46$, $p = 0.001$), with significant interaction effects found for grasses ($F_{(3,32)} = 9.86$, $p < 0.001$) but not for forbs or copperburrs. As grasses were the only dependent variable to have significant landscape type*position interactions, further tests were performed on this variable to determine the nature of the interactions. Differences were found between landscape types for table drain, fence and hinterland positions (table drain: $F_{(1,8)} = 31.42$, $p = 0.001$, fence: $F_{(1,8)} = 23.10$, $p = 0.001$, hinterland: $F_{(1,8)} = 93.08$, $p < 0.001$) (Figure 3.9), with higher values in the floodplains.

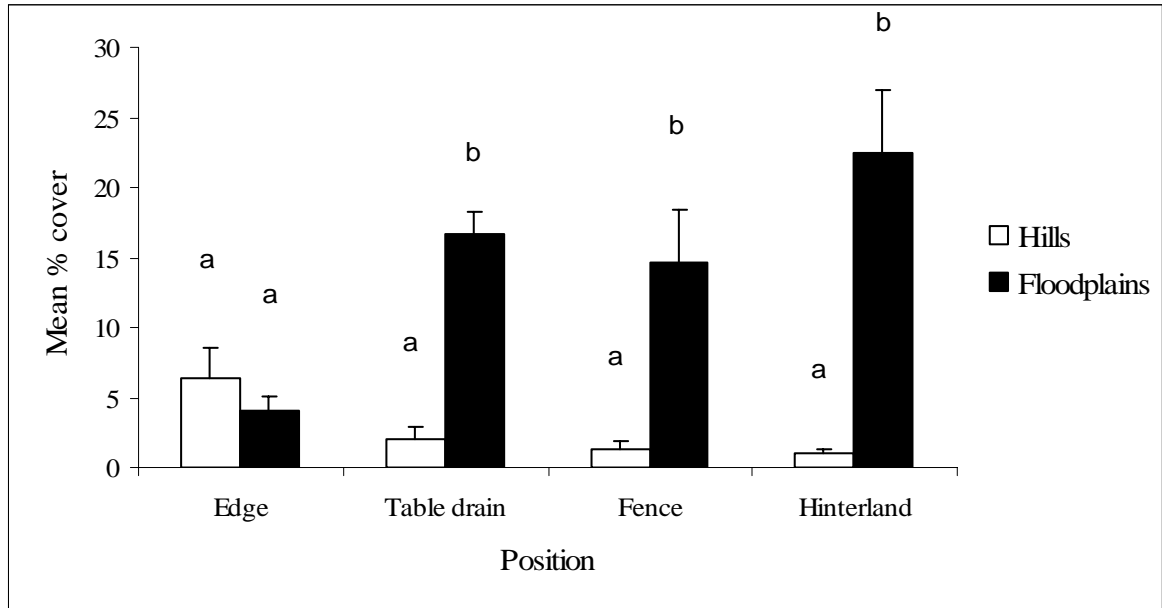


Figure 3.9: Mean % cover (+ 1 SE) for grasses at different positions relative to road in each landscape type. Different letters denote significant differences between landscape types at each position. Results are from separate one-factor Anova for each position between landscape types that followed overall significant Manova results for interaction effects.

3.3.2.2.2 Height

Significant differences for vegetation height were found between positions ($F_{(9,96)} = 2.22$, $p = 0.027$; Grass values were square-root transformed and forb values were natural-log transformed). Separate two-factor Anova for dependent variables revealed height differences for copperburrs and forbs ($F_{(3,32)} = 4.21$, $p = 0.013$ and $F_{(3,32)} = 3.48$, $p = 0.027$ respectively), with lower values of height found at the table drain compared to at the fence and hinterland positions for copperburrs and higher values of height found at the table drain compared to at the hinterland position for forbs. The discriminant analysis confirmed that copperburrs were the plant group most responsible for height differences followed by forbs and grasses, and distinguished the road edge and table drain positions from the fence and hinterland positions (one variate significant: Wilks' lambda = 0.60, $df = 9$, $p = 0.037$; different signs of functions at group centroids).

Trends existed for landscape type*position interactions ($F_{(9,96)} = 1.88$, $p = 0.065$) and grasses most likely drove these differences ($F_{(3,32)} = 5.00$, $p = 0.006$). This plant group showed differences between landscape types for table drain, fence and hinterland positions

(table drain: $F_{(1,8)} = 20.33$, $p = 0.002$, fence: $F_{(1,8)} = 7.14$, $p = 0.028$, hinterland: $F_{(1,8)} = 14.99$, $p = 0.005$), with higher values of height found in the floodplains.

3.3.2.2.3 Greenness

Significant differences for greenness were found between positions ($F_{(9,96)} = 4.42$, $p < 0.001$; Grass and forb values square-root transformed). Results from separate two-factor Anova confirmed these differences between positions for forbs ($F_{(3,32)} = 13.40$, $p < 0.001$) and copperburrs ($F_{(3,32)} = 7.48$, $p = 0.001$), finding higher greenness values for these plant groups occurring at the road edge compared to other positions, and identified similar trends for differences between positions for grasses ($F_{(3,32)} = 1.87$, $p = 0.155$) (Figure 3.10). Similarly, the discriminant analysis found differences between the road edge compared to other positions (one variate significant: Wilks' lambda = 0.39, $df = 9$, $p < 0.001$; different signs of functions at group centroids) and identified forbs as the most responsible plant group for greenness differences, followed by copperburrs and grasses.

Interactions between landscape type and position were also present ($F_{(9,96)} = 2.83$, $p = 0.005$), with two-factor Anova showing significant landscape type*position interactions for grasses and copperburrs ($F_{(3,32)} = 7.27$, $p = 0.001$ and $F_{(3,32)} = 6.18$, $p = 0.002$ respectively). Follow-up one-way Anova for grasses and copperburrs showed differences between landscape types at table drain, fence and hinterland positions for grasses (table drain: $F_{(1,8)} = 6.98$, $p = 0.030$, fence: $F_{(1,8)} = 11.23$, $p = 0.010$, hinterland: $F_{(1,8)} = 35.47$, $p < 0.001$, higher in floodplains), and at the road edge for copperburrs (road edge: $F_{(1,8)} = 11.50$, $p = 0.009$, higher in hills) (Figures 3.11).

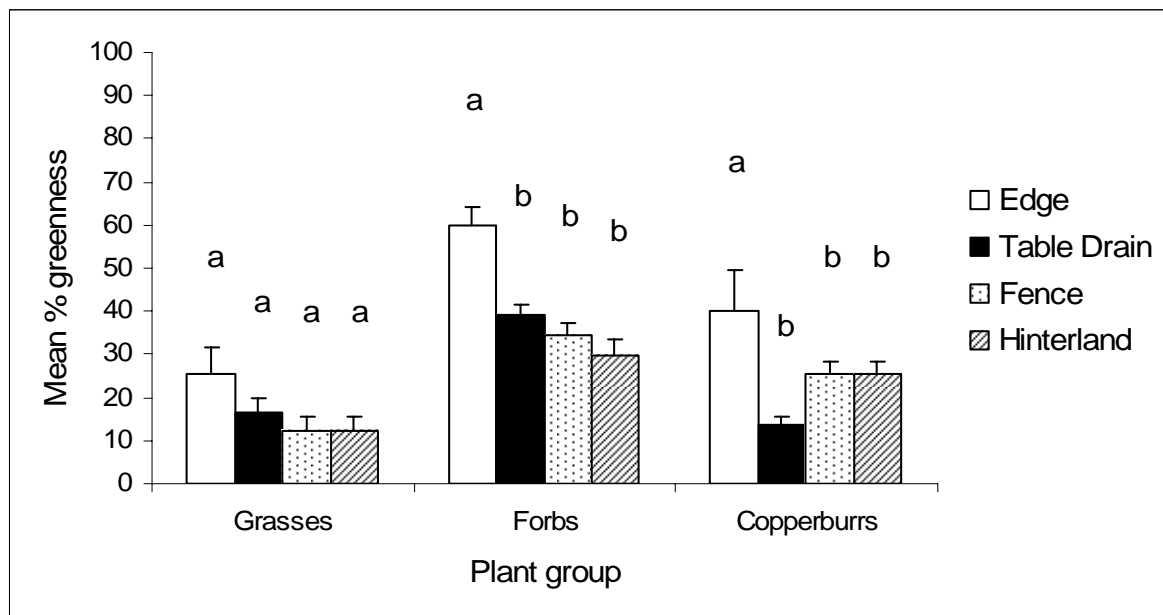


Figure 3.10: Mean % greenness (+ 1 SE) for grasses, forbs and copperburrs in each position. Different letters denote significant differences between positions for each plant group. Results are from separate two-factor Anova for each plant group between positions that followed overall significant Manova results for differences between positions.

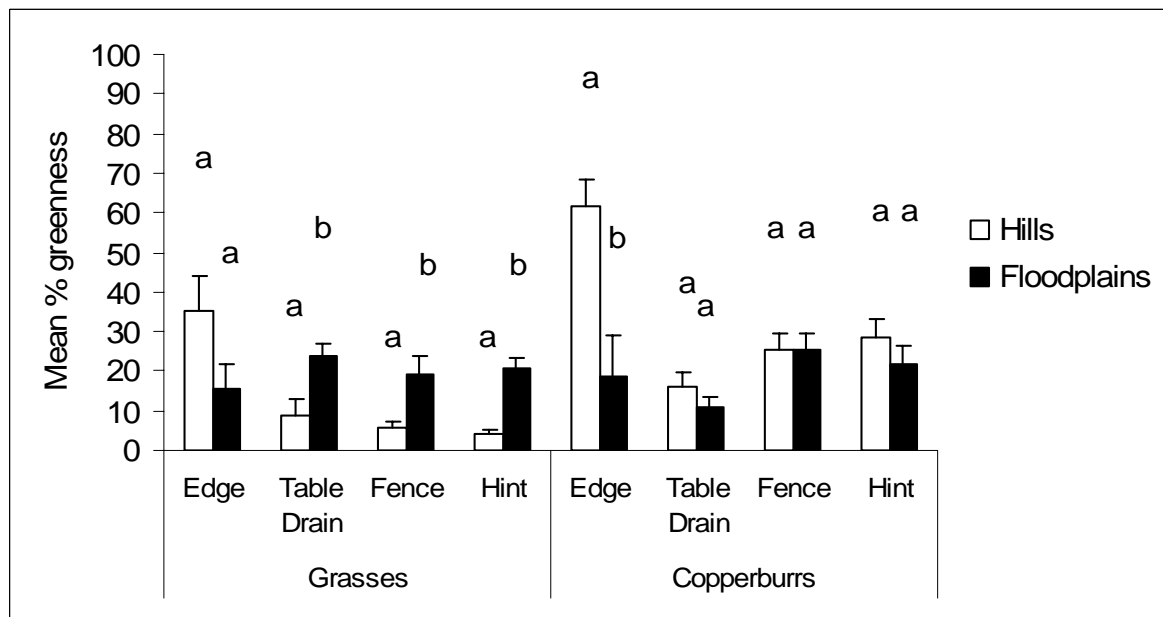


Figure 3.11: Mean % greenness (+ 1 SE) for grasses and copperburrs at different positions relative to the road in each landscape type (Hint = hinterland). Different letters denote significant differences between landscape types at each position. Results are from separate one-factor Anova for each position between landscape types that followed overall significant Manova results for interaction effects.

3.3.2.3 Soil chemistry, compaction and moisture

Significant differences were found for soil variables between positions ($F_{(33,72)} = 3.57$, $p < 0.001$; natural-log transformations used for exchangeable Ca, available P and EC). Results from separate two-factor Anova confirmed position differences for most of the dependent variables, with the exception of exchangeable Na and pH (Table 3.7). Generally, variables showed no differences between road edge and table drain positions and fence and hinterland positions, with higher values recorded at the road edge and table drain positions for exchangeable Ca and EC, and higher values recorded at the fence and hinterland positions for exchangeable K, active C, available P and nitrate (Table 3.8). Exchangeable Mg, compaction and soil moisture did not show the same patterns of differences between positions as the other variables (Table 3.8), but showed lower values of exchangeable Mg at the road edge and hinterland, lower values of compaction at the table drain, and higher values of soil moisture at the road edge compared to other positions.

Table 3.7: Results from 2-factor Anova for soil variables. Natural-log transformations were used for exchangeable Ca, available P and EC.

Variable	Landscape type		Position		Landscape type*Position	
Exchangeable Ca	$F_{(1,32)} = 1.47$	$p = 0.234$	$F_{(3,32)} = 16.02$	$p < 0.001$	$F_{(3,32)} = 2.71$	$p = 0.061$
Exchangeable K	$F_{(1,32)} = 21.31$	$p < 0.001$	$F_{(3,32)} = 20.81$	$p < 0.001$	$F_{(3,32)} = 0.41$	$p = 0.745$
Exchangeable Mg	$F_{(1,32)} = 30.00$	$p < 0.001$	$F_{(3,32)} = 3.92$	$p = 0.017$	$F_{(3,32)} = 14.47$	$p < 0.001$
Exchangeable Na	$F_{(1,32)} = 4.72$	$p = 0.037$	$F_{(3,32)} = 1.44$	$p = 0.249$	$F_{(3,32)} = 12.52$	$p < 0.001$
Active C	$F_{(1,32)} = 0.04$	$p = 0.853$	$F_{(3,32)} = 33.25$	$p < 0.001$	$F_{(3,32)} = 2.03$	$p = 0.130$
Available P	$F_{(1,32)} = 1.34$	$p = 0.256$	$F_{(3,32)} = 63.65$	$p < 0.001$	$F_{(3,32)} = 3.33$	$p = 0.032$
Nitrate	$F_{(1,32)} = 4.92$	$p = 0.034$	$F_{(3,32)} = 8.52$	$p < 0.001$	$F_{(3,32)} = 1.77$	$p = 0.172$
pH	$F_{(1,32)} = 8.65$	$p = 0.006$	$F_{(3,32)} = 1.84$	$p = 0.161$	$F_{(3,32)} = 5.50$	$p = 0.004$
EC	$F_{(1,32)} = 17.13$	$p < 0.001$	$F_{(3,32)} = 8.91$	$p < 0.001$	$F_{(3,32)} = 4.99$	$p = 0.006$
Compaction	$F_{(1,32)} = 19.98$	$p < 0.001$	$F_{(3,32)} = 10.22$	$p < 0.001$	$F_{(3,32)} = 5.48$	$p = 0.004$
Soil moisture	$F_{(1,32)} = 3.74$	$p = 0.062$	$F_{(3,32)} = 9.44$	$p < 0.001$	$F_{(3,32)} = 5.35$	$p = 0.004$

Table 3.8: Mean values (+ 1 SE) for soil variables for each position, nature of differences (from two-factor Anova between positions. Underlines indicate no differences; E = road edge, D = table drain, F = fence, H = hinterland), and order of variable influence in discriminating positions.

Variable	Edge	Table drain	Fence	Hinterland	Differences	Order of influence
Exchangeable Ca (mg/kg)	4431.10 ± 526.46	3699.22 ± 437.31	2049.40 ± 184.87	2040.36 ± 250.39	<u>ED</u> <u>FH</u>	4
Exchangeable K (mg/kg)	270.31 ± 41.33	333.89 ± 39.09	634.12 ± 62.38	663.72 ± 69.21	<u>ED</u> <u>FH</u>	3
Exchangeable Mg (mg/kg)	337.96 ± 82.29	446.24 ± 39.90	464.40 ± 26.76	385.68 ± 30.29	<u>EH</u> <u>HDF</u>	10
Exchangeable Na (mg/kg)	74.19 ± 28.00	119.96 ± 28.76	106.00 ± 23.37	87.82 ± 12.58	<u>EDFH</u>	11
Active C (mg/kg)	85.00 ± 8.45	70.50 ± 8.02	170.60 ± 8.56	176.50 ± 13.63	<u>ED</u> <u>FH</u>	2
Available P (mg/kg)	2.20 ± 0.35	1.39 ± 0.15	9.01 ± 1.04	9.27 ± 0.96	<u>DE</u> <u>FH</u>	1
Nitrate (mg/kg)	5.92 ± 0.96	4.87 ± 0.74	10.03 ± 0.71	8.81 ± 1.11	<u>ED</u> <u>FH</u>	5
pH (pH/w)	8.40 ± 0.18	8.68 ± 0.15	8.35 ± 0.11	8.34 ± 0.15	<u>EDFH</u>	9
EC (dS/m)	0.73 ± 0.27	0.34 ± 0.14	0.10 ± 0.01	0.10 ± 0.02	<u>ED</u> <u>FH</u>	6
Compaction (Kg/cm ²)	6.63 ± 1.23	3.47 ± 0.4	7.06 ± 0.41	6.77 ± 0.53	<u>D</u> <u>EFH</u>	8
Soil moisture (mm ³ /mm ³)	0.12 ± 0.02	0.09 ± 0.006	0.07 ± 0.006	0.08 ± 0.003	<u>E</u> <u>DFH</u>	7

Like the majority of separate 2-factor Anova for the dependent variables, discriminant analysis separated the road edge and table drain positions from the fence and hinterland positions (one variate significant: Wilks' lambda = 0.022, df = 33, p < 0.001; different signs of functions at group centroids) (Figure 3.12). Of the variables, available P was found to be most responsible for discriminating positions, followed by active C, exchangeable K, exchangeable Ca, nitrate, EC, soil moisture, compaction, pH, exchangeable Mg and exchangeable Na (Table 3.8).

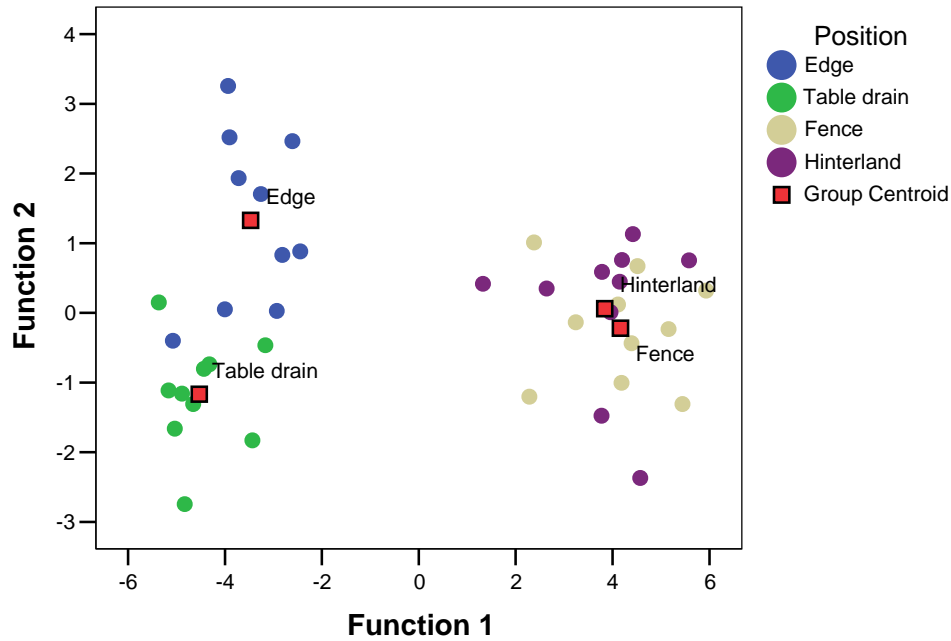


Figure 3.12: Plot of canonical discriminant functions showing separation of road edge and table drain positions from fence and hinterland positions. Only one discriminant function (Function 1) is significant.

Interactions between landscape type and position were also present for soil variables ($F_{(33,72)} = 2.29$, $p = 0.002$), and results of two-factor Anova showed significant interactions for exchangeable Mg, exchangeable Na, available P, pH, EC, compaction and soil moisture (Table 3.7). Follow-up one-factor Anova indicated that the majority of landscape type differences occurred at the road edge position, with some differences also occurring at the table drain and fence positions. Values for exchangeable Mg, exchangeable Na and pH were higher in the floodplains, while values for available P, EC, compaction and soil moisture were higher in the hills (Table 3.9).

Permutational Manova confirmed the results found by the Manova for soil variables, even though the ratio of the number of dependent variables to the number of observations was high in the Manova. Thus, highly significant differences were found between landscape types ($F_{(1,32)} = 31.66$, $p < 0.001$), positions ($F_{(3,32)} = 15.82$, $p < 0.001$, road edge and table drain different from fence and hinterland positions), and for landscape type*position interactions ($F_{(3,32)} = 4.07$, $p < 0.001$). Results from permdisp showed that these differences were not a result of differences in dispersion among groups (landscape

types: $F_{(1,32)} = 0.03$, $p = 0.865$; positions: $F_{(3,32)} = 1.37$, $p = 0.271$; landscape type*position interactions: $F_{(3,32)} = 0.97$, $p = 0.421$).

Table 3.9: Results from separate one-factor Anova at each position between landscape types for soil variables that showed significant landscape type*position interactions in original two-factor Anova. Landscape types which showed significantly higher values and trends for higher values (in brackets) are shown. Natural-log transformations were used for available P and EC.

Variable	Edge	Table drain	Fence	Hinterland
Exchangeable Mg	$F_{(1,8)}=42.54$, $p<0.001$ Floodplains	$F_{(1,8)}=16.79$, $p=0.003$ Floodplains	$F_{(1,8)}=1.42$, $p=0.267$	$F_{(1,8)}=0.73$, $p=0.419$
Exchangeable Na	$F_{(1,8)}=8.65$, $p=0.019$ Floodplains	$F_{(1,8)}=23.05$, $p=0.001$ Floodplains	$F_{(1,8)}=8.47$, $p=0.020$ Hills	$F_{(1,8)}=0.88$, $p=0.376$
Available P	$F_{(1,8)}=6.78$, $p=0.031$ Hills	$F_{(1,8)}=0.23$, $p=0.647$	$F_{(1,8)}=3.05$, $p=0.119$	$F_{(1,8)}=1.32$, $p=0.284$
pH	$F_{(1,8)}=24.59$, $p=0.001$ Floodplains	$F_{(1,8)}=13.52$, $p=0.006$ Floodplains	$F_{(1,8)}=0.33$, $p=0.582$	$F_{(1,8)}=0.15$, $p=0.711$
EC	$F_{(1,8)}=15.03$, $p=0.005$ Hills	$F_{(1,8)}=4.06$, $p=0.079$ (Hills)	$F_{(1,8)}=0.44$, $p=0.524$	$F_{(1,8)}=0.40$, $p=0.544$
Compaction	$F_{(1,8)}=16.22$, $p=0.004$ Hills	$F_{(1,8)}=1.83$, $p=0.213$	$F_{(1,8)}=0.85$, $p=0.384$	$F_{(1,8)}=2.73$, $p=0.137$
Soil moisture	$F_{(1,8)}=7.54$, $p=0.025$ Hills	$F_{(1,8)}=2.06$, $p=0.189$ (Hills)	$F_{(1,8)}=1.07$, $p=0.331$	$F_{(1,8)}=0.27$, $p=0.620$

3.3.3 Relationship between vegetation and soil variables

Regressions using soil components against vegetation variables produced results for relationships between soil and vegetation greenness for all plant groups, however, fewer relationships were found for relationships between soil and vegetation cover and height (only found for forbs and copperburrs) (Table 3.10). Plant groups showed differences in their relationships with soil components, with copperburr greenness negatively influenced by soil component 1 (pH, exchangeable Mg, exchangeable Na and compaction); pasture, grass, forb and copperburr greenness positively influenced by soil component 2 (EC, exchangeable Ca and soil moisture); and copperburr cover, height and greenness positively, and forb cover, height and greenness negatively influenced by soil component 3 (nitrate, Active C, available P, and exchangeable K) (Table 3.10, Table A3.10 in Appendix 3 for model equations).

Table 3.10: Results from regressions examining relationships between vegetation and soil variables (significant results only). Adjusted R^2 values are shown. Square-root transformations were used for copperburr cover, grass height, and grass and forb greenness values and natural-log transformations were used for grass and forb cover, and pasture and forb height values.

Variable	R^2	F values	P values	Standardised Beta values	
Forb cover	0.08	$F_{(1,38)} = 4.55$	$p = 0.039$	Component 3	-0.33
Copperburr cover	0.45	$F_{(1,38)} = 32.70$	$p < 0.001$	Component 3	0.68
Forb height	0.17	$F_{(1,38)} = 8.98$	$p = 0.005$	Component 3	-0.44
Copperburr height	0.38	$F_{(1,38)} = 24.49$	$p < 0.001$	Component 3	0.63
Pasture greenness	0.38	$F_{(1,38)} = 24.85$	$p < 0.001$	Component 2	0.63
Grass greenness	0.12	$F_{(1,38)} = 6.35$	$p = 0.016$	Component 2	0.38
Forb greenness	0.21	$F_{(2,37)} = 6.15$	$p = 0.005$	Component 3	-0.38
				Component 2	0.32
Copperburr greenness	0.46	$F_{(3,36)} = 12.03$	$p < 0.001$	Component 2	0.53
				Component 3	0.34
				Component 1	-0.33

Component 1 is positively correlated with pH, and exchangeable Mg and Na, and negatively with compaction. Component 2 is positively correlated with EC, exchangeable Ca and soil moisture. Component 3 is positively correlated with nitrate, Active C, available P, and exchangeable K.

3.3.4 Relative importance of spatio-temporal factors influencing vegetation variables

Table 3.11 shows the overall results for final models with Table 3.12 showing the model terms significantly influencing vegetation variables (see Table A3.11 in Appendix 3 for non-significant results). The spatio-temporal factors most influential on vegetation variables differed for the different plant groups (Table 3.12). What was clear, though, was that vegetation cover and height were generally more strongly influenced by spatial rather than temporal factors whereas vegetation greenness was more strongly influenced by temporal rather than spatial factors (Table 3.12). Of the temporal factors, negative relationships between days since rain and temperature with vegetation variables were generally found, while positive relationships between rainfall and vegetation variables generally occurred (exceptions to this pattern were found for pasture and grass height).

Table 3.11: Overall results from GLM examining the effects of spatio-temporal factors on vegetation variables. Adjusted R^2 values are shown. Values for copperburr greenness were square-root transformed and values for grass greenness natural-log transformed.

Variable	R^2	F values	P values
Pasture cover	0.71	$F_{(8,55)} = 20.13$	$p < 0.001$
Grass cover	0.83	$F_{(9,54)} = 34.05$	$p < 0.001$
Forb cover	0.67	$F_{(2,61)} = 63.54$	$p < 0.001$
Copperburr cover	0.43	$F_{(5,58)} = 10.60$	$p < 0.001$
Pasture height	0.57	$F_{(8,55)} = 11.52$	$p < 0.001$
Grass height	0.89	$F_{(7,56)} = 76.05$	$p < 0.001$
Forb height	0.36	$F_{(5,58)} = 8.17$	$p < 0.001$
Copperburr height	0.19	$F_{(3,60)} = 5.96$	$p < 0.001$
Pasture greenness	0.75	$F_{(5,58)} = 38.85$	$p < 0.001$
Grass greenness	0.79	$F_{(9,54)} = 28.00$	$p < 0.001$
Forb greenness	0.67	$F_{(6,57)} = 22.31$	$p < 0.001$
Copperburr greenness	0.38	$F_{(8,55)} = 5.85$	$p < 0.001$

Table 3.12: Model terms influencing vegetation variables. Values for copperburr greenness were square-root transformed and values for grass greenness natural-log transformed.

Variable	Model terms	F values	P values
Pasture cover	Landscape type	$F_{(1,59)} = 46.03$	$p < 0.001$
	Days since last rain	$F_{(1,55)} = 42.62$	$p < 0.001$
	Landscape type*Position	$F_{(6,55)} = 4.18$	$p = 0.002$
Grass cover	Landscape type	$F_{(1,59)} = 58.02$	$p < 0.001$
	Landscape type*Position	$F_{(3,54)} = 30.06$	$p < 0.001$
	Rainfall (3 months)	$F_{(1,54)} = 23.79$	$p < 0.001$
	Position	$F_{(3,59)} = 3.06$	$p = 0.035$
	Temperature (1 week)	$F_{(1,54)} = 4.47$	$p = 0.039$
Forb cover	Landscape type	$F_{(1,61)} = 82.52$	$p < 0.001$
	Days since last rain	$F_{(1,61)} = 44.55$	$p < 0.001$
Copperburr cover	Landscape type	$F_{(1,58)} = 23.68$	$p < 0.001$
	Position	$F_{(3,58)} = 8.18$	$p < 0.001$
	Rainfall (2 weeks)	$F_{(1,58)} = 4.77$	$p = 0.033$
Pasture height	Landscape type	$F_{(1,59)} = 22.86$	$p < 0.001$
	Landscape type*position	$F_{(3,55)} = 10.51$	$p < 0.001$
	Rainfall (1 week)	$F_{(1,55)} = 9.47$	$p = 0.003$
	Position	$F_{(3,59)} = 2.86$	$p = 0.045$
Grass height	Landscape type	$F_{(1,59)} = 80.34$	$p < 0.001$
	Landscape type*position	$F_{(3,56)} = 57.06$	$p < 0.001$
	Position	$F_{(3,59)} = 4.48$	$p = 0.007$
Forb height	Landscape type	$F_{(1,58)} = 21.32$	$p < 0.001$
	Position	$F_{(3,58)} = 5.07$	$p = 0.003$
	Rainfall (2 weeks)	$F_{(1,58)} = 4.33$	$p = 0.042$
Copperburr height	Position	$F_{(3,60)} = 5.96$	$p < 0.001$
Pasture greenness	Temperature (2 weeks)	$F_{(1,58)} = 45.00$	$p < 0.001$
	Rainfall (3 months)	$F_{(1,58)} = 22.52$	$p < 0.001$
	Position	$F_{(3,58)} = 22.32$	$p < 0.001$
Grass greenness	Rainfall (2 weeks)	$F_{(1,54)} = 38.49$	$p < 0.001$
	Landscape type*position	$F_{(3,54)} = 28.44$	$p < 0.001$
	Landscape type	$F_{(1,59)} = 15.13$	$p < 0.001$
	Position	$F_{(3,59)} = 3.76$	$p = 0.015$
	Temperature (1 week)	$F_{(1,54)} = 4.61$	$p = 0.036$
Forb greenness	Temperature (1 month)	$F_{(1,57)} = 32.71$	$p < 0.001$
	Rainfall (3 months)	$F_{(1,57)} = 23.47$	$p < 0.001$
	Position	$F_{(3,57)} = 10.29$	$p < 0.001$
	Landscape type	$F_{(1,57)} = 5.01$	$p = 0.029$
Copperburr greenness	Temperature (3 months)	$F_{(1,55)} = 22.18$	$p < 0.001$
	Landscape type*position	$F_{(3,55)} = 3.34$	$p = 0.026$
	Landscape type	$F_{(1,59)} = 4.83$	$p = 0.032$

3.3.5 Relationship between soil moisture and spatio-temporal factors

Soil moisture was influenced by both temporal and spatial factors, with rainfall explaining most of the variation (positive relationship), followed by position (higher at the edge), landscape type (higher in the hills), and temperature (negative relationship) (Table 3.13). Trends for landscape type*position interactions and last rain amount (positive relationship) influencing soil moisture levels also existed.

Table 3.13: Results from GLM examining effects of factors and variables on soil moisture. The final model accounted for 55 % of variation ($\text{Adj } R^2 = 0.510$, $F_{(6,49)} = 12.35$, $p < 0.001$).

Model Terms	F values	P values
Rainfall (2 months)	$F_{(1,49)} = 21.47$	$p < 0.001$
Position	$F_{(3,49)} = 4.72$	$p = 0.006$
Landscape type	$F_{(1,49)} = 6.38$	$p = 0.015$
Temperature (2 weeks)	$F_{(1,49)} = 5.15$	$p = 0.028$
Landscape type*position	$F_{(3,46)} = 2.64$	$p = 0.061$
Last rainfall amount	$F_{(1,48)} = 2.90$	$p = 0.095$

3.3.6 Comparisons of greenness between mown and unmown quadrats

Apart from grasses, where unmown quadrats in the hills were significantly higher in greenness compared to mown quadrats in the hills ($t = -2.68$, $df = 11$, $p = 0.021$; unmown quadrats = 54.37 ± 6.09 % green, mown quadrats = 32.83 ± 3.65 % green), no other plant group exhibited significant differences in greenness between mown and unmown quadrats when entire datasets were used in analyses (Tables A3.12 to A3.15 in Appendix 3). However, there was a trend for higher pasture greenness in mown quadrats in the floodplains compared to unmown quadrats in the floodplains ($t = 1.79$, $df = 14$, $p = 0.095$; mown quadrats = 60.90 ± 4.38 % green, unmown quadrats = 50.99 ± 4.49 % green). Similarly, no differences in greenness were found between mown and unmown quadrats for any plant group when datasets from the first and second surveys were used in analyses.

A significant difference between mown and unmown quadrats was found for pasture greenness in the floodplains when the dataset from the last survey was used in analysis ($t = 2.78$, $df = 14$, $p = 0.015$), with higher greenness values found in mown

quadrats (mown quadrats = 60.16 ± 6.09 % green, unmown quadrats = 43.47 ± 5.40 % green). This result was most likely influenced by forbs in the floodplains, which showed trends for higher greenness in mown quadrats ($t = 2.03$, $df = 12$, $p = 0.065$; mown quadrats = 63.27 ± 6.71 % green, unmown quadrats = 49.10 ± 7.33 % green) during the same period.

3.3.7 Comparisons of plant diversity between mown and unmown quadrats

A list of the species found in the mown and unmown quadrats is provided in Table A3.16 in Appendix 3. No differences in diversity were found between mown and unmown quadrats when entire datasets or datasets from the first and second vegetation surveys were used in analyses (Table A3.17 in Appendix 3). However, when the dataset from the last survey was used in analyses, significant differences were found (landscape types combined: $p = 0.035$, hills: $p = 0.039$), with mown quadrats showing higher diversity indices compared to unmown quadrats (landscape types combined: $D = 25.18$ compared to 16.13 ; hills: $D = 16.26$ compared to 9.21 for mown and unmown quadrats respectively).

3.4 Discussion

This study showed that an arid-zone road modified the immediate road verge and found that the extent of these modifications occurred at slightly different scales on the physical, chemical, and biological environments. The study revealed that landscape types influenced the effects of the road, which complicated interpretations of the effects of an arid-zone road on the immediate road verge, and found that the underlying causes for enhanced vegetation quality at the roadside differed from those identified in other ecosystems. In addition, management of the roadside vegetation by mowing influenced vegetation quality and diversity differently across landscapes. These results highlight the importance of examining the effects of roads and road management practices on habitats across landscapes and ecosystems. Understanding how the effects of roads and road management practices impact different landscapes and ecosystems is essential for designating the best locations for new roads to conserve natural habitats and for shaping road management frameworks for existing roads to maintain biodiversity.

3.4.1 Effects of the road on vegetation and limitations of some vegetation measures

Comparisons of vegetation at both fine and local scales were useful in determining the extent and nature of habitat modification by the road. This is because while both methods were designed to detect differences in vegetation in relation to the road in two landscape types, comparisons at the fine-scale gave information for actual patterns occurring at the roadside with increasing distance from the road edge while comparisons at the local-scale allowed for the examination of the wider effects of the road on the surrounding landscape. In addition, fine-scale comparisons distinguished the road as responsible for creating edge effects from another type of disturbance, since comparisons between metres within monitoring areas at the fence (slightly disturbed) and hinterland (little disturbed) showed no differences for the majority of vegetation variables and plant groups. However, while the study attempted to compare vegetation at three levels (plant cover, structure and quality via measurements of plant cover, height and greenness) and subsequently relate patterns of vegetation at these levels with spatio-temporal factors, only one vegetation variable (vegetation greenness) was useful for detecting real patterns of vegetation change at both fine and local scales, which could also be related to spatio-temporal factors.

There are two possible reasons as to why measurements of vegetation cover and height were not helpful in this study. The first is that arid-zone plants have a tendency to remain intact after senescence. Thus, high values of cover and height would not necessarily reflect increases in plant cover and growth as plants would have the same values regardless of their state (alive or dead). This was clearly illustrated in the fine-scale comparisons of plant growth at the roadside where peaks occurred in pasture and grass cover and grass height around 9-15 m (Figures 3.3-3.5). These peaks probably represented plants that had grown during favourable conditions and then died, since plant greenness (high values of which would indicate plant growth) in the same area did not also increase for any plant group (Figure 3.6 for pasture greenness).

Secondly, the study grouped plants into broad categories without any regard for their life forms (annual or perennial). This probably affected comparisons of plant cover and height at both the fine and local scales. At the fine-scale, the cover of forbs, grasses and pasture, and the height of grasses were lower at the road edge compared to metre intervals

further from the road along roadside transects in the floodplains (Tables 3.3 and 3.4). This may have been due to the presence of smaller annual plants (for example *Enneapogon* species and *Chamaesyce drummondii*) at the road edge compared to larger perennial plants (for example *Astrebla* species and *Brachycome ciliaris*) further from the road. At the local-scale, the cover of pasture and grasses and the height of grasses were higher with increasing distance from the road in the floodplains, with no such patterns displayed in the hills (Figures 3.8 and 3.9). These patterns were most likely due to the presence of perennial *Astrebla* species, which were not only present exclusively in the floodplains, but also present further from the road edge in the floodplains. This study does not have any quantitative data to support the presence and distribution of annual or perennial plants with distance from the road, but the presence and distribution of annual and perennial plants, particularly the perennial *Astrebla* species in the floodplains can be seen clearly in Figure 3.13. In addition, studies of the effects of roads on plants in other arid areas (e.g. Mojave desert) have shown that annual plants colonise road edges more readily than perennial plants (Brooks and Lair, 2005) and that re-colonisation of the roadside by perennial plants after their removal following road construction does not occur for long periods of time (Lovich and Bainbridge, 1999).

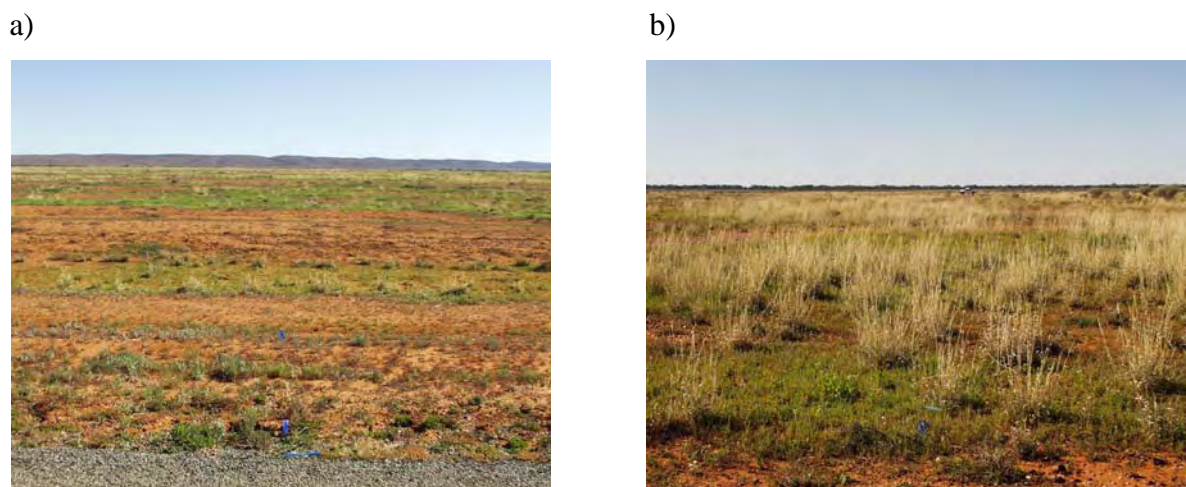


Figure 3.13: Photo along a road transect showing plants with annual life forms (a) and along a hinterland transect showing plants with perennial life forms (b) in the floodplains.

As measurements of plant cover and height were not useful for examining the effects of the road and other spatio-temporal factors on arid-zone plant growth, further

discussions will focus on the effects of the road and other spatio-temporal factors on the quality (greenness) of arid-zone plants. This will be discussed in more detail following a discussion of the effects of the road on soil variables.

3.4.2 Effects of the road on soil

The road exerted a wide influence from its edge on the majority of soil variables. Where the road significantly influenced soil variables, differences to the road edge were generally from as far as 50 m from the road (from the monitoring areas at the fence and onwards into the hinterland). A noteworthy exception to this generalisation was soil moisture, where values at the road edge were also significantly different to those at the table drain. The wide area over which the road influenced soil variables in this study contrasts to the areas found in other studies, where concentrations of salts and nutrients were significantly different to the road edge at much closer distances from the road edge (salts: at 15 m in McBean and Al-Nassri's (1987) study and 6 m in Spencer and Port's (1988) study; nutrients: from 6 m in Spencer and Port's (1988) study).

Also in contrast with the findings of other studies (other than Norton and Stafford Smith's (1999) study in central arid Australia) is the finding that many soil variables, particularly soil nutrients, had lower concentrations at the roadside compared to areas further from the road. Generally, roads concentrate nutrients, salts and pollutants along their margins since nutrients, salts and pollutants originating from motor vehicles, the road surface itself, and roadside management are transported short distances from roads through the air or in runoff (Forman *et al.*, 2003). An explanation for the observed patterns in this and Norton and Stafford Smith's (1999) study may lie in the modifications made to the physical and chemical environments around the road during road construction and processes unique to the arid zone. When the study road was built, the upper layers of soil at the sides of the road (up to 20 metres away from the road) were removed to not only raise the height of the road before the road surface was compacted and sealed with bitumen, but also to create a table drain alongside the road (G. Baker, NSW Roads and Traffic Authority, Western Division, pers comm.; see section 2.2.1.1 for more details on road construction). In the arid zone, nutrients are highly concentrated in the upper layers of the soil profile, much more so than in soil profiles in other ecosystems (Charley and Cowling, 1968; Friedel,

1981; West, 1991). This is because soil biota, which facilitate the accumulation of organic matter and soil nutrients and together make up a biological soil crust in the arid-zone, are more highly concentrated at the upper layers of the soil in the arid-zone due to the shallow depths of soil wetting in arid areas (biological activity can only occur in the presence of water, Charley and Cowling, 1968; Whitford, 1996; Belnap *et al.*, 2003). As such, removal of even the top 5 cm of the soil profile also removes the nutrients present there (Charley and Cowling, 1968; Friedel, 1981). Continuing low levels of nutrients would be maintained at the road edge and table drain after road construction as the subsequent recovery of previous soil structure, formation of biological soil crusts, and accumulation of nutrients are extremely slow in arid lands (Charley and Cowling, 1968; Lovich and Bainbridge, 1999). Any nutrients that might accumulate from the breakdown of litter by soil biota (Friedel, 1981) would be rapidly used up by plants, further preventing a buildup of nutrients at the road edge.

Removal of the top layer of the soil profile is less likely to have as strong an effect on salt levels in the arid zone. This is because unlike nutrients, salts leach through the soil profile rather than accumulate in the top layers of the soil profile. Salts do not move deep into the soil profile, however; rather salts in arid lands accumulate at relatively shallow depths due to the shallow infiltration depths of water (Cloudsley-Thompson and Chadwick, 1964; West, 1991). It is not surprising then, that this study did not find differing levels of sodium or magnesium between positions relative to the road, nor that the study found higher levels of calcium at the roadside compared to areas further from the road. The study did find lower levels of potassium at the roadside compared to areas further from the road which contrasted with the pattern found for the other salts. This result may have been associated with potassium's value to plants: potassium is an essential macronutrient for plants (Gourley, 1999) and its uptake from the soil increases with plant activity (West, 1991). Since plant activity was high at the roadside (as evidenced by the generally higher plant quality at the roadside), it is possible that plants were removing potassium from the soil in this area. The technique used to estimate EC may have confounded the values for EC in this study. The method used (a simple 1:5 water extraction method) is extremely biased when there are high levels of calcium present (J. Triantafilis, School of Biological, Earth and Environmental Sciences, UNSW, pers comm.), and thus results may not have been an

accurate representation of actual saltiness. Sodium is a better measure of saltiness; if levels of sodium were instead used as a measure of saltiness, roadside areas would show no differences in saltiness compared to areas further from the road.

Results found for soil physical properties (moisture and compaction) with distance from the road are compatible with our knowledge of the effects of roads (Forman *et al.*, 2003) and the process of arid-zone road construction. Higher levels of soil moisture at the road edge relative to areas further from the road were most likely due to water running off the impermeable road surface towards its edges, resulting in higher amounts of water being received at the road edge compared to the other areas not receiving extra runoff (Norton and Stafford Smith, 1999). Higher soil compaction at the road edge compared with in the table drain was probably the result of road construction, where soils underneath the road and at its edge were compacted before the road was sealed with bitumen. Findings that soil compaction were no different at the road edge compared to areas further from the road at the fence and hinterland areas may have been due to soils at the fence and hinterland areas remaining undisturbed by road construction and hence retaining soil crusts. Soil crusts increase soil stability (Graetz and Tongway, 1986; Belnap *et al.*, 2003) and this may have affected measurements of soil compaction.

The concentrations and properties of some soil variables were influenced by landscape type which complicated interpretations of the overall effect of the road. Soils at the road edge were more compacted in the hills than in the floodplains (Table 3.9). This was most likely due to the extra layer of gravel used in road construction in the hills but not in the floodplains (G. Baker, NSW Roads and Traffic Authority, Western Division, pers comm.; see section 2.2.1.1 for more details on road construction). The differing effect of position relative to the road on soil moisture levels in the two landscape types may have been influenced by levels of magnesium and sodium. Levels of magnesium and sodium were higher at the roadside in the floodplains compared to in the hills, with levels of magnesium also remaining relatively constant between areas relative to the road in the floodplains. High levels of magnesium and sodium decrease soil stability and hence the ability of water to infiltrate through the soil (Cloudsley-Thompson and Chadwick, 1964; Voortman *et al.*, 2002). This may account for higher soil moisture levels at the roadside in the hills compared to in the floodplains and the more constant soil moisture levels across all

positions relative to the road in the floodplains. Furthermore, higher soil moisture levels at the roadside in the hills and more constant soil moisture levels at all positions relative to the road in the floodplains may have been due to more water being channeled onto the road from roadside cuttings that were present in the hills but absent in the floodplains (see section 2.2.1.4 for more details). Higher levels of phosphorus at the road edge in the hills compared to the floodplains are more difficult to account for. Phosphorus was possibly transported in water to the road edge in the hills as the movements of nutrients are usually closely associated with water (Harrington *et al.*, 1984; James *et al.*, 1995). This explanation loses strength though, with the finding that no such differences were found for nitrogen and active carbon (an index for soil quality; Knopp *et al.*, 2000) at this area. In fact, examination of the data for phosphorus suggests that the significant interaction results may not have been accurate (Type 1 error) as patterns at the positions relative to the road in the hills closely mirrored those in the floodplains (Hills: road edge = 2.9 ± 0.5 , table drain = 1.4 ± 0.2 , fence = 7.4 ± 1.5 , hinterland = 10.1 ± 1.0 ; Floodplains: road edge = 1.5 ± 0.3 , table drain = 1.3 ± 0.2 , fence = 10.7 ± 1.1 , hinterland = 8.4 ± 1.7).

3.4.3 Effects of the road on vegetation quality and the relationship between vegetation quality and spatio-temporal factors

Two clear outcomes of the results discussed so far are that the road influenced soil properties, and that landscape type interacted with road effects. The possible reasons for these results have just been discussed. To understand the reasons for the effects of the road on plant quality, however, one must consider the relationships between plant quality and soil variables, between plant quality and larger spatio-temporal factors, and between soil moisture and spatio-temporal factors. This study showed that temporal factors (temperature and rainfall) had stronger influences on plant quality than spatial factors (distance from the road, landscape type and their interactions) (Table 3.12), but that spatial factors also regulated the availability of water in the soil (Table 3.13) that primarily influenced the quality of pasture, grasses and copperburrs (Table 3.10). In other words, water availability was the main driving force for enhancing plant quality, and the road influenced the quality of all vegetation groups through its effects on redistributing water. Thus, the different way in which the road distributed water across landscapes types was reflected by the different

patterns found for the quality of grasses and copperburrs in relation to the road across landscape types.

The patterns for the quality of neither pasture or forbs followed the pattern of soil moisture distribution. However, pasture quality was strongly influenced by soil moisture levels (Table 3.10), and showed trends for landscape type*position interactions ($p = 0.092$) such that patterns for pasture quality were similar to patterns for grasses and copperburrs across landscapes. The quality of forbs was most strongly influenced by nutrient levels, and this relationship was negative. It is difficult to account for this result: perhaps grouping forbs together into a single category complicated results since the group comprised of a diverse range of dicotyledons and consequently the correlation with nutrient levels was erroneous. After all, nutrients explained only 12 % of variation (of the 21% of variation explained; Table 3.10), and forb quality, like the quality of other plant groups, was also strongly influenced by temperature and rainfall in spatio-temporal analyses (Table 3.12). Relationships between soil moisture and forb greenness should nevertheless be made cautiously; in Witte's (2004) study, weak relationships between forb biomass and rainfall were found. She attributed this result to forbs being mainly annual in growth form, and other variables such as temperature may have been equally or more important to forbs as rainfall. Indeed, this study found that forb greenness correlated most strongly to ambient temperatures (Table 3.12).

This study's result of water mainly driving plant quality, plus findings of other arid-zone studies where water has also been the driving force for enhanced plant growth along roads (Lightfoot and Whitford, 1991; Lovich and Bainbridge, 1999; Norton and Stafford Smith, 1999; Brooks and Lair, 2005) contrast with the results of studies of the effects of roads in other ecosystems. In studies conducted by Port and Thompson (1980), Spencer and Port (1988), Spencer *et al.* (1988), and Angold (1997) there was evidence that higher soil nitrogen levels enhanced plant growth along roads, not water levels. The different underlying causes of enhanced plant quality at roadsides most probably reflect the factors important to plant growth in the different ecosystems. In the arid zone, the quality of vegetation is primarily driven by water availability (which is in turn influenced by rainfall patterns, soil characteristics, and topography), with nutrients a secondary influence (Noy-Meir, 1973; Westoby, 1980; Harrington *et al.*, 1984; Stafford Smith and Morton, 1990).

Additions of water via the re-distributing effects of roads therefore have a stronger influence on plant quality than nutrient additions (the effect of the study road did not increase nutrient levels though due to the process of arid-zone road construction discussed above). In many other ecosystems, nutrients are the limiting factor driving plant growth and additions of nutrients have a stronger influence on plant growth than additions of water. Thus, although there are many examples where roads enhance plant quality, the underlying causes for enhancement are related to both the effects of roads on distributing water and nutrients in different ecosystems, as well as an ecosystem's response to additional water and nutrients.

3.4.4 Effects of mowing on roadside vegetation quality and diversity

Besides the changes in vegetation at the roadside compared to areas further from the road, roadside vegetation was further influenced by management practices along the road, albeit slightly, with mowing increasing pasture quality in the floodplains and plant diversity in the hills. These results may be attributed to differences in the amounts of vegetation removed in mown quadrats, as well as differences in soil moisture levels in the two landscape types. In the hills, both mown and unmown quadrats had low initial plant cover so mowing had a minor effect on vegetation removal. This contrasted with the situation in the floodplains where plant cover along the road was high and mowing resulted in a major reduction in plant cover. Vegetation growth can be stimulated by the removal of plant matter (Cousins, 2006), so the differences in plant cover in mown and unmown quadrats in the floodplains may explain the significant difference in plant quality between the quadrats in this landscape type. The significantly higher plant diversity in mown quadrats relative to unmown quadrats in the hills but not in the floodplains may be due to the higher soil moisture levels present at the road edge in the hills compared to in the floodplains (Table 3.9). With water available to plants in both mown and unmown quadrats in the hills, water may not have been limiting; rather, nutrients may have limited the germination of new plant species in the hills. As nutrients from plant material are broken down by micro-organisms in the soil in the presence of water (Friedel, 1981), and excised plant material was present in the mown quadrats from mowing, more nutrients may have been available to plants in mown quadrats relative to unmown quadrats in the hills, accounting for the greater plant

diversity result. By contrast, soil moisture levels were low along the road in the floodplains. Even if nutrients were higher in mown quadrats, nutrient additions would not have stimulated the germination of new plant species in the floodplains until water became less limiting.

3.4.5 Management implications

The larger spatial scale of the study road's influence on roadside vegetation and soils compared to those found in other studies confirmed the sensitivity of arid areas to resource additions (Noy-Meir, 1974; Stafford Smith and Morton, 1990) and disturbance (Charley and Cowling, 1968; Johns *et al.*, 1984; Lovich and Bainbridge, 1999). Although the influence of the road on vegetation extended to only 15 m from the road in this study, which is consistent with the distances found in other studies (5-10 m in Port and Thompson's (1980) study and 3.5-9 m in a study by Spencer *et al.* (1988)), the influence was greater on soils (see 3.4.2), and roads in arid zones may represent a major source of disturbance, with this disturbance having implications for the integrity of natural ecosystem functions. Large-scale disruptions of the natural patterning of arid landscapes could lead to degradation as healthy arid landscapes supporting a diversity of flora and fauna depend on water and nutrients being unevenly distributed at the small-scale (Stafford Smith and Morton, 1990; James *et al.*, 1995; Ludwig and Tongway, 1995). Any disruption to the spatial heterogeneity of landscapes may result in situations where landscapes lose their ability to capture, store and recycle nutrients (Lechmere-Oertel *et al.*, 2005). This study's findings of greater disruptions to the natural spatial patterning in the hills compared to in the floodplains therefore have implications for future road construction projects in arid ecosystems. If the aim is to reduce the impact of roads on arid ecosystems and to conserve the heterogeneous distribution of resources inherent in healthy arid ecosystems, roads should be constructed in floodplains where roads have a lesser impact on redistributing water. This strategy of avoiding particular areas in which roads are constructed is the most effective planning strategy designed to counteract the adverse impacts of roads on the natural landscape (Cuperus *et al.*, 1999).

Roadside management practices of mowing further complicated the response of vegetation along roadsides, increasing plant quality at the roadside in the floodplains which

otherwise would not have differed from the quality of plants further away from the road, and increasing plant diversity in the hills. Whether these results of management are beneficial or not depends on what is being considered. If conservation managers are concerned with conserving arid ecosystem functions and minimising the impact of roads on fauna, new roads should be constructed in the floodplains (as discussed above), and mowing of the roadside vegetation should not be performed. This is because increases in plant quality at the road edge as a result of mowing is likely to influence the distributions, behaviours and population dynamics of fauna (Spellerberg, 2002), possibly attracting fauna to the road edge and placing them at risk of being involved in collisions with passing vehicles (Lee *et al*, 2004). However, if managers are concerned with maintaining the diversity of plants along roadsides, then mowing roadside vegetation along existing roads in the hills might be considered.

3.4.6 Conclusion

In summary, the road increased vegetation quality and influenced the physical and chemical environments along its edge. Effects of the road on vegetation quality differed among the two arid landscape types. Combined with the different underlying cause of habitat modification compared to those identified in other ecosystems, this study highlights the need of investigating the effects of roads with consideration of the landscapes and ecosystems that roads traverse. The impact of road management practices also need to be investigated more thoroughly before road management frameworks can be created as effects are also likely to differ among landscapes and ecosystems.

Chapter 4

Kangaroo use of the road

4.1 Introduction

The effects of roads and traffic on fauna are many and varied (Andrews, 1990; Trombulak and Frissell, 2000; Spellerberg, 2002; Forman *et al.*, 2003). Some of their more significant effects are their impacts on faunal movements: fauna may change their movement patterns around roads such that their overall abundances decrease or increase in the vicinity of roads relative to the hinterland, and fauna may change their movement patterns across roads such that their frequencies of road crossings decrease or increase (Forman and Alexander, 1998; Spellerberg, 1998). Faunal movement changes around and across roads may impact the health and stability of populations, especially if shifts in movement are disproportionate between ages and sexes: movements away from roads (exacerbated by decreased movements across roads) may result in faunal populations on either side of roads becoming effectively fragmented (Reijnen *et al.*, 1995; Gerlach and Musolf, 2000; Dyer *et al.*, 2002; Shine *et al.*, 2004; Steen and Gibbs, 2004), and movements towards roads (exacerbated by increased movements across roads) may result in higher rates of faunal mortality as fauna come into contact with vehicles using roads (Rosen and Lowe, 1994; Aresco, 2005; Boarman and Sazaki, 2006; Ramp *et al.*, 2006). Moreover, altered faunal movements may have community-level impacts as species within communities may have different responses to roads (Meunier *et al.*, 1999a, b; Goosem, 2000, 2001; Vega *et al.*, 2000; Gutzwiller and Barrow, 2003; Lee *et al.*, 2004). These population and community effects are by no means local. Road networks now permeate ecosystems worldwide; thus faunal movement shifts around roads are of global significance and mitigating their negative impacts must occur on larger regional or landscape scales.

Possible causative factors for faunal movements away from, towards and across roads have been identified in previous road reviews (Trombulak and Frissell, 2000; Spellerberg, 2002; Forman *et al.*, 2003). For large mammals, movements shift away from roads mainly due to disturbances caused by vehicular traffic (volume, noise, movements,

and emissions; Grover and Thompson, 1986; McLellan and Shackleton, 1988; Czech, 1991; Thurber *et al.*, 1994; Mace *et al.*, 1996; Dyer *et al.*, 2002), but also due to the sudden convergence of contrasting microclimates and habitats around roads (Van Dyke *et al.*, 1986; Lovallo and Anderson, 1996). Movements shift toward roads due to higher levels of resources (e.g. food or shelter) that are available near roads compared to areas further from roads (Coulson, 1989; Lee *et al.*, 2004). Movements across roads occur if different resources are available on opposite sides of roads (Klöcker, 2002) or if large mammals are dispersing or migrating (Groot Bruinderink and Hazebroek, 1996; Dyer *et al.*, 2002). However, large mammal movements in relation to roads are affected to varying degrees by the scale of microclimate/microhabitat differences around roads, the levels of disturbance along roads, the width of roads, the resources available at roadsides and across roads, and the requirements to cross roads (e.g. to disperse or find mates) (Bennett, 1991; Van Langevelde and Jaarsma, 1995). Some of these factors, such as the scale of microhabitat changes and the availability of resources around and across roads are affected by the ecosystems traversed by roads. This is because roads interact with ecological processes unique to ecosystems and this influences the magnitude of road effects (Gutzwiller and Barrow, 2003; Brooks and Lair, 2005). Because of the influence of ecosystems on road effects that in turn influence large mammal movements, it is essential that the effects of roads on large mammal movements be investigated on an ecosystem-specific basis. Without this knowledge, mitigating the negative impacts of altered faunal movements around roads can not be undertaken with confidence.

An ecosystem in which large mammal movements are impacted by roads yet remains little studied is an arid ecosystem (Brooks and Lair, 2005). Roads in arid ecosystems may not be high in density, but arid ecosystems cover up to one third of the earth's land surface (Kinlaw, 1999), so are ecosystems in which the effects of roads should be studied. Arid-zone roads may influence large mammal movements in various ways. Firstly, the open nature of arid ecosystems may allow large mammals to detect disturbances from large distances so areas near roads could be perceived as risky (Lima and Dill, 1990) and avoided. Secondly, while microhabitat changes may not be as obvious around arid-zone roads compared to roads in more heavily vegetated ecosystems, simple factors like higher temperatures radiated from dark, sealed road surfaces compared to natural surfaces of a

higher albedo may attract or repel mammals depending on ambient conditions, as they have been found to do for small mammals (Goosem, 2000). Thirdly, vegetation at roadsides that are higher in quality and productivity compared to vegetation further from roadsides due to roads in arid areas channelling water toward roadside vegetation (Chapter 3; Lightfoot and Whitford, 1991; Lovich and Bainbridge, 1999; Norton and Stafford Smith, 1999; Lee *et al.*, 2004) could be used as a food resource by large mammalian herbivores (Coulson, 1989; Osawa, 1989; Lee *et al.*, 2004), especially since high quality forage of nutritional value are preferred over lower quality forage in arid herbivores such as kangaroos (Dawson and Ellis, 1994, 1996). Finally, water pooling on arid-zone roads could attract large mammals to roadsides as water is limiting in arid ecosystems (Noy-Meir, 1973; Harrington *et al.*, 1984; Stafford Smith and Morton, 1990).

Since arid-zone roads have the capacity to alter large mammal movements around them with potentially serious consequences on populations, the nature of large mammal movements around arid-zone roads should be known. Thus, this study focused on four kangaroo species in arid Australia and investigated their use of an arid-zone road. The aims were: 1) to determine temporal and spatial variation in density, near and away from an arid-zone road, for four sympatric kangaroo species 2) to relate such variation in kangaroo densities to factors such as species, age and sex, proximity to the road, traffic volume, and climate (especially rainfall), 3) to investigate variations in kangaroo movements across an arid-zone road, and 4) to relate these variations in kangaroo road crossings with temporal factors (especially rainfall).

4.2 Methods

4.2.1 Kangaroo density data

Weekly daytime (commencing at first light) and night-time (commencing 2 h after sunset) counts of kangaroos were conducted within 24 h of each other between March 2003 and November 2004 (83 weekly surveys altogether with 6 surveys forfeited due to poor weather conditions; see Table A4.1 in Appendix 4 for dates). Day and night counts were performed to obtain information about possible changes in kangaroo densities at different times of day. Both counts were conducted along two transects to obtain information for

densities relative to distance from the road: one along the 21.2 km study road (see section 2.2 for details) and the other along a parallel 10 km dirt track located approximately 500 m from the road (hereafter referred to as the hinterland transect). Since the hinterland transect was only about 3 m wide, not heavily compacted, and used infrequently by station staff (usually with motorbikes), both microhabitat changes at the interface of the transect with the surrounding landscape and disturbance levels from traffic were low. The hinterland transect was therefore assumed to represent the hinterland area in general (although it is recognised that there was still a low level of disturbance along the transect). In order to compare kangaroo densities between the two transects, only counts along the stretch of road parallel to the hinterland transect (also spanning 10 km) rather than along the entire road were considered in analysis (Figure 4.1) for weeks where data existed for both transects (total of 78 weeks during the day and 77 weeks during the night). Kangaroo counts that fell within equivalent road stretches were easily determined as the distances of these road sections from the start and end of the entire road transect were known. Unfortunately, there was no way of avoiding the problems of pseudo-replication in this study (see Hurlbert, 1984); marking individuals that had previously been counted so that they could be recognised in future counts was not feasible as this would have required tagging of kangaroos on a large-scale over a large area, and increasing the number of spatial replicates was impractical due to issues such as excessive travel time and limited access to the hinterland. However, some authors such as Oksanen (2001, 2004) do not consider pseudo-replication to be a major problem in large-scale community or ecosystem studies, and believe pseudo-replication to be preferable to increasing the number of spatial replicates (as spatial scales relevant for the predictions to be tested should not be sacrificed).

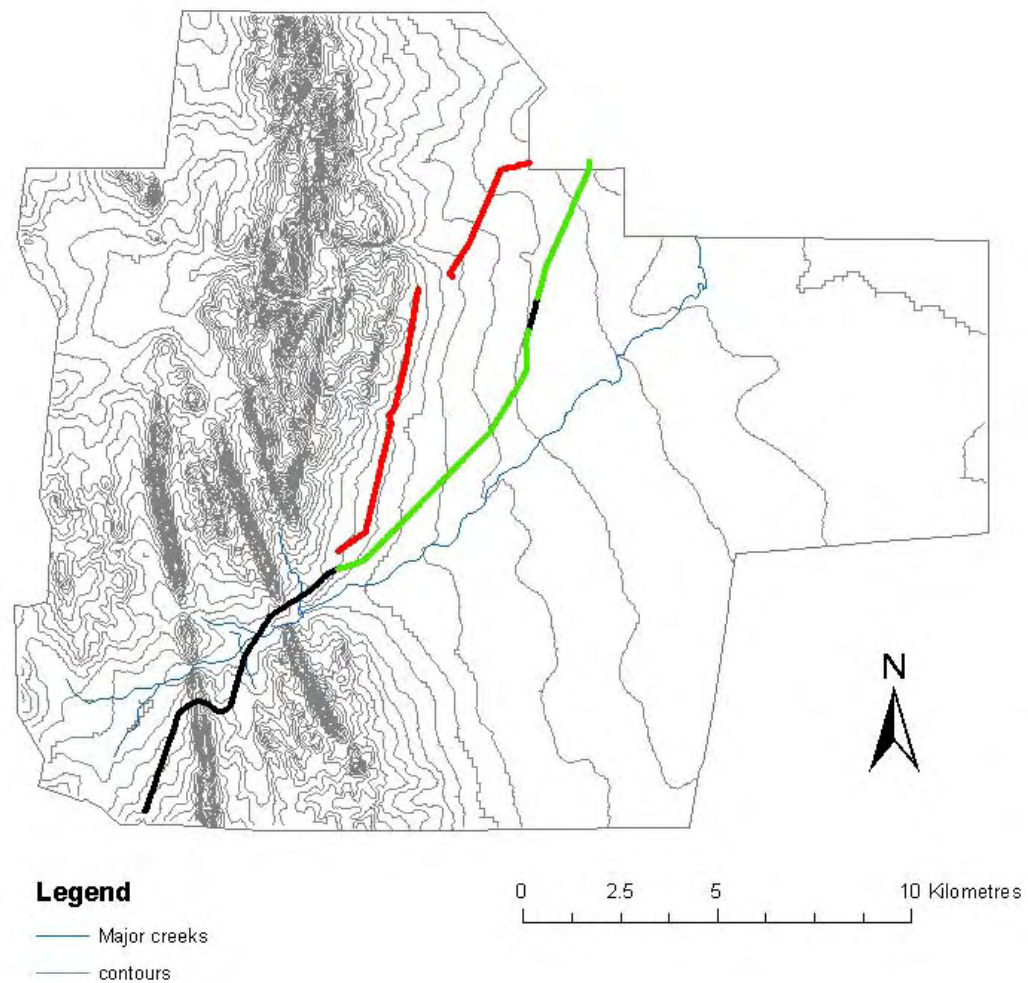


Figure 4.1: Topographic map of Fowlers Gap Arid Zone Research Station showing road and hinterland transects. Sections of road transect used for comparisons with hinterland transect are shown in green; remaining sections of Silver City Highway are shown in black; hinterland transect is shown in red.

Kangaroo population densities during the day were estimated using a line transect method. Line transect methods are more time-consuming compared to some other methods of density estimation, such as strip transect methods, since distance measurements from the observer must be recorded for detected objects. However, unlike strip transects where all objects in an area must be detected for accurate density estimates, some objects can be missed when using line transect methods (Southwell, 1989). Underlying the theory of distance sampling is the concept of a detection function, $g(y) = \text{probability}\{\text{detection} \mid \text{distance } y\}$ with detection usually decreasing with increasing distance from the line. This theory is accurate provided three main assumptions are met: objects on the actual

line are detected with certainty, objects are detected at their original location, and measurements are exact (Buckland *et al.*, 1993; Southwell, 1994). In this study, all assumptions were met as kangaroos are large and easily seen due to the open habitat in the study area and their conspicuous hopping gait, and measurements of radial distance and sighting angle were accurately taken with a rangefinder (Bushnell 2000 laser rangefinder) and protractor, respectively. Radial distances and sighting angles were recorded for every kangaroo and group of kangaroos seen along transects (distance to the approximate centre of the group measured for groups of kangaroos). Kangaroos were regarded as belonging to a group if individuals were within 50 m of each other (Croft, 1980). The kangaroo species and age/sex class of individuals were also recorded where accurately identifiable (at times, sex determination was not accurate amongst sexes of similar size). Approximately two and a half hours were needed to complete transects.

Kangaroo densities for each species (km^{-2}) were calculated using the program DISTANCE 4.0. Prior to calculation, *Macropus giganteus* and *M. fuliginosus* were pooled into a single category (grey kangaroos) as numbers of *M. giganteus* were low and there were many instances where *M. giganteus* and *M. fuliginosus* could not be reliably distinguished without stopping for intensive observation and thus confounding a requirement of the line transect method to travel at a constant speed. In DISTANCE, data were treated as clusters, and radial distances and sighting angles were converted to perpendicular distances to determine the detection function and calculate densities. Pilot runs of the data with different methods of truncation, grouping intervals and models revealed that the best models were achieved with data truncated to exclude the last 10% of distances and data grouped into twenty-five 10-m intervals. A hazard rate model with a cosine adjustment factor was the best of the available models giving consistently low Akaike's Information Criterion values. In addition, this combination of data truncation, data grouping and use of the hazard rate model produced the most precise models (lowest coefficients of variation) and used the least number of parameters to estimate kangaroo densities.

Kangaroo population densities during the night were estimated using a strip transect method as kangaroos could not be seen beyond the distance illuminated by the headlights of the car. Spotlighting was not conducted due to the constraints placed on a single researcher

driving and counting kangaroos. Kangaroos were counted and identified to species (with age/sex determined where possible) within a 40 m strip (20 m on either side of transect line). *M. giganteus* and *M. fuliginosus* were again grouped into one category of grey kangaroos as distinguishing between the species was not reliable for reasons given above. Night transects took approximately two hours to complete. Densities were calculated as the number of kangaroos km^{-2} (number of kangaroos within a 0.4 km^2 strip as only the last 10 km of road included in analyses; see earlier in this section).

Both day and night transects were conducted by driving a standard four-wheel drive diesel vehicle (Nissan Navara single cab tray-top/pick-up) at about 25 km h^{-1} and scanning for kangaroos. The order and direction of road and hinterland transects were alternated between weeks to account for differences in starting time and direction. To control for possible disturbances caused to kangaroos while travelling to the start of transects before beginning surveys, a 10-minute waiting period was established to allow time for disturbed kangaroos to settle.

4.2.2 Kangaroo road crossing data

A fence running parallel to the road (approximately 50 m away from the road; see section 2.2.1.4) was checked in order to detect regular kangaroo crossing points. Areas where kangaroos crossed typically had deep and obvious depressions in the ground under the fence ('slip-through') from frequent kangaroo use, as well as high concentrations of kangaroo scats and tracks leading to and away from that point in the fence. Trailmasters (mounted on metal stakes approximately 50 cm from ground level) were placed at these areas (Figure 4.2) and logged data for approximately two years between February 2003 and February 2005. Trailmasters (Goodson & Associates Inc., Kansas) are infrared devices which detect the passing of animals and record the date and time of these events. Both active and passive Trailmasters were used (Models TM1500 and TM550 respectively): active Trailmasters detect animals as they interrupt an infrared beam passing between a transmitter and receiver component; passive Trailmasters detect animals by a combination of heat and movement from animals within a narrow wedge-shaped field projecting approximately 20 m from the face of the Trailmasters' (oriented along the fence line and

offset about 1 m from the slip-through in this study). To prevent repeated counts of individual kangaroos, all Trailmasters were configured with a 5 second delay.

Only nighttime crossings were included in analyses (one hour before sunset to one hour after sunrise; sunrise and sunset times for Fowlers Gap calculated using a computer application from the Astronomical Applications Department, US Naval Observatory, here and subsequent usage) as passive Trailmasters registered many spurious counts during the day from convection currents of hot air. In addition, the numbers of crossings per night were standardised by dividing the total number of crossings per night by the number of working Trailmasters, and the average numbers of crossings per week calculated from standardised per night numbers were used in analyses (week = Monday to Sunday for this and subsequent weekly variables). Standardisations were necessary since the number of working Trailmasters varied throughout the study in an inconsistent pattern (e.g. if Trailmasters ran out of memory space, further data logging was prevented). In total, 82 weeks of data were collected across a 90-week period.

The numbers of kangaroo crossings at the fence provided an index of the numbers of kangaroos crossing the road. While it is recognised that some kangaroos may not have crossed the road once they crossed the fence, the fence and road were in close proximity to each other, suggesting that they were associated. It was not feasible to test the assumption of an association between fence and road crossings through direct observation, but the presence of tracks and scats to the road edge gave confidence to the assumption that kangaroos crossed the road after crossing the fence. Further, the presence of water troughs on the opposite side of the road, which typically attract kangaroos, provided strong incentives for kangaroos to cross the road following fence crossings.

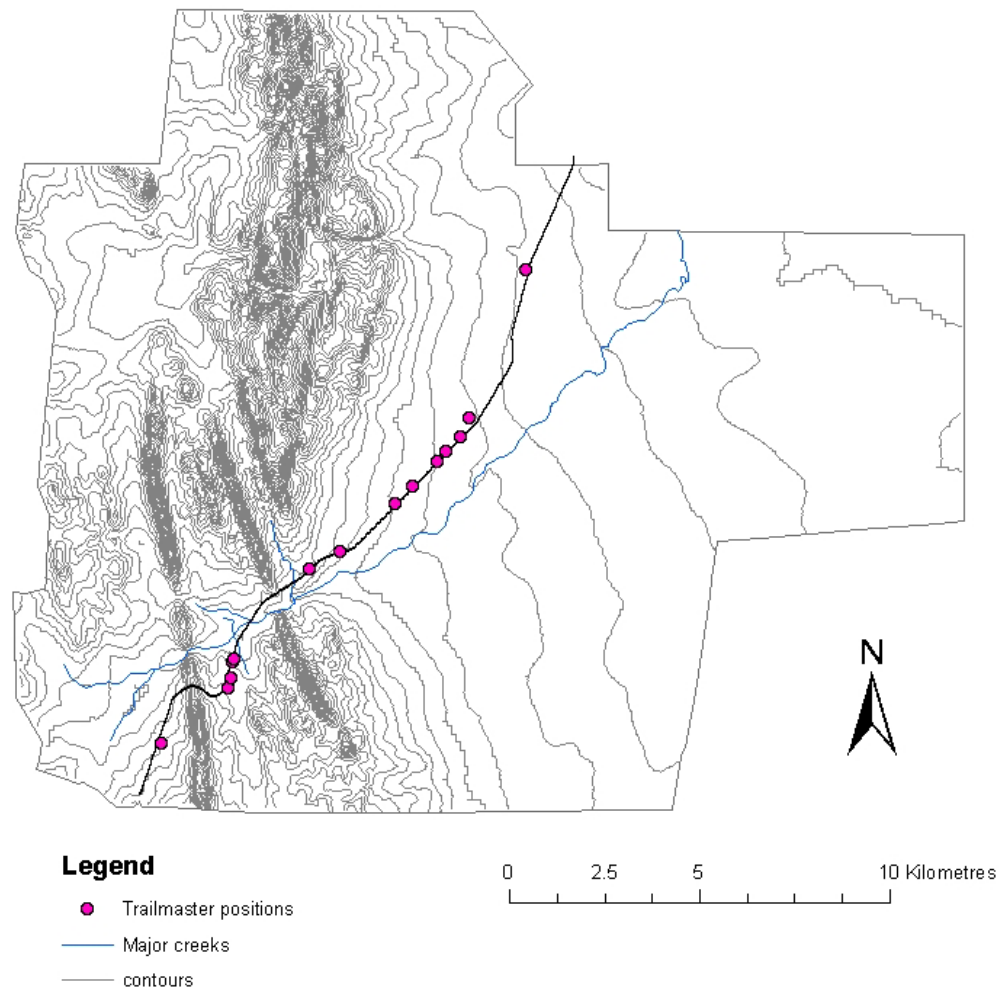


Figure 4.2: Topographic map of Fowlers Gap Arid Zone Research Station showing the locations of Trailmasters along the fence. The Silver City Highway is shown in black.

4.2.3 Weather data

Data on temperature, humidity, wind speed, barometric pressure, dewpoint and rainfall were collected on an hourly and daily basis via an automatic weather station (WM-918) located at Fowlers Gap Homestead. These variables were considered important in influencing kangaroo use of the road and kangaroo movements around the road as these weather variables were found to influence kangaroo movements and distributions in other studies, such as Montague-Drake's (2003) study in the nearby Sturt National Park. Weekly averages for weather variables (other than rainfall where total rainfall was calculated) were computed. Variables (other than rainfall) were then reduced to components using principal

component analysis (PCA, conducted in SPSS for Windows V13.0) as they were highly correlated to one another, and these components were used in analyses (see section 3.2.3.3 for more details of use of PCAs and conducting PCAs; unlike section 3.2.3.3, the number of components extracted was based on Kaiser's criterion as communalities after extraction were greater than 0.7).

The 11 weather variables were reduced to three components and these accounted for 89.65% of total variance. There were strong extraction communalities for all variables (above 0.7 with majority of variables well above 0.8), indicating that high amounts of variability were accounted for and that the extracted components represented the variables well. Component 1 was negatively correlated with maximum and minimum humidity, and positively correlated with maximum and minimum temperature, maximum heat index and minimum windchill; Component 2 was negatively correlated with minimum and maximum barometric pressure and positively correlated with maximum wind gust; and Component 3 was positively correlated with minimum and maximum dewpoint (see Table A4.2 in Appendix 4 for correlations between weather variables and extracted components).

4.2.4 Traffic data

Traffic data were logged continuously between February 2003 and November 2004 using a traffic monitor (Metrocount Vehicle Classifier System 5600 series) that recorded the time, date and speed of vehicle passage, and classified vehicles to 12 type/size classes. As similar volumes and frequencies of motorcycles were present on the road and hinterland track (relatively low compared to other vehicular traffic) and exact counts of motorcycles were not made on the hinterland transect, motorcycles were excluded from analyses and traffic volumes per total day and per night were calculated for remaining vehicles on the road (MCReport, version 2.25.7132.0; no other vehicles regularly used the hinterland track). Total (24 h) day traffic included all vehicles throughout the day and night (calculated from 1200 h on day 1 to 1200 h on subsequent day) and night-time traffic was defined as all vehicles between two hours before sunset and two hours after sunrise. Weekly averages were used in analyses.

4.2.5 Data analysis

4.2.5.1 Factors influencing kangaroo densities

A univariate general linear model (GLM, conducted in SPSS for Windows V13.0) was used to examine how kangaroo densities varied between kangaroo species, transects (this reflected proximity to road; see section 4.2.1), times of day, rainfall, traffic volume and various weather variables (reduced weather components). Examination of how kangaroo densities varied according to age/sex was not possible as too many kangaroos could not be accurately identified into age/sex classes (especially during night counts). Repeated measures models were not employed as is usually recommended when single subjects have been monitored over different conditions (kangaroos along the same transects over different times; Green, 1993; Field, 2000) since reduced weather components were included in the analysis and it is not possible to run repeated measures models when there are also covariables in the model. This is a potential limitation in analysis; however, including weather components and rainfall in the analysis rather than a simple temporal factor as a repeated measure (for example, season) was appropriate to this study as rainfall is the primary driving force for the biota in arid areas, with factors such as season only of secondary importance after rainfall (Stafford Smith and Morton, 1990).

In the analysis, rainfall was included as two separate factors (current total weekly rainfall and total rainfall over the last 2 weeks) where levels of factors could either be rain or no rain. Both rainfall factors were examined as kangaroo densities may be influenced by rainfall immediately (as water becomes available for drinking) as well as by rainfall lags (as forage becomes available after plants respond to rain: 2 weeks as established for kangaroos' preferred forage type, grass, in Chapter 3; Dawson, 1998). The use of categorical data rather than exact values of rainfall were employed to increase the chance of detecting an effect of rain on kangaroo densities; the magnitude of the response in this study was not considered as important as detecting if a response occurred at all.

Model terms were added into the GLM using a stepwise technique, with all terms and interactions initially entered into the model and dropped if not significant at $p < 0.05$. The final model was that which included terms for which elimination would have reduced the explanatory power of the model (that is, the model that accounted for the most variation;

Adjusted R^2 used, Quinn and Keough, 2002). Since the aim of this study was to determine kangaroo species' use of the road relative to surrounding areas, only significant interactions with transect and species were investigated (significant main effects were not of interest). If significant interaction effects with transect and species were detected for factors, differences between the levels of the interacting factors were tested for each species separately (one-factor Anova). If variables were contained in interactions, the nature of the relationship (between the levels of the interacting factors tested for each species separately) was determined from the sign of β calculated using regression analysis.

All assumptions for GLM were checked (see section 3.2.3.4 for details of procedures and steps taken if assumptions were violated). Reported significance values of interactions were derived from the final model, whereas significance values of terms contained in interactions were derived from a model run for these terms without interactions. Statistics for non significant terms were obtained by re-running the final model containing all significant terms with each non significant term included individually.

4.2.5.2 Factors influencing kangaroo road crossings

A univariate GLM was also used to examine how the average weekly number of kangaroo crossings varied with rainfall (same rainfall factors as used in kangaroo density analysis), night time kangaroo densities, night time traffic volumes and weather variables (reduced PCA components, see above in weather data). Like the kangaroo density analysis, repeated measures models were not employed. Model terms were added into the GLM using a stepwise technique (see 4.2.5.1). The nature of significant differences was assessed with Bonferroni corrected post hoc comparisons for factors and the sign of β calculated using regression analysis for variables. Checks of assumptions were made with steps taken to correct violations of assumptions as necessary (see section 3.2.3.4 for details of procedures). Reported values and statistics for significant terms were derived from final models and values for non significant terms were obtained by re-running the final model containing all significant terms with each non significant term included individually. As no traffic data was available after November 2004, a truncated dataset (to the end of November 2004) was used in analysis. This dataset was a subset of kangaroo crossing data taken from Trailmasters positioned within the area covered by the hinterland transect.

4.3 Results

4.3.1 Kangaroo densities

A total of 3661 kangaroos of four species were counted during the day (1407 along the road transect and 2254 along the hinterland transect) compared to 299 kangaroos counted during the night (151 along the road transect and 148 along the hinterland transect). Kangaroo densities (all species combined) averaged 3.5 ± 0.2 kangaroos km^{-2} along the road and 7.4 ± 0.5 kangaroos km^{-2} in the hinterland during the day compared to 4.7 ± 3.0 kangaroos km^{-2} along the road and 4.5 ± 1.7 kangaroos km^{-2} in the hinterland during the night (mean \pm 95% confidence intervals).

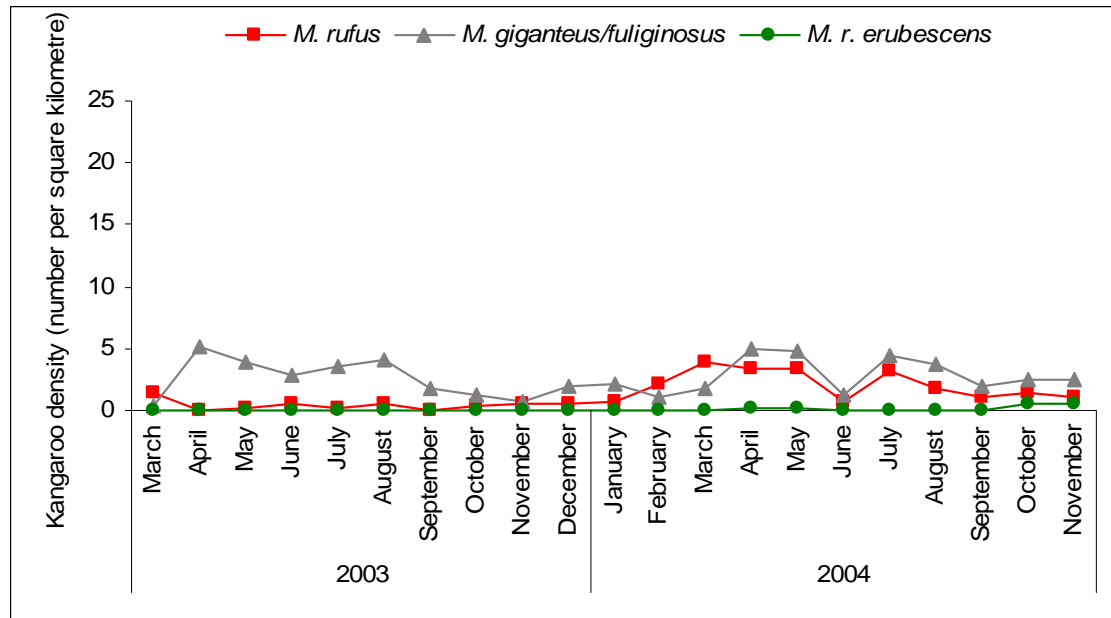
Macropus rufus densities showed clear changes over time, grey kangaroos displayed less marked changes and *M. robustus erubescens* showed hardly any changes in densities (Figure 4.3). Thus, in 2003, *M. rufus* densities were low relative to 2004 along both road and hinterland transects and exhibited no large fluctuations. In 2004, however, *M. rufus* densities increased along both transects. Grey kangaroo densities were relatively consistent over time, but a dip in density occurred along the road transect between the end of 2003 and beginning of 2004, with a peak in density seen along the hinterland track during the same period. These patterns of kangaroo densities over time were derived from day surveys rather than from night surveys as estimates of kangaroo densities during the day were more reliable for picking up trends (larger sample size). Nonetheless, similar trends in kangaroo densities were observed during the night.

Increases in *M. rufus* densities over time occurred soon after young-at-foot kangaroos were first observed in their population (Figure 4.4). Young-at-foot kangaroos were also observed within the grey kangaroo population, but no obvious relationship with their densities could be drawn. No young-at-foot were ever observed in the *M. r. erubescens* population.

Females dominated the *M. rufus* population along both the road and hinterland transects, although this dominance was more evident along the hinterland transect (Figure 4.5). The opposite pattern was seen among *M. r. erubescens*, where males represented the entire *M. r. erubescens* population along the road and dominated the population along the hinterland transect (Figure 4.6). Sample sizes, however, were extremely small for *M. r.*

erubescens (n = 7 and n = 40 during entire study along road and hinterland transects, respectively). Sexes of grey kangaroos are not discussed as they could not always be reliably distinguished.

(a)



(b)

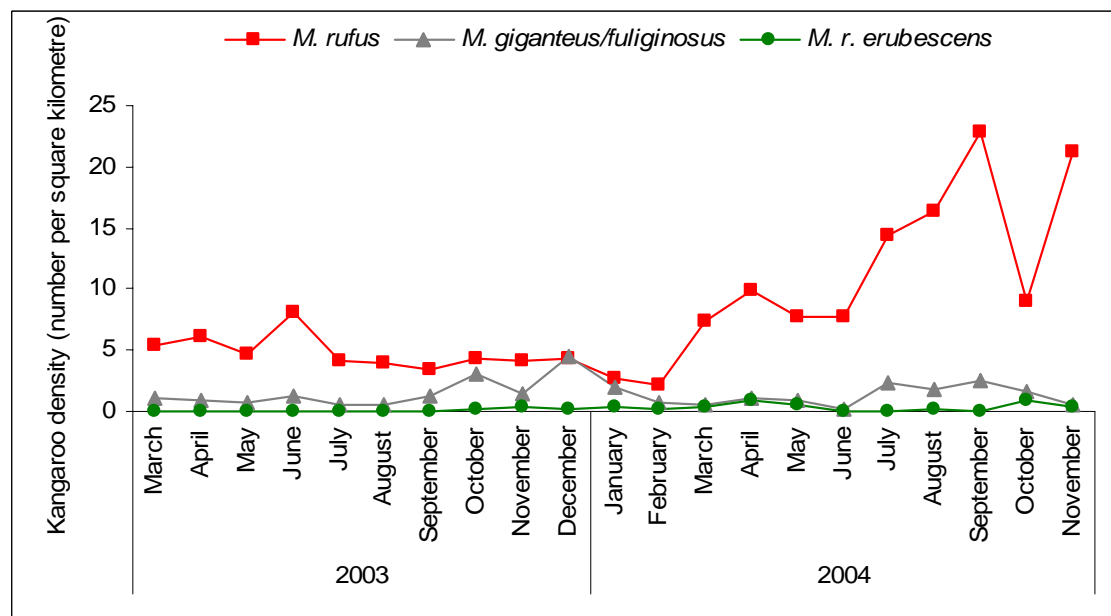
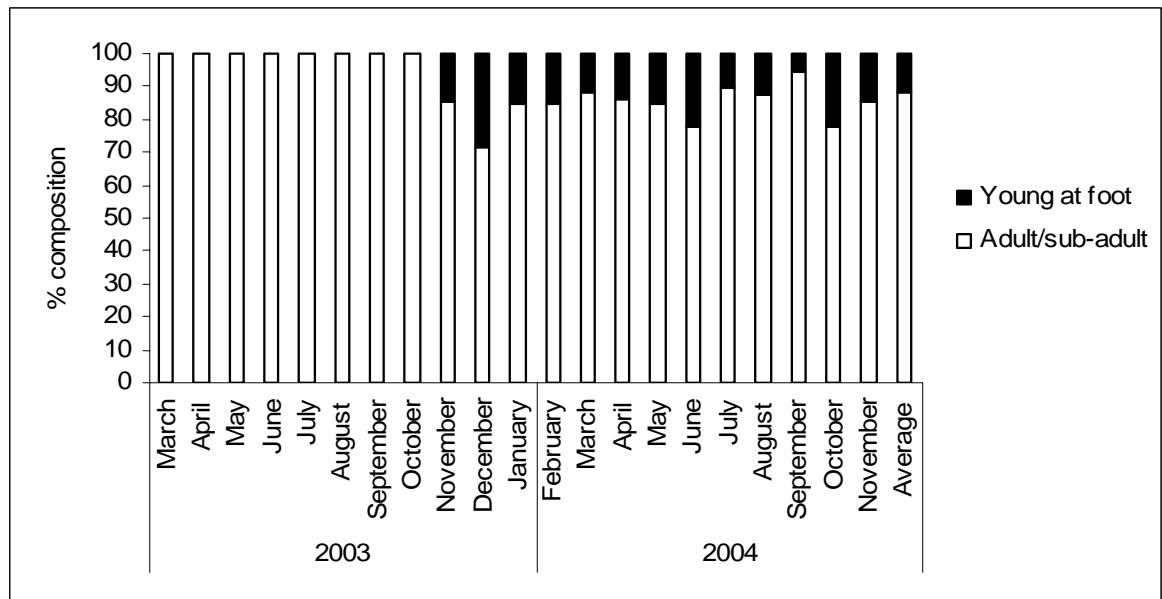


Figure 4.3: Mean monthly kangaroo densities along the road transect (a) and hinterland transect (b) during the day.

(a)



(b)

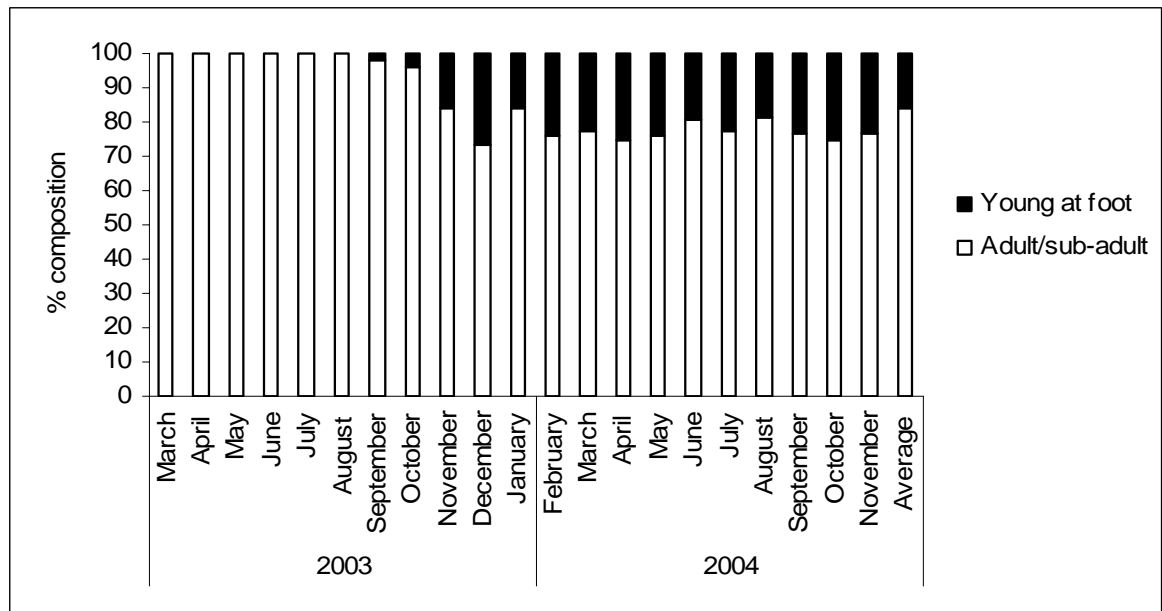
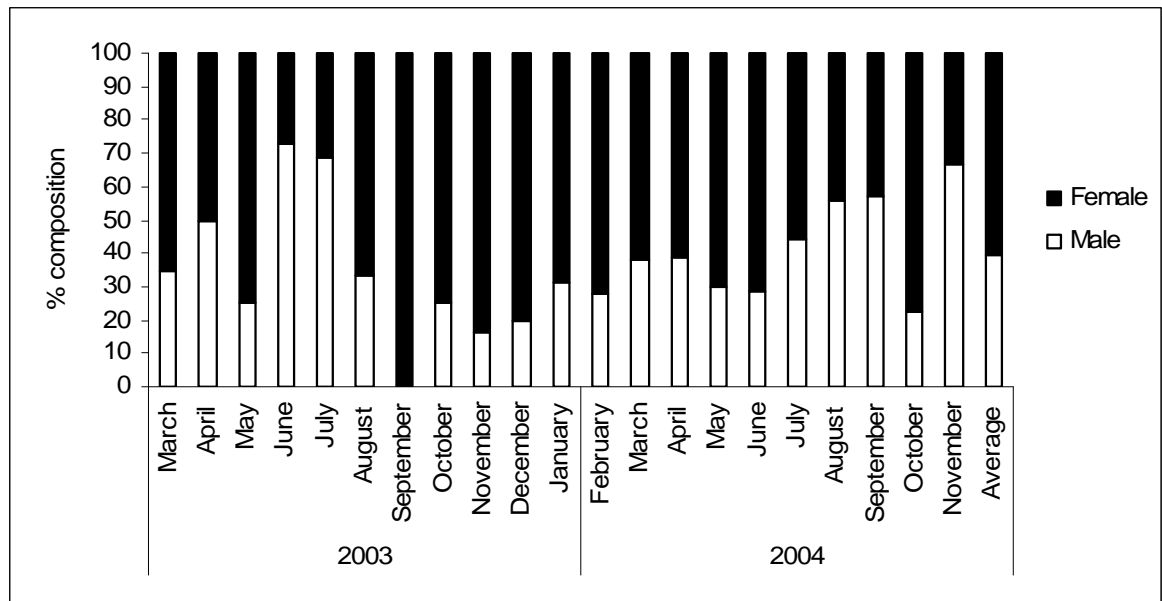


Figure 4.4: Percentage composition of adults/sub-adults relative to young-at-foots for *Macropus rufus* along the road transect (a) and hinterland transect (b) during the day.

(a)



(b)

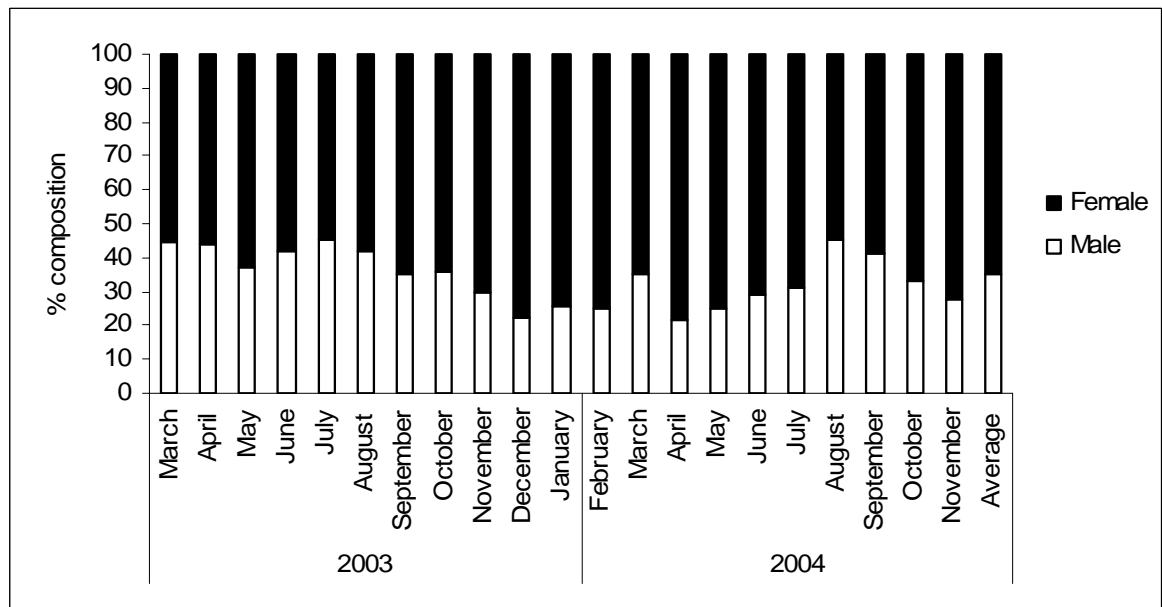
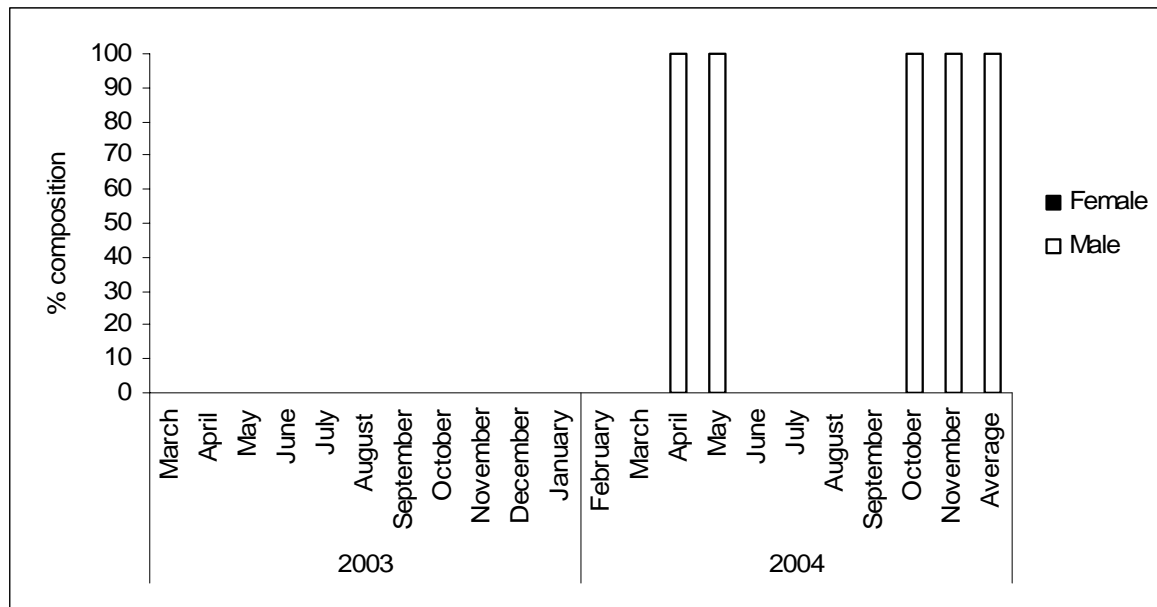


Figure 4.5: Percentage composition of males relative to females for *Macropus rufus* along the road transect (a) and hinterland transect (b) during the day.

(a)



(b)

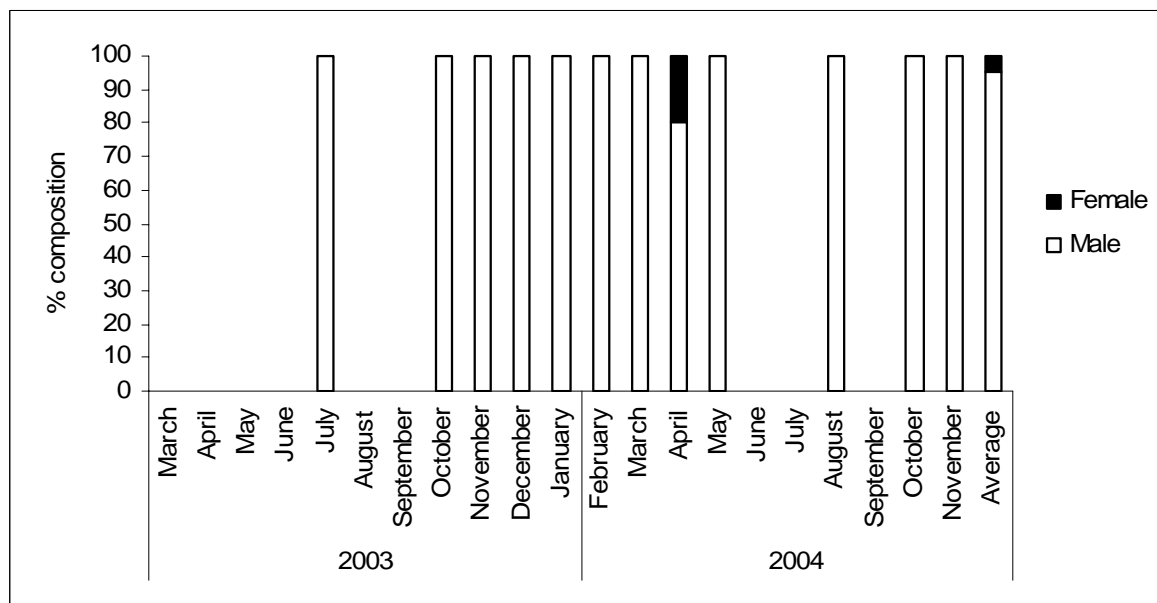


Figure 4.6: Percentage composition of males relative to females for *Macropus robustus erubescens* along the road transect (a) and hinterland transect (b) during the day.

4.3.2 Factors influencing kangaroo densities

GLM revealed significant differences in kangaroo densities for a number species*transect (*factor/variable) interactions (Table 4.1). Examination of species*transect interactions only revealed that *M. rufus* densities were significantly higher along the

hinterland transect compared to the road transect ($F_{(1,308)} = 56.01$, $p < 0.001$) and that grey kangaroo densities were significantly higher along the road transect compared to the hinterland transect ($F_{(1,308)} = 8.86$, $p = 0.003$) (Figure 4.7).

Table 4.1: Results from GLM examining effects of various factors, factor interactions (with species), and variables on kangaroo densities (non significant interactions not shown). The final model accounted for 40 % of variation ($\text{Adj } R^2 = 0.399$, $F_{(24,893)} = 26.41$, $p < 0.001$). Density values were natural-log transformed. Significant model terms of interest are shown in **bold**.

Model Terms	F values	P values
Species	$F_{(2,911)} = 135.09$	$p < 0.001$
Transect	$F_{(1,911)} = 20.83$	$p < 0.001$
Time of day	$F_{(1,911)} = 48.46$	$p < 0.001$
Total weekly rainfall	$F_{(1,892)} = 1.98$	$p = 0.160$
Total rainfall over last 2 weeks	$F_{(1,911)} = 5.60$	$p = 0.018$
Total number of vehicles (total day)	$F_{(1,892)} = 0.71$	$p = 0.400$
Total number of vehicles (night)	$F_{(1,892)} = 0.19$	$p = 0.667$
Component 1 (humidity and temperature)	$F_{(1,893)} = 0.61$	$p = 0.437$
Component 2 (barometric pressure and wind gust)	$F_{(1,892)} = 0.001$	$p = 0.973$
Component 3 (dewpoint)	$F_{(1,893)} = 14.33$	$p < 0.001$
Species*Transect	$F_{(2,893)} = 46.54$	$p < 0.001$
Species*Transect*Time of day	$F_{(5,893)} = 13.53$	$p < 0.001$
Species*Transect*Total rainfall over last 2 weeks	$F_{(5,893)} = 2.63$	$p = 0.022$
Species*Transect* Component 1	$F_{(5,893)} = 2.75$	$p = 0.018$

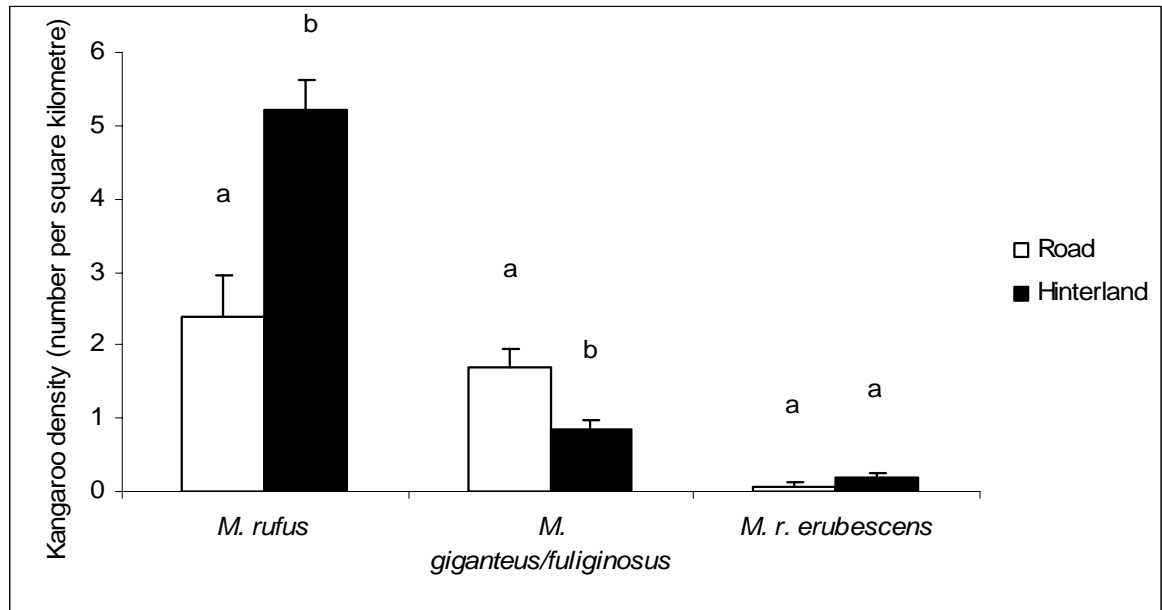


Figure 4.7: Mean densities per species (+ 1 SE) along the road and hinterland transects. Letters denote significant differences between transects for each species. Results are from separate one-factor anovas for each species between transects that followed significant results for species*transect interactions.

A significant interaction occurred for species between the road and hinterland transects and between different times of day. Grey kangaroo densities were higher during the day compared to during the night along both transects (road: $F_{(1,153)} = 34.78$, $p < 0.001$, hinterland: $F_{(1,153)} = 19.42$, $p < 0.001$). Similarly, *M. rufus* densities along the hinterland transect were higher during the day compared to during the night ($F_{(1,153)} = 27.95$, $p < 0.001$). Along the road transect however, *M. rufus* densities were higher during the night compared to during the day (difference not significant: $F_{(1,153)} = 0.07$, $p = 0.797$, Figure 4.8).

A significant interaction also occurred for species between road and hinterland transects and between rain occurrences. Thus, the densities of all kangaroo species were higher when no rain fell over the last 2 weeks in the hinterland (differences were significant for *M. rufus* and grey kangaroos; *M. rufus*: $F_{(1,153)} = 7.67$, $p = 0.006$, grey kangaroos: $F_{(1,153)} = 4.53$, $p = 0.035$; trend for significant differences for *M. r. erubescens*: $F_{(1,153)} = 3.34$, $p = 0.070$). Conversely, along the road, densities of all kangaroo species were higher when rain fell over the last 2 weeks (differences not significant; *M. rufus*: $F_{(1,153)} = 0.28$, $p = 0.599$, grey kangaroos: $F_{(1,153)} = 0.47$, $p = 0.495$, *M. r. erubescens*: $F_{(1,153)} = 0.37$, $p = 0.545$) (Figure 4.9).

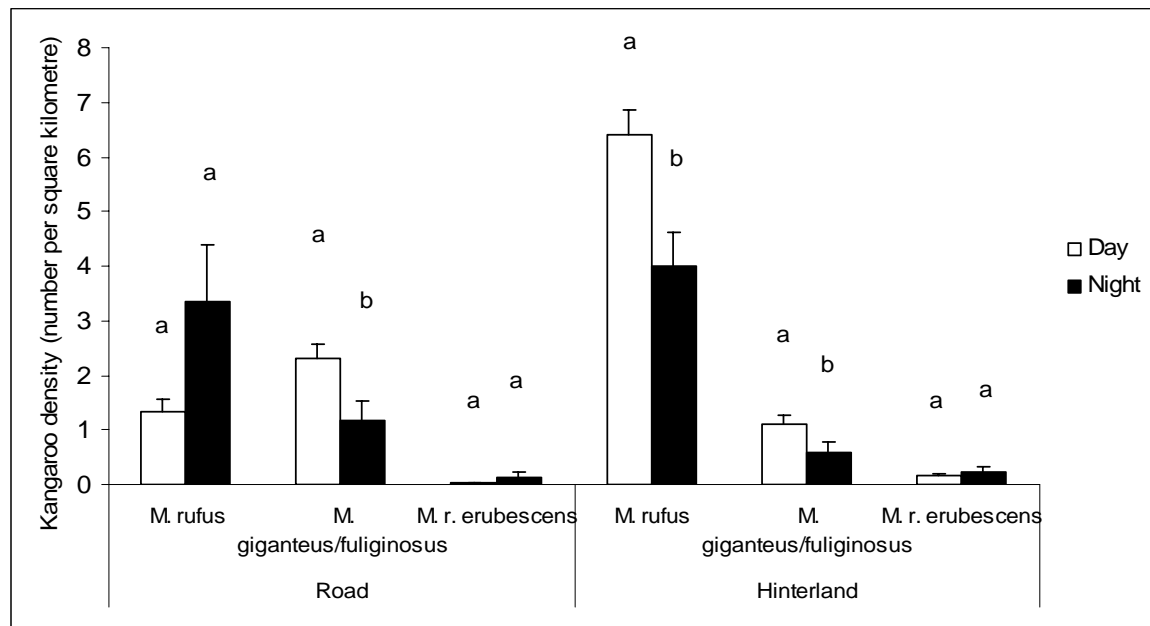


Figure 4.8: Mean densities per species (+ 1 SE) along the road and hinterland transects during the day and night. Letters denote significant differences between times of day for each species along the two transects. Results are from separate one-factor anovas for each species between times of day along road and hinterland transects that followed significant results for species*transect*time of day interactions.

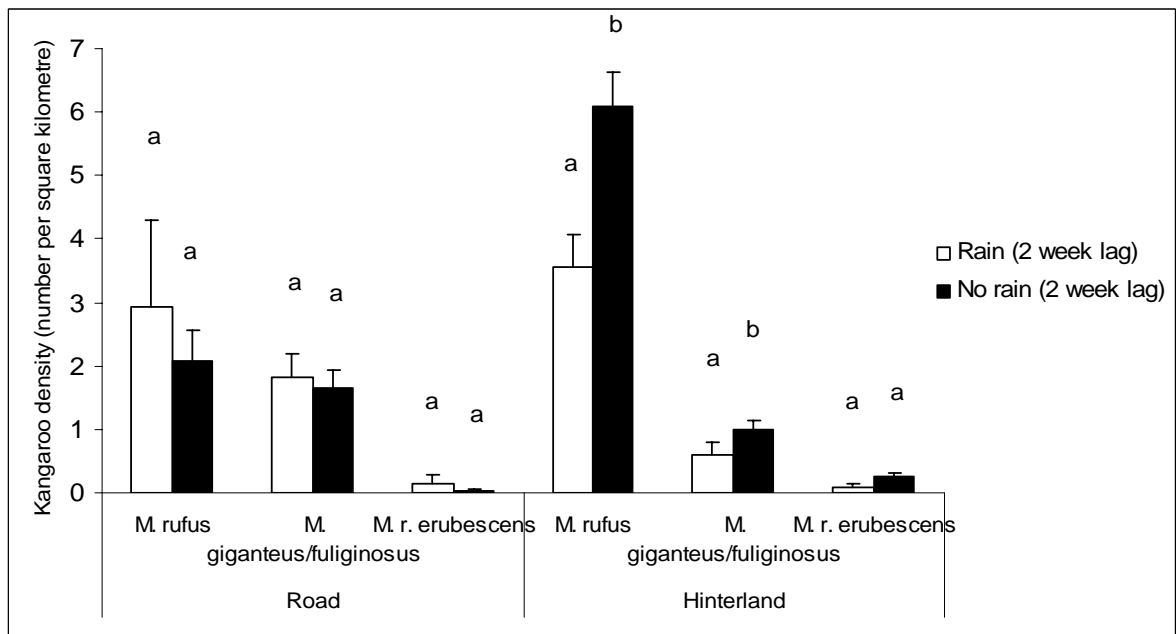


Figure 4.9: Mean densities per species (+ 1 SE) along the road and hinterland transects when rain and no rain fell over the last 2 weeks. Letters denote significant differences between rain occurrences for each species along the two transects. Results are from separate one-factor anovas for each species between rain occurrences along road and hinterland transects that followed significant results for species*transect*total rain over the last 2 weeks interactions.

Finally, interactions occurred for species between road and hinterland transects with increases or decreases in humidity and temperature. Thus, the densities of all kangaroo species increased in the hinterland with decreases in humidity and increases in temperature, maximum heat index and minimum windchill (differences not significant for all species; *M. rufus*: $F_{(1,153)} = 1.36$, $p = 0.246$, grey kangaroos: $F_{(1,153)} = 1.21$, $p = 0.274$, *M. r. erubescens*: $F_{(1,153)} = 3.12$, $p = 0.079$). Conversely, along the road, the densities of all kangaroo species increased with increases in humidity and decreases in temperature, maximum heat index and minimum windchill (differences significant for grey kangaroos only; *M. rufus*: $F_{(1,153)} = 0.35$, $p = 0.558$, grey kangaroos: $F_{(1,153)} = 9.33$, $p = 0.003$, *M. r. erubescens*: $F_{(1,153)} = 1.74$, $p = 0.189$).

Both maximum and minimum weekly temperature and humidity levels, as well as maximum heat loads and minimum windchill loaded on Component 1. Thus, details of the nature of the influence of Component 1 were not entirely clear (e.g. whether the densities of kangaroo species along transects were influenced by hot and dry days, hot and dry nights, or both were not known). GLM revealed no species*transect*time of day*Component 1 interactions; nevertheless, to further tease out the nature of the influence of Component 1, investigations of the relationships between kangaroo species along the transects and “daytime” and “night-time” elements of Component 1 were made. The daytime component was derived by reducing average weekly maximum temperature, minimum humidity and maximum heat index to one component (89.24 % variance explained), while the night-time component was derived by reducing average minimum temperature, maximum humidity and minimum windchill to one component (87.68 % variance explained) (PCA, conducted in SPSS for Windows V13.0; number of components extracted based on Kaiser’s criterion; orthogonal varimax rotation not performed since only one component extracted for day and night; communalities after extraction for both day and night components above 0.8; Tables A4.3 and A4.4 in Appendix 4 for correlations between variables and extracted components).

Patterns in species densities along transects were similar during both the daytime and night-time. Thus, like the results for Component 1, the densities of all kangaroo species increased in the hinterland with decreases in humidity and increases in temperature during both the daytime and night-time (differences not always significant; daytime: *M. rufus*: $F_{(1,153)} = 2.46$, $p = 0.119$, grey kangaroos: $F_{(1,153)} = 4.87$, $p = 0.029$, *M. r. erubescens*: $F_{(1,153)}$

= 7.18, $p = 0.008$; night-time: *M. rufus*: $F_{(1,153)} = 0.08$, $p = 0.782$, grey kangaroos: $F_{(1,153)} = 1.95$, $p = 0.165$, *M. r. erubescens*: $F_{(1,153)} = 4.69$, $p = 0.032$). Conversely, along the road, the densities of all kangaroo species increased with increases in humidity and decreases in temperature during both the daytime and night-time (differences significant for grey kangaroos only; daytime: *M. rufus*: $F_{(1,153)} = 0.66$, $p = 0.418$, grey kangaroos: $F_{(1,153)} = 8.93$, $p = 0.003$, *M. r. erubescens*: $F_{(1,153)} = 1.08$, $p = 0.311$; night-time: *M. rufus*: $F_{(1,153)} = 1.85$, $p = 0.175$, grey kangaroos: $F_{(1,153)} = 11.15$, $p = 0.001$, *M. r. erubescens*: $F_{(1,153)} = 2.15$, $p = 0.145$).

4.3.3 Kangaroo road crossings

The average number of road/fence crossings per week fluctuated over the study and ranged between 0 and 53 crossings per week (Figure 4.10). On average, 17.1 ± 1.2 kangaroos crossed the road/fence per week.

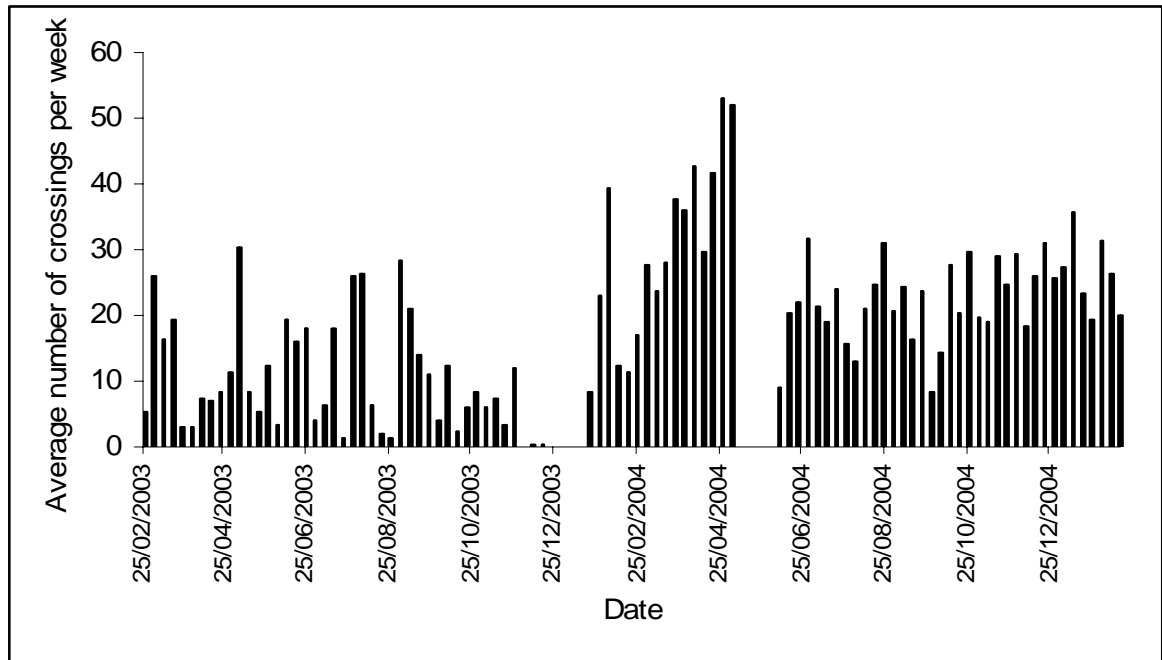


Figure 4.10: Average number of kangaroo road/fence crossings per week between February 2003 and February 2005. Data missing between 17/12/2003 and 22/01/2004 and between 10/05/2004 and 8/06/2004.

4.3.4 Factors influencing kangaroo road crossings

GLM revealed that the number of kangaroo crossings per week was influenced by barometric pressure and wind gust (Component 2), and dewpoint (Component 3) (Table 4.2, Figures 4.11 and 4.12). In addition, there were trends for a significantly higher number of kangaroo crossings per week when no rain fell over the last 2 weeks compared to when rain fell (13.1 ± 2.2 and 7.6 ± 0.5 kangaroo crossings per week respectively) and for a positive relationship between the number of kangaroo crossings per week and night time kangaroo densities in the hinterland. Total weekly rainfall, night time kangaroo densities along the road, the night time number of vehicles, and humidity and temperature (Component 1) did not influence the number of kangaroo crossings per week (Table 4.2).

Table 4.2: Results from GLM examining the effects of rainfall, kangaroo density, traffic volume and other weather variables on the number of kangaroo road crossings per week. The final model accounted for 18 % of variation ($\text{Adj } R^2 = 0.179$, $F_{(2,66)} = 8.42$, $p = 0.001$). Values for the number of kangaroo crossings were square-root transformed. Significant model terms are shown in **bold**.

Model Terms	F values	P values
Total weekly rainfall	$F_{(1,65)} = 0.20$	$p = 0.656$
Total rainfall over last 2 weeks	$F_{(1,65)} = 3.46$	$p = 0.067$
Night time kangaroo density along the road	$F_{(1,65)} = 2.09$	$p = 0.153$
Night time kangaroo density in the hinterland	$F_{(1,65)} = 3.23$	$p = 0.077$
Night time total number of vehicles	$F_{(1,65)} = 1.55$	$p = 0.218$
Component 1 (humidity and temperature)	$F_{(1,65)} = 0.65$	$p = 0.424$
Component 2 (barometric pressure and wind gust)	$F_{(1,66)} = 8.03$	$p = 0.006$
Component 3 (dewpoint)	$F_{(1,66)} = 9.89$	$p = 0.002$

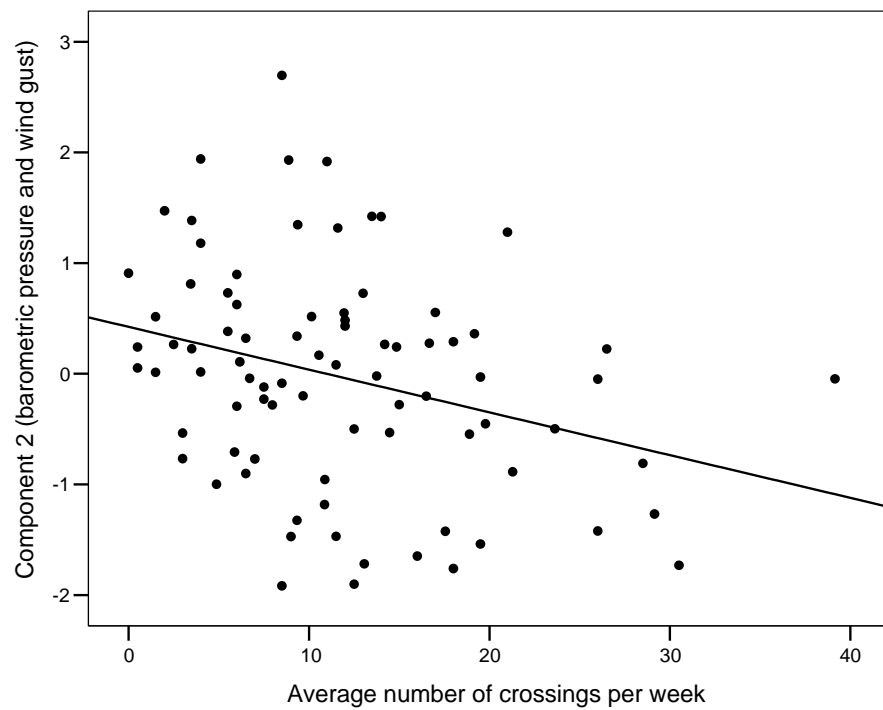


Figure 4.11: Relationship between the average number of crossings per week and Component 2 (negatively correlated with minimum and maximum barometric pressure and positively correlated with maximum wind gust).

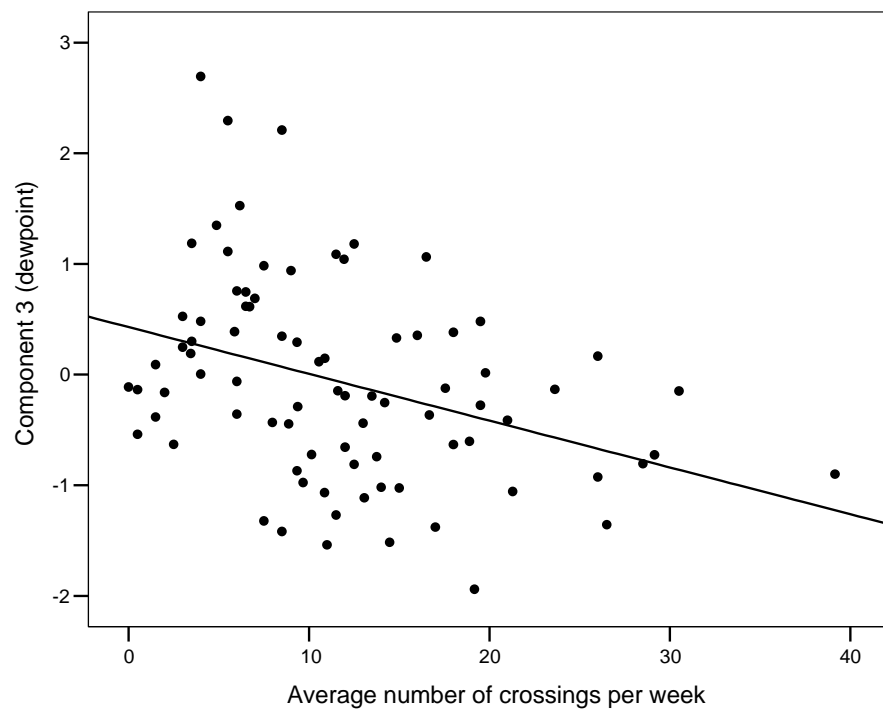


Figure 4.12: Relationship between the average number of crossings per week and Component 3 (positively correlated with minimum and maximum dewpoint).

4.4 Discussion

This study showed that an arid-zone road influenced kangaroo densities but revealed no overall shift in kangaroo movements either away from or towards the road. Kangaroo densities near and away from the road varied depending on the availability of high quality forage at the road (as revealed from relationships with 2-week lags in rainfall that drive the growth of forage; Chapter 3) and ambient temperatures, with *M. rufus* densities additionally influenced by their diurnal sheltering/resting and nocturnal foraging areas, and kangaroo road crossing frequencies varied with wind gust and dewpoint. As there was no overall shift away from the road by kangaroos, and kangaroos regularly crossed the road, arid-zone roads probably do not fragment kangaroo populations on either side of roads. Arid-zone roads probably do not represent sink areas for kangaroo populations either as there was no overall movement shift towards the road by kangaroos. However, interpretations of results should be made cautiously: changes in environmental condition typical of the arid zone could influence kangaroo movements; kangaroo mortality rates along the road could be high even if kangaroo densities were low as kangaroos may not perceive traffic along the road as dangerous enough to avoid; increases in traffic could further increase kangaroo mortality rates along the road; and differential mortality could also occur, changing population demographic structure and community composition.

4.4.1 Kangaroo densities over the study

Of the kangaroo species, only *M. rufus* displayed changes in overall density over the study period, with densities increasing in the latter half of the study. A possible explanation for the observed pattern may be that the densities of *M. rufus* at the beginning of the study were low due to high mortality resulting from the drought of 2002/2003, and increases in densities during the latter part of the study reflected natural population growth in *M. rufus*. Support for this explanation comes from the NSW National Parks and Wildlife Service which recorded a drop in the *M. rufus* population to almost half their population between June 2002 and June 2003 (records from aerial surveys of the Broken Hill kangaroo anagement block), and from observations made in the current study where increases in *M. rufus* densities occurred shortly after the appearance of young-at-foot in their population. That the densities of grey kangaroos and *M. r. erubescens* were not observed to follow the

same pattern as *M. rufus* may have been due to the fact that grey kangaroos reproduce more slowly in comparison to other kangaroo species (the more common of the grey kangaroos, *Macropus fuliginosus*, lacks embryonic diapause, generally breeds on a seasonal basis, and young-at-foot remain with their mothers for longer periods of time compared to other kangaroo species; Dawson, 1998), and that both the road and hinterland transects ran through areas where *M. r. erubescens* were not common (*M. r. erubescens* are more common in the western, hilly sections of the study site compared to the eastern alluvial plains; Croft, 1991b, see also section 2.1.1 for details). Thus, although grey kangaroos and *M. r. erubescens* also suffered high mortality as a result of the 2002/2003 drought (NSW National Parks and Wildlife Service), counts did not reflect low densities that may have subsequently increased.

In addition to the above explanation, the overall density patterns in *M. rufus* over the study period may have been due to many *M. rufus* moving away from the study site prior to and during the 2002/2003 drought in search for forage, returning only when conditions on the study site improved (possibly after heavy rains in February 2003 where 79.8 mm of rain fell, or after April 2003 where 14.4 mm of rain was followed by 25 mm of rain in May 2003), with the influx of returning *M. rufus* augmenting the natural increase in the *M. rufus* population. Support for this explanation comes from other studies, which indicate that *M. rufus* are highly selective feeders, preferring to feed on grasses (Bailey *et al.*, 1971; Dawson and Ellis, 1994; Moss and Croft, 1999), as well as a mobile species that move quickly in response to distant rainfall driving the growth of grasses (Newsome, 1965; Priddell, 1988) or to areas in better condition outside their core habitats (Clancy and Croft, 1992; Dawson, 1998). In comparison to *M. rufus*, grey kangaroos are more generalist in their diets, able to take in browse in addition to pasture (Barker, 1987; Norbury, 1987), and are relatively sedentary, even when conditions are poor (Jarman and Taylor, 1983; Arnold *et al.*, 1992). Similarly, *M. r. erubescens* are relatively sedentary, and females may even decrease their home-ranges during times of food shortage (Croft, 1991b). Thus, due to their sedentary behaviours and responses to food shortages, neither grey kangaroos nor *M. r. erubescens* showed density increases due to immigration during the latter part of the study period.

4.4.2 Effects of rainfall lag and forage at roadsides on kangaroo densities and movements

Kangaroo densities, and to a lesser extent kangaroo movements in the vicinity of and across the road, were influenced by the availability of high quality grass at the roadside, with higher densities and increased movements occurring at the road when grass was available at the road and lower densities and decreased movements occurring at the road when grass was less available. These results were inferred from the fact that kangaroo densities were higher along the road and lower in the hinterland and that the frequency of kangaroo road crossings increased when rain fell over the last two weeks compared to when no rain fell over the last two weeks; that the quality of grasses are highly correlated to rainfall over the last two weeks (positive relationship; Chapter 3); and that the quality of grasses two weeks after rain were most likely higher along the road compared to in the hinterland due to the greater amounts of water received at the road edge (due to the road preventing infiltration and collecting water at its surface that is then channelled towards its edges). As kangaroos usually select grasses that are high in quality and nutritional value (Dawson and Ellis, 1994, 1996; Dawson, 1998), greater numbers of kangaroos moving to the road and harvesting limited, higher quality grasses (that are also high in water, thereby reducing a kangaroo's reliance on free water; Green, 1989) along the road when available are hardly surprising. Also not surprising are the results of higher kangaroo densities in the hinterland and lower kangaroo movements at the road when grass quality along the road was not significantly enhanced by rainfall. Decision making theory predicts that animals making any behavioural decisions should perform the behaviour until the marginal benefits of the behaviour equal the marginal costs (e.g. the sum of the energetic, predation, reproduction and missed opportunity costs; Lima and Dill, 1990; Kotler and Blaustein, 1995). Thus, when limited amounts of high quality grass were available along the road, the benefits of harvesting the grass must have outweighed the combined costs of being in the road vicinity. Kangaroo densities and movements probably decreased along the road as the benefits of harvesting grasses that may not have been significantly higher in quality along the road compared to in the hinterland were outweighed by the combined costs of being along the road. This pattern of movement towards roads depending on the availability and quality of forage has been observed in other studies, where various kangaroo species

(Coulson, 1989; Osawa, 1989; Lee *et al.*, 2004) and baboons (*Papio hamadryas* (Linnaeus); Drews, 1995) also moved to the road edge when higher quality grass was available at the roadside compared to areas further from the road.

4.4.3 Effect of ambient temperature on kangaroo densities and movements

One of the costs of being along the road compared to in the hinterland may have been the greater amounts of heat radiated from the road to its vicinity on hot days and nights, as kangaroo densities decreased along the road and increased in the hinterland with increases in ambient temperature during both daytime and night-time hours (another cost may be disturbance caused by traffic; see section 4.4.6). While road temperatures relative to temperatures in the hinterland were not measured, it is likely that more heat was radiated from the road surface during daytime hours due to the dark road surface being of a lower albedo than surrounding natural surfaces, thus increasing temperatures in the road vicinity. During night-time hours, greater amounts of heat from the road surface compared to natural surfaces would continue to be radiated to the road vicinity due to the slow release of heat from the road. A possible reason for why more kangaroos might avoid the high temperatures given off from the road during hot days and nights may be that during the hotter months of the year, road temperatures must have been in excess of 45 °C during the day and 20 °C during the night (as air temperatures on Fowlers Gap already exceed 45 °C and 20 °C during the day and night in summer respectively; see section 2.1.6.2). Temperatures this high are usually avoided by kangaroos, who usually deal with high temperatures by resting in cooler microclimates, such as under shrubs and trees and within caves during the hottest times of day, becoming active only when ambient temperatures decrease (McCarron and Dawson, 1989; Watson and Dawson, 1993) as more water is required to thermoregulate in high temperatures (Montague-Drake, 2003) and water is limited in arid ecosystems (Stafford Smith and Morton, 1990). While higher road temperatures may have been a cost to kangaroos on hot days and nights, higher road temperatures may have been beneficial to kangaroos on cooler days and nights. Kangaroo densities increased along the road and decreased in the hinterland with decreases in ambient temperatures, and it is possible that more kangaroos moved to the warmer areas near the road during these times to increase body temperatures without using their own energy

stores to generate heat, as they are also known to use heat from the sun to increase body temperatures with minimal energetic expenditure (Dawson, 1998).

Although kangaroo densities were influenced by ambient temperatures, kangaroo road crossing frequencies were not similarly affected. This result is unexpected given that kangaroo movements and kangaroo densities are related and the temperature of roads may influence kangaroo road crossings more than kangaroo densities (due to kangaroos that are crossing roads having to come into direct contact with roads). However, the needs of kangaroos to move across the landscape to reach their preferred destinations (with suitable microclimates) probably outweighed the costs of temporarily being in the road microclimate on hot days, thereby resulting in no significant differences in crossing frequency with ambient temperatures. In addition, kangaroo road crossing frequencies were only recorded during night-time hours when kangaroos are active, and while ambient temperatures affected kangaroo densities during both daytime and night-time hours, road temperatures during the night would have been less extreme than daytime hours and thus may not have represented a major deterrent to road crossings. Moreover, the trailmasters may have only been measuring the crossings of *M. rufus* (trailmasters do not distinguish between species) as *M. rufus* densities were high along the road at night and the influence of ambient temperatures on *M. rufus* densities were not statistically significant (unlike the significant influence on grey kangaroos and *M. r. erubescens*).

4.4.4 Effect of species on kangaroo densities and movements

The different habitat preferences of the kangaroo species, along with the behaviour and diets of all of the kangaroo species may explain why only *M. rufus* densities differed between daytime and night-time hours at road and hinterland areas. *Macropus rufus*, grey kangaroos and *M. r. erubescens* mainly rest during the day and forage during the night (*M. rufus*: Watson and Dawson, 1993; *M. giganteus*: Southwell, 1987; *M. fuliginosus*: Arnold *et al.*, 1992; Coulson, 1993a; *M. r. erubescens*: Ealey, 1967; Croft, 1991b) and usually separate their diurnal sheltering or resting areas from their nocturnal foraging areas (the shift between resting and foraging areas is most likely to do with thermoregulation; Croft, 1991b; Coulson, 1993a). As *M. rufus* prefer open areas and grey kangaroos prefer areas with more cover (Priddel, 1988; Dawson, 1998), higher densities of *M. rufus* in the

hinterland and grey kangaroos along the road during the day probably reflected these species' preferred daytime sheltering or resting areas (the hinterland was more open and the road was lined in part by shrubs, see sections 2.2.1.2 and 2.2.1.4 and also 2.1.5). The higher densities of *M. rufus* along the road during the night may have been the result of their moving towards the road vicinity to forage as *M. rufus* select high quality forage (Dawson and Ellis, 1994; Moss and Croft, 1999) and vegetation at road edges is typically higher in quality compared to areas further from the road (due to the road's redistribution of water towards its edges that enhances vegetation; Chapter 3; Lee *et al.*, 2004). Densities of grey kangaroos were also higher along the road during the night and thus no density shifts reflective of distinct diurnal sheltering and nocturnal foraging areas were found. However, grey kangaroos did not have to move very far to access forage at the road from their sheltering areas along the road, so sheltering and foraging areas in the study area may not have been very distinct. Other studies have also found differences between daytime and night-time usage of road areas for species. For example, swamp wallabies (*Wallabia bicolor*; Osawa, 1989), grizzly bears (*Ursus arctos* Ord; McLennan and Shackleton, 1988) and black-backed jackal (*Canis mesomelas* (Schreber); Newmark *et al.*, 1996) use roads more often at night compared to during the day as darkness provides cover for these species while they use resources available along roads.

4.4.5 Effects of other weather components on kangaroo movements

The significant relationships between kangaroo road crossing frequency and weather components 2 (associated with barometric pressure and wind gust) and 3 (associated with dewpoint), where kangaroo road crossings increased with decreases in wind gust and dewpoint and decreased with increases in wind gust and dewpoint, confirmed results of other studies which examined the relationships between kangaroo movements and environmental conditions (Croft, 1980; Southwell, 1987; Montague-Drake, 2003). Kangaroos usually increase their movements when wind gusts are low as dangers can be more readily detected during these times. Strong winds interfere with the hearing of kangaroos so kangaroos respond by being more alert and restricting their movements (Croft, 1980). In addition, kangaroos travel to water when they do not acquire enough water in their diets (Montague-Drake, 2003). That kangaroo crossings increased when dewpoint was

low and decreased when dewpoint was high suggests that kangaroos were seeking water since rain is unlikely to fall when dewpoint is low and high dewpoint indicates imminent rainfall. If rain was about to fall, kangaroos would have no need to move to water troughs located across the road as water would most likely be available in pools on the ground.

4.4.6 Factors that did not influence kangaroo densities and movements

Contrary to expectations, kangaroo densities and kangaroo road crossing frequencies were not influenced by traffic volume along the road. Other studies with higher traffic volumes have clearly found that large mammal movements and densities are influenced by traffic (Rost and Bailey 1979; Van Dyke *et al.*, 1986; McLellan and Shackleton, 1988; Czech, 1991; Thurber *et al.*, 1994; Lovallo and Anderson, 1996; Mace *et al.*, 1996; Dyer *et al.*, 2002). This suggests that kangaroos do not perceive traffic as a great risk and that traffic disturbance does not by itself deter kangaroos from moving towards the road, and agrees with the findings of Cronin *et al.* (1998) and Yost and Wright (2001) where densities of caribou (*Rangifer taradus*) at road areas and their use of road areas also did not differ from those at areas further away from roads. Possible reasons for why kangaroo densities and movements were not influenced by traffic on the road are that vehicles may appear relatively static to kangaroos in comparison to other dangers, such as their natural predators that exhibit more motion in their bodies, and also lack organic scent (as suggested by Whittington *et al.*, 2004), so were not avoided. Indeed, it has often been observed that kangaroos will allow vehicles to approach closer than a person on foot before taking flight (Croft, 1980). However, care should be taken when interpreting results: although no relationships were found between traffic and kangaroo densities and road crossings, kangaroos may still be influenced by traffic. Kangaroos display a variety of behaviours towards approaching vehicles, and many of these behaviours indicate that kangaroos regard approaching vehicles as dangerous (Brown, 2001; Chapter 5). In addition, average traffic volume during the study was low (58.7 ± 1.7 vehicles per day), as were those in Cronin *et al.* (1998) and Yost and Wright (2001), and infrequently dispersed so may not have been great enough to elicit an overall response by way of a movement shift from kangaroos.

Besides traffic volume, total rainfall had no effect on kangaroo densities or kangaroo movements to the road, and this is unexpected given that water is limited in arid ecosystems and more water would be expected to pool on impervious road surfaces after rain compared to more permeable natural surfaces in the hinterland. However, it is possible that after small rain events, water did not pool on the road surface as heat from the road may have evaporated any water, so no differences in amounts of water occurred between road and hinterland surfaces that may influence kangaroo densities. Similarly, after larger rain events, water would have been available both on the road and in the hinterland, so differences in amounts of water between the areas would be minimal and would not influence kangaroo densities. Neither of the weather components associated with barometric pressure and windgust (2), or dewpoint (3), influenced kangaroo densities. This result may be attributed to the fact that none of these weather variables are likely to affect microhabitats around roads.

4.4.7 Effects of the road on kangaroo populations

As no distinct overall movement shift either away from or towards the road was found, it is tempting to suggest that arid-zone roads neither fragment kangaroo populations on either side of roads, nor increase kangaroo mortality rates, and that kangaroo populations are likely to persist near road areas (Jaeger *et al.*, 2005). However, there are several reasons for why these results should be interpreted cautiously. Firstly, arid ecosystems in Australia are characterised by extended and extreme drought periods (Stafford Smith and Morton, 1990). Drought periods influence local kangaroo movements, particularly those of *M. rufus* (Dawson, 1998) and male *M. r. erubescens* (Clancy and Croft, 1992), with movements towards roads increasing during drought as kangaroos harvest limited forage present along road edges (Coulson, 1989; Lee *et al.*, 2004). Increases in kangaroo movements towards the road (and thus densities along the road) during drought periods could lead to increases in mortality compared to periods of non-drought as more kangaroos are present along the road that could collide with vehicles using the road (Lee *et al.*, 2004). Thus, the road could represent an ecological trap for kangaroos during drought periods as their evolved foraging habits during droughts that are normally correlated with

reproductive success could instead result in high adult mortality (Schlaepfer *et al.*, 2002; Aresco, 2004; Ramp *et al.*, 2006).

Secondly, kangaroo mortality rates along the road could be high even if kangaroo densities were low if kangaroos do not perceive traffic along the road as dangerous or exhibit responses towards vehicles that are counteractive to increasing their safety (Chapter 5). Fauna along roads with low and infrequent traffic often suffer from high mortality as fauna do not learn to perceive the road and traffic as dangerous enough to avoid (Ramp *et al.*, 2005). Slight increases in traffic could further exacerbate this situation (provided that increases were not great enough to elicit road avoidance behaviour; Seiler, 2005), increasing kangaroo mortality rates along the road as more traffic would be present along the road that could collide with kangaroos (Forman and Alexander, 1998; Trombulak and Frissell, 2000; Chapter 5).

Thirdly, male *M. rufus* and *M. r. erubescens* were proportionally higher and female *M. rufus* and *M. r. erubescens* proportionally lower along the road, and young-at-foot *M. rufus* (which are still dependent on their mothers and hence found in association with them) were proportionally lower compared to their respective proportions in the hinterland over the study period. These results suggest that spatial selection by the sexes occurred, which was made more pronounced if female *M. rufus* also had young-at-foot, and may be attributed to the riskier behaviour of male kangaroos relative to female kangaroos (Arnold *et al.*, 1994; Coulson, 1997; Lintermans and Cunningham, 1997; Lee *et al.*, 2004), and the solitary behaviour of female kangaroos with young-at-foot (Jarman and Coulson, 1989). Male kangaroos generally have greater food requirements compared to female kangaroos due to their larger body sizes (Priddel, 1986) and may have harvested available food at roadsides to maintain their food intake, despite the costs of being in the road environment. Female kangaroos with young-at-foot tend to isolate themselves from other kangaroos to increase the safety of their young (Croft, 1980; Jarman and Coulson, 1989; Banks, 2001) and may have moved to areas further from roads where disturbance levels were lower. If more male kangaroos are killed along the road relative to females due to collisions with passing vehicles, *M. rufus* and *M. r. erubescens* populations could be disproportionately skewed, leading to demographic changes (Lee *et al.*, 2004; see also Chapter 5). Finally, kangaroo species could differ in their susceptibility of being killed by passing vehicles.

Thus, if a kangaroo species suffered higher mortality rates compared to another species, changes could occur in local kangaroo communities near roads (Lee *et al.*, 2004; see also Chapter 5).

4.4.8 Conclusion

In summary, kangaroos displayed no overall movement shift either away from or towards the road but rather varied their movements and densities in relation to the road depending on various factors. Changes in environmental condition typical of arid ecosystems may influence kangaroo movements and densities around arid-zone roads, and factors other than high kangaroo densities may influence kangaroo mortality along arid-zone roads. Thus, generalisations regarding the overall effects of arid-zone roads on kangaroo movements and their subsequent population and community effects should be made cautiously.

Chapter 5

Patterns, causes and effects of kangaroo-vehicle collisions

5.1 Introduction

The effects of roads and traffic on fauna are many and varied (Andrews, 1990; Trombulak and Frissell, 2000; Spellerberg, 2002; Forman *et al.*, 2003). Mortality of fauna via collisions with motor vehicles (often referred to as wildlife roadkill) is probably the most obvious of these, influencing species from a range of faunal groups worldwide such as amphibians (Fahrig *et al.*, 1995; Hels and Buchwald, 2001), reptiles (Rosen and Lowe, 1994; Bonnet *et al.*, 1999; Haxton, 2000; Aresco, 2005), birds (Hernandez, 1988; Massemin and Zorn, 1998; Mumme *et al.*, 2000), and mammals (Drews, 1995; Clarke *et al.*, 1998; Inbar and Mayer, 1999; Philcox *et al.*, 1999; Caro *et al.*, 2000; Huijser and Bergers, 2000; Jones, 2000; Joyce and Mahony, 2001; Bo Madsen *et al.*, 2002; Saeki and MacDonald, 2004). Large numbers of wildlife roadkill have been documented (Bennett, 1991; Putman 1997; Forman *et al.*, 2003; Ramp *et al.*, 2005) and coupled with small or rare populations that may be additionally fragmented by roads (Jaeger *et al.*, 2005), mortality of fauna via collisions with vehicles has the potential to negatively impact faunal populations (Jones, 2000; Mumme *et al.*, 2000; Dique *et al.*, 2003; Aresco, 2005) and thus affect changes at the community level (Lee *et al.*, 2004).

Investigations have been conducted on a wide range of topics surrounding the issue of roadkill including the patterns and causes of roadkill (Groot Bruinderink and Hazebroek, 1996; Hubbard *et al.*, 2000; Jones, 2000), the costs of roadkill on humans and wildlife (Conover *et al.*, 1995; Conn *et al.*, 2004; Williams and Wells, 2005) and the effectiveness of various abatement technologies used to mitigate the frequency of roadkill (Brown *et al.*, 2000; Bender, 2001; Clevenger *et al.*, 2001; Blackwell *et al.*, 2002; Taylor and Goldingay, 2003; Jaeger and Fahrig, 2004). However, there is a surprising lack of information on variation among ecosystems on the numbers and patterns of roadkill (Brooks and Lair, 2005), faunal behaviour as a causal factor of roadkill (Forman *et al.*, 2003), and the effects of roadkill on faunal population size, demography, and health (Bennett, 1991; Underhill

and Angold, 2000; Spellerberg, 2002; Forman *et al.*, 2003) and on communities (but see Lee *et al.*, 2004), and this constrains the development of strategic management frameworks for mitigating roadkill.

There is an increasing recognition that the ecological effects of roads, including roadkill, should be investigated on an ecosystem-specific basis (Clark *et al.*, 2001; Gutzwiller and Barrow, 2003; Brooks and Lair, 2005). Roads in some ecosystems may provide resources at their edges that are more valuable to fauna than those in other ecosystems (Garland and Bradley, 1984; Trombulak and Frissell, 2000), so draw fauna to roads in these ecosystems and place them at a higher risk of collisions with vehicles (Trombulak and Frissell, 2000; Brooks and Lair, 2005). Alternatively, habitats around roads in some ecosystems may be more modified by disturbance than others, resulting in fauna shifting their movements away from roads and placing them at a lower risk of collisions with vehicles (see Chapter 4; Reijnen *et al.*, 1995; Mace *et al.*, 1996). Related to differences in the patterns and causes of roadkill in various ecosystems are differences in faunal behaviour. Certain species or individuals of particular ages or sexes may differ in their use of road areas depending on the ecosystem that the roads traverse, resulting in some being at more risk than others in collisions with vehicles (Coulson, 1997; Lee *et al.*, 2004; Aresco, 2005). Once in the road vicinity, species or individuals of particular ages or sexes could differ in their behaviours along roads and towards approaching vehicles that could additionally influence their susceptibility of becoming roadkill (Horejsi, 1981; Jones, 2000; Brown, 2001). Recent studies have indicated that high mortalities from collisions with vehicles can have strong impacts on local populations (Rosen and Lowe, 1994; Underhill and Angold, 2000), at times causing local extinctions (Jones, 2000) or affecting the viability of local populations (Lunney *et al.*, 2002). Effects on local populations can lead to community level effects, as the impact of roadkill may affect the populations of sympatric species differently, leading to changes in their proportional makeup (Lee *et al.*, 2004). Thus, as generalisations of the patterns, causes and effects of roadkill cannot be made across ecosystems and species, there is a need for more comprehensive study of effects of roadkill in different ecosystems, focussing also on behaviour as a causal factor of roadkill and their effects on populations and communities.

Limited studies on the patterns, causes and effects of roadkill have been conducted in arid ecosystems (Rosen and Lowe, 1994; Boarman and Sazaki, 1996; Klöcker, 2002; Lee *et al.*, 2004). Roadkill rates may be high along roads in arid areas as herbivorous fauna are attracted to the higher quality forage present at arid-zone road edges relative to the lower quality forage in areas further away from roads (Lightfoot and Whitford, 1991; Lee *et al.*, 2004; Chapters 3 and 4). This effect may be accentuated in drought when overall availability of forage is low (Klöcker, 2002; Lee *et al.*, 2004), given that high quality forage is preferred by arid herbivores such as kangaroos (Dawson and Ellis, 1994, 1996), thereby placing them at high risk of collisions with vehicles. Water pooling on roads may also attract fauna to roads in arid ecosystems where water is limiting (Noy-Meir, 1973; Harrington *et al.*, 1984; Stafford Smith and Morton, 1990), which could similarly increase their susceptibility of becoming roadkill. In addition, feeding and resting sites and limited water resources for herbivorous fauna that are already patchily distributed in the arid zone (Stafford Smith and Morton, 1990; Ludwig and Tongway, 1995) may be located on opposite sides of arid-zone roads, which could lead to an increased risk of roadkill as fauna cross roads to get to these sites and resources. Such effects may vary between species and individuals of different age and sex within a species leading to differential use of roadside resources or frequency of road crossings and susceptibility to becoming roadkill (Klöcker, 2002; Lee *et al.*, 2004). Moreover, differences in behaviour towards approaching vehicles may influence roadkill. Thus, roadkill may impact population size and demographics, and community structure.

In order to build on current knowledge of the patterns, causes and effects of roadkill in arid ecosystems to assist in the development of strategic management of roadkill, this study focused on roadkill of four kangaroo species in arid Australia. The aims of the study were: 1) to quantify roadkill for four sympatric kangaroo species along an arid-zone road, 2) to relate roadkill frequencies with spatial factors, such as road features and vegetation quality at an arid-zone road edge, 3) to relate roadkill frequencies with temporal factors such as climate variation, traffic variables and kangaroo densities, 4) to investigate kangaroo behaviour in response to an approaching vehicle, 5) to relate roadkill frequencies with kangaroo flight behaviour towards an approaching vehicle, and 6) to determine whether any species or age/sex classes are more likely to be killed than others and thus

ascertain the effects of roadkill on the demography of kangaroo populations and on kangaroo communities.

5.2 Methods

5.2.1 Roadkill data

Data for roadkilled kangaroos were collected over 21 months between February 2003 and November 2004. Checks along the road (see section 2.2 for details) for roadkilled kangaroos were conducted every second day from a standard vehicle (see section 4.2.1) travelling at low speed. For each roadkill, the date, location (Garmin GPS II), species, and sex were recorded. When present and relatively undamaged, the heads of kangaroos were collected for an estimation of age by molar progression (after Kirkpatrick, 1965). This method of aging kangaroos is not available for *M. fuliginosus*. However, as *M. fuliginosus* is closely related and similar to *M. giganteus*, the method for aging *M. giganteus* was used for aging *M. fuliginosus*.

5.2.2 Road feature variables

Five hundred and forty-seven points were logged along the road at a rate of every 10 seconds while driving at a constant speed of 25 km/h with a GPS data logger (DGPS-XM-XE, R.I. Keskull) attached to a GPS receiver (Garmin II Plus). Road features at every one of these points were categorised as water sources, man-made obstructions to kangaroo movements, areas of low driver visibility, and combinations of features, and their proportional representation along the road was calculated. Water sources along the road included a wide range of features associated with water and ranged from ephemeral creeks, water drainage channels (eg. culverts), and natural and artificial water sources (for stock) located as far as 200 m from the road (see section 2.2.1.3 for details; Figure 2.6) (although some water sources were located quite far from the road, evidence from Chapter 4 suggests that kangaroos move across roads to these areas to drink). Man-made obstructions to kangaroo movements included stockraces and road cuttings where fences and steep rock faces at the roadside prevented kangaroos from quickly moving away from the road (stockraces are 50-m long fences positioned 1 m from both sides of the road, designed to turn sheep away from the road; see section 2.2.1.4 for details). Curves, borrow pits and

dense shrubs lining the road (shrubby areas; see section 2.2.1.3 for details) were all areas of low driver visibility due to the reduction in drivers' line of sight in curves and the obscuring of kangaroos in the low relief of borrow pits (areas excavated for road construction purposes) and in shrubby areas by vegetation.

5.2.3 Vegetation data

Vegetation data at roadside areas were collected at each roadkill site and at a randomly selected site along the road (random non-kill site) within 1-2 days of discovering a roadkilled kangaroo. Random non-kill sites were selected from 547 previously logged points along the road (see above in section 5.2.2 for details of logging points). Plants were classified as grasses, forbs, copperburrs, round-leaved chenopods (bluebushes), or flat-leaved chenopods (saltbushes) as these groups generally represent the variety of life forms present in rangeland plant communities adapted to arid conditions (Harrington *et al.*, 1984, Dawson and Ellis, 1994; see Table 3.1 in vegetation chapter for more details on plant categories).

At each site, the cover, height and greenness of each plant type were estimated per meter along two 30-m transects orientated perpendicular to the direction of the road (height measured for vegetation structure, and greenness measured for vegetation quality; replicate transects located on either side of the road). This was achieved by laying a 30-m tape across the vegetation and estimating the % cover (proportion of the tape intersected by the plant), height to the nearest 5 cm, and % greenness (0%, 1-20%, 21-40%, 41-60%, 61-80% or 81-100%) in each meter interval. The % greenness of plants were assessed within plant groups as the maximum greenness of one plant group was not necessarily the same maximum greenness attained by another plant group. The mean height and greenness within a metre were weighted by cover if more than one stand of a plant type was measured. Mean values across replicates were calculated to represent a site, and grasses, forbs and copperburrs were pooled into a single "pasture" category for analyses.

5.2.4 Kangaroo densities

Kangaroos were counted along the study road and densities were estimated using the methods outlined in the previous chapter (section 4.2.1) to determine the composition of

the kangaroo source population along the road as it ran through two landscape types (hills and floodplains). Kangaroo densities along the road were derived from the full 83 weeks of data collected between March 2003 and November 2004 (see Table A4.1 in Appendix 4 for dates).

5.2.5 Weather and traffic data

Details of the collection of weather data and the weather variables and factors used in analyses can be found in the previous chapter (section 4.2.3). Similarly, details of traffic data collection and traffic variables used in analyses are outlined in section 4.2.4.

5.2.6 Kangaroo behavioural data

Data for kangaroo behaviour towards an approaching vehicle were collected over approximately two years between March 2003 and February 2005. Data were collected along the same road and hinterland transects used for kangaroo counts. Drives along transects were conducted at various times of day and at different speeds from a standard vehicle (see section 4.2.1). If a kangaroo took flight from the approaching vehicle, the vehicle was stopped and the initial distance between the vehicle and kangaroo before flight was recorded (Bushnell 2000 rangefinder) along with the initial angle of the kangaroo from the vehicle (relative to north) and the position of the vehicle (Garmin GPS II receiver). In addition, the final distances and angles of kangaroos from the vehicle after flight were recorded. Total distances travelled by kangaroos during flight were later calculated using a custom designed *Microsoft Visual Basic* 6.0 application using simple trigonometry.

If a kangaroo did not take flight, the vehicle was stopped when the kangaroo was alongside the vehicle (that is, when the kangaroo was perpendicular to the direction of transects), and its distance and angle from the vehicle and the vehicle's position were recorded. In addition, the behaviour of kangaroos during approach was recorded (included behaviours such as foraging, grooming, fighting; see Croft 1980 for details and descriptions of behaviours exhibited by kangaroos). Other variables measured (for both kangaroos that took flight and kangaroos that did not take flight) included the species and age/sex of the kangaroo, whether the kangaroo belonged to a group, and whether the kangaroo was initially in cover (within 2 m of vegetation or rocks that obscured more than 30% of a

kangaroo). Unfortunately, as for kangaroo counts (see section 4.2.1), there was no way of avoiding the problems of pseudo-replication in this study, but considering that behavioural observations were conducted over relatively large spatial scales, pseudo-replication may not have been overly problematic (Oksanen, 2001, 2004).

5.2.7 Data analysis

5.2.7.1 Spatial patterns of roadkills

5.2.7.1.1 Effects of road features on roadkill frequency

The frequency of roadkills occurring within each type of roadside feature was calculated, and chi-square tests (exact tests with 10, 000 Monte Carlo simulations and the likelihood ratio statistic used to account for the small sample size, SPSS for Windows V13.0) were used to compare the frequencies of roadkills within these features to their expected frequencies based on the proportional representation of the features along the road. Ten features were used in the comparisons and included obstructions, obstructions plus water sources, obstructions plus curves, water sources, water sources plus curves, water sources plus borrow pits, areas of dense vegetation (shrubby areas plus borrow pits), curves, curves plus borrow pits, and residual sections of the road with no features (see section 5.2.2 for details of features). As many features occurred in combination with other features, further comparisons were made for features separately (obstructions vs. no obstructions, water sources vs. no water sources, curves vs. no curves, borrow pits vs. no borrow pits, and shrubby areas vs. no shrubby areas).

5.2.7.1.2 Vegetation at roadkill versus non-roadkill sites

Friedman's tests were used to determine differences in pasture between metre intervals at both roadkill and random non-kill sites, with Dunn's post-hoc test used to reveal where differences lay (significant when $p < 0.05$; Siegel and Castellan, 1988). Only differences between the first metre interval to the other metre intervals and pasture greenness were considered as only pasture at the road edge relative to pasture further from the road edge was of interest (as an attractant to kangaroos) and greenness was a good measure of plant quality (see Chapter 3 for details). Comparisons of pasture greenness

between roadkill and random non-kill sites were made using paired t-tests, using the mean values per metre calculated for pasture greenness at all roadkill and random non-kill sites.

5.2.7.2 Temporal patterns of roadkills

Binary logistic regressions (stepwise forward likelihood method, conducted in SPSS for Windows V13.0) were used to model the probability of a roadkill occurring per week (all kangaroos combined and per species; multiple linear regression not used due to low roadkill numbers per week). Predictors entered into the logistic models were the night-time densities of kangaroos along the road (per species densities entered as appropriate), the average speeds of vehicles during the day and night, the average numbers of vehicles during the night, total current weekly rainfall, total rainfall over the last two weeks, and the weather components. For the model for all species combined, the average number of road crossings (see Chapter 4) was also included. No interactions were examined in the analysis as the combined influences of variables were not regarded to change the probability of a roadkill occurring. Predictors included in the final model were those which were individually significant at $p < 0.05$ (significance statistics for the model log-likelihood ratios, G^2 were used, not for the Wald statistic, as standard errors become inflated when the regression coefficient, β is large resulting in the Wald statistic being underestimated; Field 2000), and included terms for which elimination would have reduced the explanatory power of the model (R_L^2 used, Quinn and Keough, 2002).

To determine the effect of a predictor on the probability of kills occurring, odds ratios ($\text{Exp } \beta$) were used, with values greater than 1 indicating that the predictor increased the probability of a roadkill occurring and values less than 1 indicating the opposite. Checks of model accuracy and assumptions for logistic regressions were made after running the regression. Two measures were used to assess model accuracy and identify influential cases: $Dfbeta$, an analogue of Cook's statistic standardised by its standard error, and leverage measures (values greater than 1 for $Dfbeta$, and values twice the average leverage values are a concern). Outliers were removed if influential cases were found. Checks of collinearity were made by examining Pearson's correlations (Field, 2000; Quinn and Keough, 2002). If variables were found to be highly correlated, the variable that correlated less strongly to the dependent was removed as a predictor.

5.2.7.3 Kangaroo behaviour towards an approaching vehicle

5.2.7.3.1 Influence of night-time versus daytime, and species on kangaroo behaviour

While it is acknowledged that night-time observations of kangaroo behaviour towards an approaching vehicle may have yielded biased results due to only a small area being illuminated by the vehicle's headlights at night (where the behaviour of kangaroos outside of the headlights would be missed), observations of behaviours exhibited during the night were nevertheless deemed as valid for comparisons with behaviours exhibited both within night-time hours and between night-time and daytime hours. Indeed, such comparisons were the only way to determine whether night-time and daytime influenced kangaroo behaviours towards an approaching vehicle as the subsequent analysis for determining the influences of other factors on kangaroo behaviour towards an approaching vehicle is restricted to daytime hours (see section 5.2.7.3.2). This is because these behaviours would be those seen by drivers of oncoming vehicles, and these drivers would be the people involved with dealing with kangaroo behaviour towards oncoming vehicles. Chi-square tests (exact tests with 10, 000 Monte Carlo simulations and the likelihood ratio statistic used to account for the small sample size, SPSS for Windows V13.0) were used to compare the frequencies of behaviours exhibited by kangaroos towards an approaching vehicle between the day and night (pooled across species), and between species during the day and night (only two behaviours: flight and no flight examined). Chi-square tests were used to compare the frequencies of flight directions taken by kangaroos relative to an approaching vehicle between the day and night (pooled across species), with comparisons of flight direction (only two directions: across and away examined) between species also made for daytime and night-time.

5.2.7.3.2 Influence of other factors on kangaroo flight

For an examination of the other factors influencing kangaroo behaviour towards an approaching vehicle (besides night-time versus daytime and species, see section 5.2.7.3.1), a binary logistic regression (stepwise forward likelihood method, conducted in SPSS for Windows V13.0) modelling the probability that a kangaroo would take flight from an approaching vehicle based on various categorical and continuous predictors was used. Prior

to analysis, data were examined to ensure that adequate numbers of observations existed for each level of categorical predictor and for combinations of categorical predictors. If numbers of observations were low, observations were regrouped into broader categories. In addition, continuous data were examined to determine whether their effects on flight were linear. If effects were non-linear, data were grouped into biologically meaningful categories for analysis as interpretations of interactions of non-linear predictors and other variables are difficult. Data exclusions were performed for cases where the genders of kangaroos were unknown, and for night-time observations during which very few high speed drives were conducted and where kangaroos outside of the area illuminated by the vehicle's headlights were not detected.

Predictors entered into the logistic model were time of day (dawn and dusk), site (road and hinterland), speed of the approaching vehicle (continuous variable, ranging from 20 to 80 km/h), distance from the approaching vehicle when flight occurred/closest distance to the approaching vehicle if no flight occurred (continuous variable), kangaroo species (*M. rufus*, grey kangaroos and *M. r. erubescens*), kangaroo age/sex (adult/sub-adult male, adult/sub-adult female, and young-at-foot), group size (one, two and greater than two), presence of cover (yes and no), and season (summer, autumn, winter and spring). Season was considered in this analysis rather than weather variables because fine-scale differences in temperature or rainfall were not considered to significantly influence kangaroo flight behaviour, an anti-predator strategy which should be more or less independent of small changes in environmental conditions. Only biologically meaningful interactions with species were examined in the analysis as the combined influences of other interacting factors were not regarded to change the probability of a kangaroo taking flight. Predictors included in the final model were those which were individually significant at $p < 0.05$ (significance statistics for the model log-likelihood ratios, G^2 were used; see above in section 5.2.7.2), and included terms for which elimination would have reduced the explanatory power of the model (R_L^2 used, Quinn and Keough, 2002).

Significance statistics for Wald were used to determine if the levels within categorical predictors differed from each other in predicting the probability of flight (for predictors that had more than 2 categories). Contrasts between all levels within predictors were achieved by changing reference categories from first to last (predictors with 3

categories) and by recoding categories to contrast remaining categories against each other (predictors with 4 categories). To determine the effect of a predictor on flight, odds ratios ($\text{Exp } \beta$) were used, with values greater than 1 indicating that the predictor increased the probability of kangaroo flight and values less than 1 indicating the opposite. Interactions were difficult to interpret from the regression output; thus chi-square tests were used to determine differences within predictors influencing the probability of flight (exact tests with the likelihood ratio statistic used to account for small sample sizes within some categories; Field, 2000), with the signs of standardised residuals used to determine significant increases or decreases in flight probability. Checks of model accuracy and assumptions for logistic regressions were made after running the regression (see above in section 5.2.7.2 for procedures used and steps taken if assumptions were violated, Field, 2000; Quinn and Keough, 2002). As the model contained categorical predictors, checks of collinearity were additionally made using Cramer's V measure of strength of association for categorical predictors against categorical predictors (Field, 2000; Quinn and Keough, 2002).

5.2.7.4 Relationship between kangaroo flightiness and roadkill frequency

As there was no way to directly relate kangaroo roadkill frequency with the tendency for kangaroos to take flight, it was difficult to determine whether kangaroo flightiness influenced roadkill. However, two other measures of kangaroo flightiness were also measured that could be related to roadkill frequency: the initial distance to flight when flight occurred, and the distance travelled during flight. If species differ in measures of kangaroo flightiness, patterns of species flightiness occur in the same pattern among all measures of flightiness, and there is a relationship between some of these measures and roadkill frequency, it is possible to infer that there is a relationship for all of these measures with roadkill frequency.

To determine if the initial distance to flight and the distance travelled by a kangaroo were influenced by species, univariate GLM (conducted in SPSS for Windows V13.0) were performed. Models also included other influencing factors such as time of day, site, kangaroo age/sex, group size, the presence of cover, season, and the speed of an approaching vehicle (initial distance also included in model for the distance travelled by a kangaroo as an influencing factor). Data where age/sex and distance travelled were

unknown as well as night-time observations were excluded from the analysis. Model terms were added into GLM using a stepwise technique, with all terms and interactions initially entered into models and dropped if not significant at $p < 0.05$. The final models were those which included terms for which elimination would have reduced the explanatory power of the models (Adjusted R^2 used, Quinn and Keough, 2002). Only biologically meaningful interactions with species were investigated, although none were found to be significant. If significant differences were found for species, Bonferroni corrected post hoc comparisons were used to determine where differences lay (Bonferroni's test controls Type 1 error very well and has good power when the number of comparisons is small, Field, 2000). All assumptions for GLM were checked (see section 3.2.3.4 for details of procedures and steps taken if assumptions were violated). Statistics for non-significant terms were obtained by re-running the final model containing all significant terms with each non-significant term included individually. Results for the factors influencing the initial distance to flight and the distance travelled during flight are given in Tables A5.1 and A5.2 in Appendix 5.

5.2.7.5 Population demographic and community effects of roadkill

Comparisons of the numbers of species and sexes killed with their respective numbers in the source populations were made using chi-square tests where the numbers in source population were calculated by multiplying the average species and sex proportions found in the source populations by the total number of kills (hills and floodplains landscape types considered separately). Exact tests with 10, 000 Monte Carlo simulations were used to account for the small sample size (SPSS for Windows V13.0). The numbers of *Macropus giganteus* and *M. fuliginosus* killed were pooled together for analyses as the two species were not distinguished from each other during kangaroo counts. In addition, only the sex frequencies for *M. rufus* and *M. robustus erubescens* were compared as sex determination of *M. giganteus* and *M. fuliginosus* in the source population was not accurate amongst males and females of similar size. Separate comparisons of the frequencies of species killed were made with their respective numbers in the source populations estimated during the day and night.

5.3 Results

5.3.1 Numbers, species, sex and age of roadkills

A total of 92 roadkilled kangaroos were found during the study period (Figure 5.1) which averaged 4.4 kangaroos killed per month ($0.007 \text{ roadkills day}^{-1} \text{ km}^{-1}$), and kills usually occurred during night-time hours. *Macropus rufus* made up the majority of kills, followed by *M. fuliginosus*, *M. r. erubescens* and *M. giganteus* (Table 5.1). Kills of *M. rufus* and *M. fuliginosus* were divided equally between sexes (slight female bias for *M. fuliginosus*). In contrast, more males were killed compared to females among *M. giganteus* and *M. r. erubescens* (Table 5.1). For information on how kills related to species abundances, see section 5.3.6.

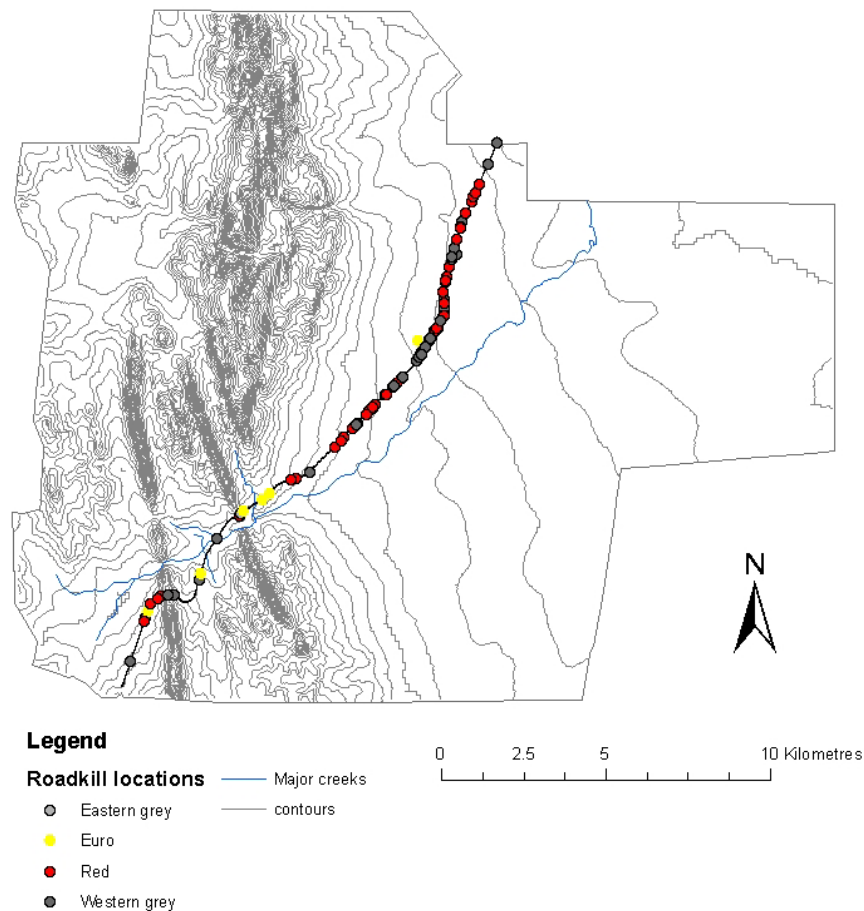


Figure 5.1: Topographic map of Fowlers Gap Arid Zone Research Station showing location of road-killed kangaroos along the Silver City Highway (black line) between February 2003 and November 2004.

Table 5.1: Percentage of kangaroo species killed and percentage composition of males and females killed per species.

Species	Total (n = 92)	* Females (n = 35)	* Males (n = 42)
<i>Macropus rufus</i>	48	50	50
<i>M. fuliginosus</i>	39	53	47
<i>M. giganteus</i>	4	25	75
<i>M. robustus erubescens</i>	9	0	100

* Excludes individuals where sex was indeterminate due to condition of carcass (n = 15).

Roadkilled kangaroos were aged between one and ten years (median = 2, mode = 1, Figure 5.2). When examined per species, roadkilled *M. rufus* and *M. fuliginosus* were made up of mostly young individuals, with 83 % and 71 % of all *M. rufus* and *M. fuliginosus* (n = 34 and 27 for roadkilled individuals of known age, respectively) aged between one and three (*M. rufus*: 56 %, 21 % and 6 %; *M. fuliginosus*: 26 %, 30% and 15 % for ages one, two and three). Roadkilled *M. r. erubescens* were aged 3 and 4 (25 % and 75%, respectively; n = 4 for individuals of known age). Ages of roadkilled *M. giganteus* were unknown.

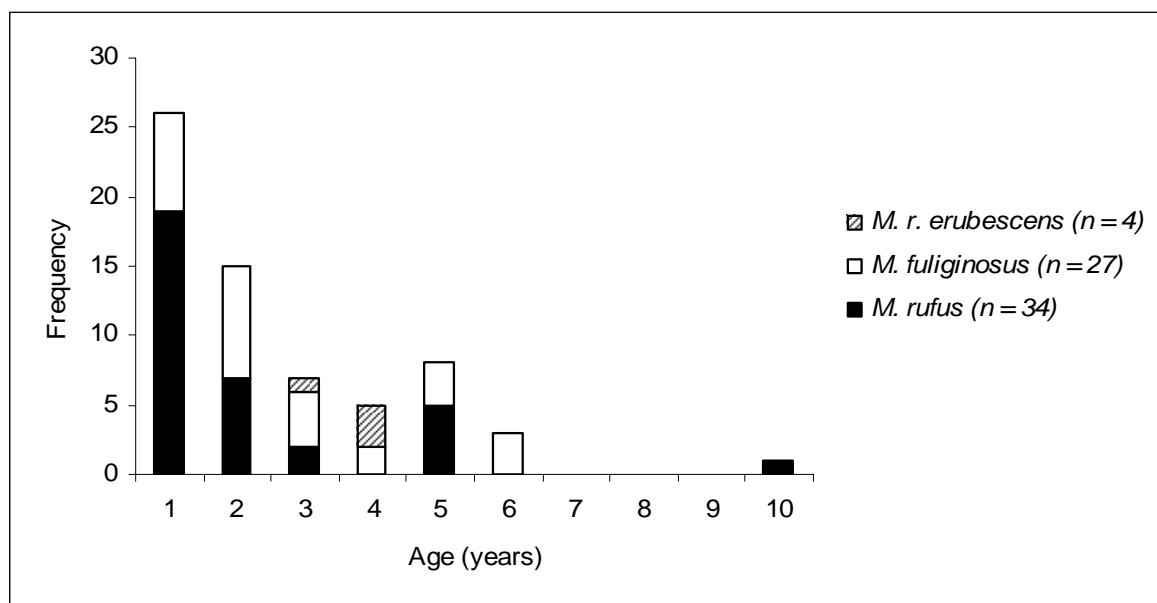


Figure 5.2: Age distribution of roadkilled kangaroos (ages of roadkilled *Macropus giganteus* were unknown).

5.3.2 Spatial patterns of roadkills

5.3.2.1 Effects of road features on roadkill frequency

There was a trend for kangaroos to be killed in areas of dense vegetation lining the road (shrubby areas) more often than expected ($\chi^2 = 16.73$, $df = 9$, $p = 0.075$; observed: 26, expected: 8). Separate analyses for the presence/absence of an individual feature (Table 5.2) revealed only a significant increase in kills in shrubby areas (observed = 15, expected = 5) relative to non-shrubby areas.

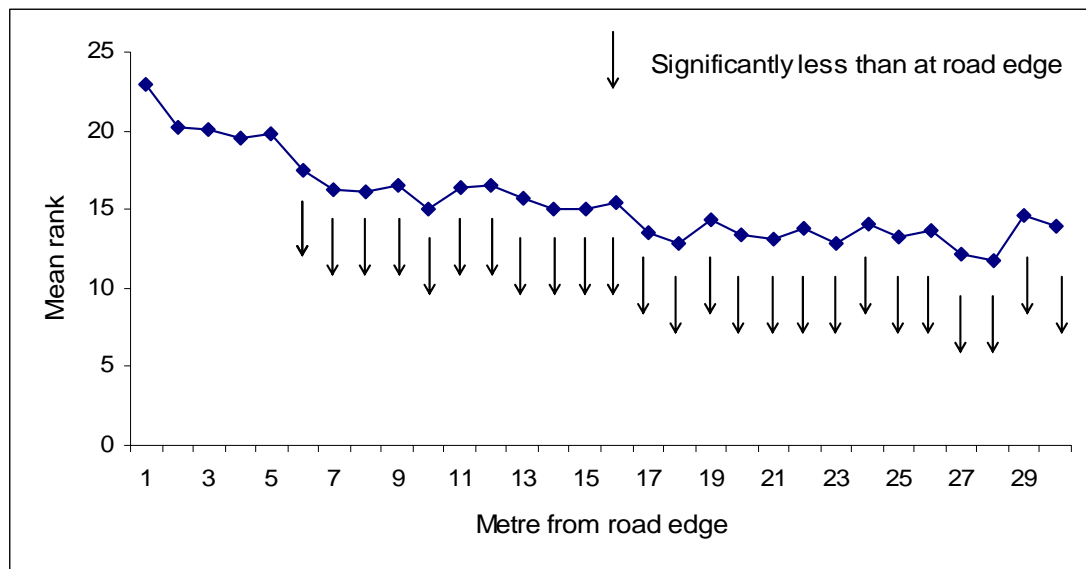
Table 5.2: Results from chi-square analyses comparing kill frequencies in two categories of features present vs. no features present. Significant results shown in **bold**.

Road feature	χ^2	Degrees of freedom	P values
Obstructions	1.92	1	0.237
Water sources	0.03	1	1
Curves	2.06	1	0.211
Borrow pits	2.52	1	0.190
Shrubby areas	5.84	1	0.031

5.3.2.2 Vegetation at roadkill versus non-roadkill sites

Pasture greenness was significantly higher at the road edge compared to the majority of metre intervals out to 30 m from the road at both roadkill and random non-kill sites (Friedman $_{(1,29)} = 175.12$, $p < 0.001$ and Friedman $_{(1,29)} = 131.42$, $p < 0.001$, respectively). Figure 5.3 shows these patterns for changes in greenness values with distance from the road, with mean ranks reflecting higher or lower greenness values (see section 3.2.3.1). However, comparisons of entire transects at kill and random non-kill sites revealed that pasture greenness was significantly higher at kill sites ($t = 7.98$, $df = 29$, $p < 0.001$; kill sites = 48.8 ± 1.2 %, non-kill sites = 43.7 ± 1.3 %). This was also the case for comparisons of pasture greenness at the edge only (first 4 metres) between transects ($t = 3.02$, $df = 3$, $p = 0.057$; kill sites = 61.2 ± 3.5 %, non-kill sites = 58.1 ± 4.4 %).

(a)



(b)

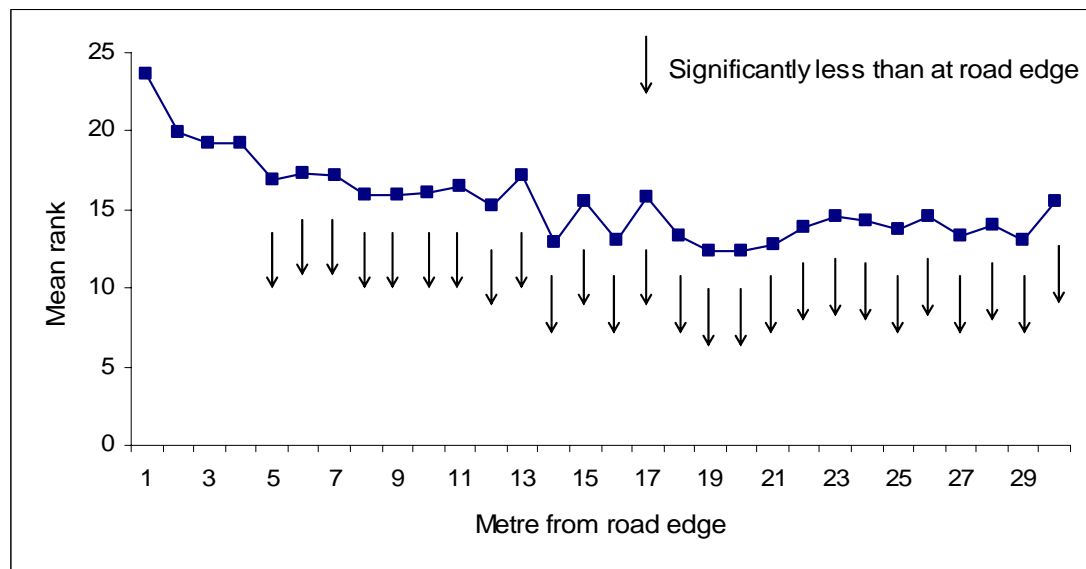


Figure 5.3: Plot of mean ranks of pasture greenness against the perpendicular distance from the road edge at roadkill sites (a) and random non-kill sites (b). Arrows indicate significantly lower mean ranks from the first metre (Dunn's post-hoc tests).

5.3.3 Temporal patterns of roadkills

Logistic regression revealed that the likelihood of a kill occurring per week (all species combined) was influenced by the night-time density of kangaroos ($G^2 = 17.53$, $df = 1$, $p = 0.001$), night-time traffic volume along the road ($G^2 = 21.19$, $df = 1$, $p < 0.001$), and

the weather component (2) associated with barometric pressure and wind gust ($G^2 = 6.23$, $df = 1$, $p = 0.013$), with the final model accounting for 38 % of variation ($R_L^2 = 0.375$, $\chi^2 = 38.43$, $df = 3$, $p < 0.001$). Increases in all variables increased the probability of a kill occurring ($\text{Exp}\beta = 1.50$, 1.44 and 2.23 for the night-time density of kangaroos, night-time traffic volume and Component 2, respectively; equation: $y = 1/(1 + e^{-5.76 + 0.41*\text{night-time density} + 0.37*\text{night-time traffic volume} + 0.80*\text{Component2}})$). Other weather variables did not influence the probability of a kill occurring, even when total rainfall and total rainfall over the last two weeks were categorised into rain/no rain, nor did vehicle speed or the frequency of kangaroo movements across the road.

The probability of a kill occurring for *M. rufus* per week was influenced by the night-time densities of *M. rufus* along the road ($G^2 = 29.55$, $df = 1$, $p < 0.001$) as well as the weather component (1) associated with temperature and humidity ($G^2 = 4.29$, $df = 1$, $p = 0.038$; the final model accounted for 32 % of variation: $R_L^2 = 0.318$, $\chi^2 = 32.05$, $df = 2$, $p < 0.001$). High night-time densities of *M. rufus* increased the probability of a kill occurring ($\text{Exp}\beta = 1.95$) and high temperatures and low humidity decreased the probability of a kill occurring ($\text{Exp}\beta = 0.52$, equation: $y = 1/(1 + e^{-1.93 + 0.67*\text{night-time density} - 0.65*\text{component1}})$). As both maximum and minimum temperature and humidity levels and maximum heat load and minimum windchill loaded on Component 1, further analysis investigating the nature of the influence of Component 1 on the probability of *M. rufus* being killed was performed using “daytime” and “night-time” components of Component 1 (see section 4.3.2 and Tables A4.3 and A4.4 in Appendix 4 for details). Night-time temperature and humidity influenced the probability of *M. rufus* being killed ($G^2 = 5.63$, $df = 1$, $p = 0.018$) suggesting that high night-time temperature and low night-time humidity decreased the probability of a kill occurring (rather than daytime temperature and humidity; $\text{Exp}\beta = 0.56$). Weather components associated with barometric pressure, wind gust and dewpoint, rainfall, traffic volumes and vehicle speeds did not influence the probability of a kill occurring.

The probability of a kill occurring for grey kangaroos per week was influenced by the night-time traffic volume along the road ($G^2 = 22.21$, $df = 1$, $p < 0.001$) and the weather component (2) associated with barometric pressure and wind gust ($G^2 = 7.37$, $df = 1$, $p = 0.007$), with the final model accounting for 23 % of variation ($R_L^2 = 0.227$, $\chi^2 = 23.40$, $df = 2$, $p < 0.001$). Increases in night-time traffic volume and decreases in barometric pressure

and increases in wind gust increased the probability of a kill occurring ($\text{Exp}\beta = 1.32$ and 2.16 for night-time traffic volume and weather component associated with barometric pressure and wind gust respectively, equation: $y = 1/(1 + e^{-4.72 + 0.28*\text{night-time traffic volume} + 0.77*\text{component}^2})$). Weather components associated with temperature and humidity, and dewpoint, rainfall, vehicle speeds and the night-time densities of grey kangaroos did not influence the probability of a kill occurring. No model could be constructed for predicting the probability of a kill occurring for *M. r. erubescens*.

5.3.4 Kangaroo behaviour towards an approaching vehicle

5.3.4.1 Influence of night-time versus daytime, and species on kangaroo behaviour

Kangaroos displayed a higher proportion of flight compared to vigilance or other behaviours during the night, and a higher proportion of vigilance compared to flight or other behaviours during the day (Figure 5.4). Significantly more kangaroos took flight and significantly less showed vigilance or other behaviours during the night compared to during the day ($\chi^2 = 193.72$, $df = 2$, $p < 0.001$; $n = 5,482$). Significant differences (only flight and no flight examined, with vigilance and other behaviours clumped for no flight) existed between species: during the day *M. rufus* (34 %) took flight more often than grey kangaroos (23 %; $\chi^2 = 57.45$, $df = 2$, $p < 0.001$; euros: 35 %; $n = 5,132$), while during the night *M. rufus* (81 %) took flight more often than *M. r. erubescens* (19 %; $\chi^2 = 75.88$, $df = 2$, $p < 0.001$; grey kangaroos: 68 %; $n = 360$).

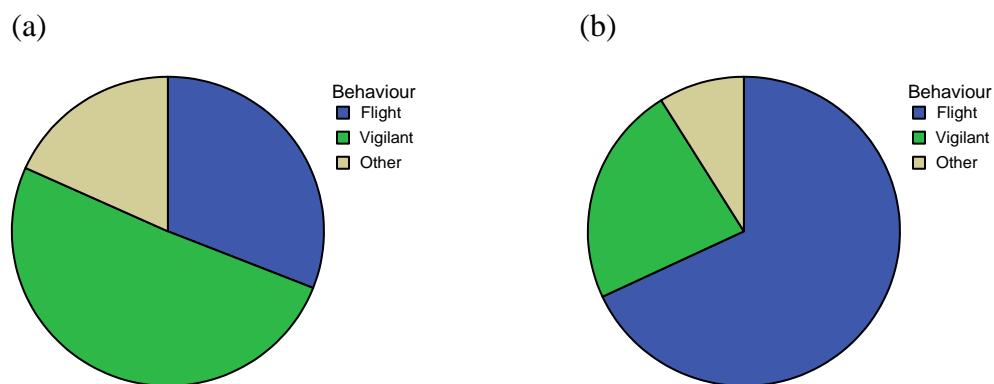


Figure 5.4: Proportional makeup of behaviours exhibited by kangaroos during the day (a) and night (b).

Kangaroos fled away from an approaching vehicle more often than across, parallel and towards the direction of an approaching vehicle during both the day and night (Figure 5.5). However, more kangaroos took flight across the direction of an approaching vehicle and less took parallel flight during the night compared to the day ($\chi^2 = 19.67$, $df = 3$, $p < 0.001$; $n = 1,831$). No differences in flight direction (only across and away examined) were found between species during either the day or night (day: $\chi^2 = 0.85$, $df = 2$, $p = 0.670$, $n = 1,535$; night: $\chi^2 = 0.35$, $df = 2$, $p = 0.878$, $n = 244$).

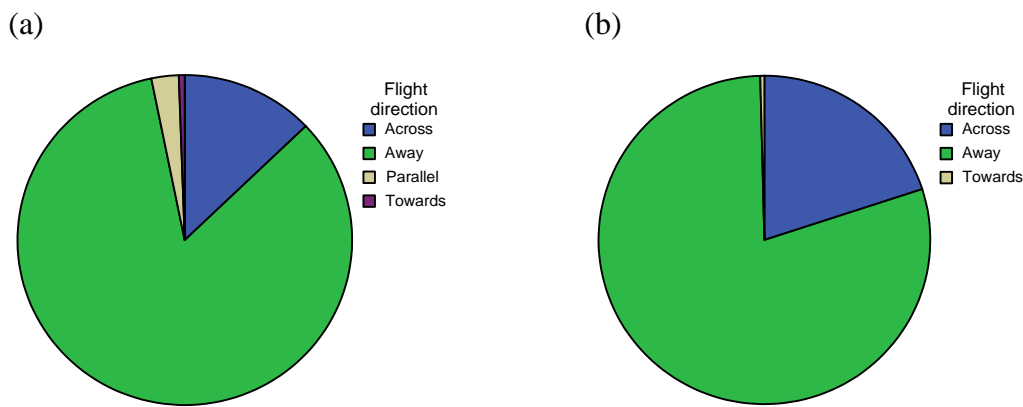


Figure 5.5: Proportional makeup of flight directions taken by kangaroos during the day (a) and night (b).

5.3.4.2 Influences of other factors on kangaroo flight

Site, season and species*cover and species*group size interactions had significant effects on the probability of a kangaroo taking flight (Table 5.3). Likewise, speed of the approaching vehicle and distance from the vehicle had significant effects on the kangaroo flight response (Table 5.3). The odds that a kangaroo took flight in the hinterland was almost three times higher than that of the odds of flight occurring in a similar area sampled along the road ($\exp \beta = 2.93$). The probability of flight was also found to be higher in spring compared to the other seasons (spring vs. summer: Wald = 14.71, $df = 1$, $p < 0.001$; spring vs. autumn: Wald = 15.66, $df = 1$, $p < 0.001$; spring vs. winter: Wald = 20.85, $df = 1$, $p < 0.001$; no differences between autumn, summer and winter in predicting the probability of flight: autumn vs. summer: Wald = 0.02, $df = 1$, $p = 0.893$; autumn vs. winter: Wald = 2.23, $df = 1$, $p = 0.135$; summer vs. winter: Wald = 1.72, $df = 1$, $p = 0.190$), although the odds of flight occurring were not that much higher in spring ($\exp \beta$ only slightly greater

than 1 for all comparisons). For the continuous predictors, the probability of flight was higher when the approaching vehicle was travelling at low speeds, and when kangaroos were closer to the approaching vehicle ($\exp \beta = 1.01$ and 0.99 , respectively).

Table 5.3: Results for the final logistic regression modelling the probability of a kangaroo taking flight (non significant interactions not shown; non significant predictors show scores not G^2 values). The final model accounted for 6% of variation ($R_L^2 = 0.063$, $\chi^2 = 256.13$, $df = 12$, $p < 0.001$). Significant model terms are shown in **bold**.

Model Terms	G^2	Score	df	P values
Time of day		0.37	1	$p = 0.543$
Site	128.48		1	$p < 0.001$
Speed of approaching vehicle	36.17		1	$p < 0.001$
Distance from approaching vehicle	47.34		1	$p < 0.001$
Species		0.21	2	$p = 0.899$
Age/sex		0.45	2	$p = 0.798$
Group size		4.45	2	$p = 0.108$
Cover		0.70	1	$p = 0.405$
Season	24.23		3	$p < 0.001$
Species*Cover	21.93		2	$p < 0.001$
Species*Group size	22.29		4	$p < 0.001$

Cover had a significant effect on the probability of grey kangaroos taking flight ($\chi^2 = 14.28$, $df = 1$, $p < 0.001$) with flight occurring more often when there was no cover (Figure 5.6). Cover had no effect on the probability of *M. rufus* or *M. r. erubescens* taking flight (*M. rufus*: $\chi^2 = 0.17$, $df = 1$, $p = 0.688$, *M. r. erubescens*: $\chi^2 = 1.80$, $df = 1$, $p = 0.209$). Similarly, group size had a significant effect on the probability of grey kangaroos taking flight ($\chi^2 = 18.28$, $df = 2$, $p < 0.001$) with flight occurring more often when kangaroos were in group sizes of one and two (Figure 5.7). Group size had no effect on the probability of *M. rufus* or *M. r. erubescens* taking flight (*M. rufus*: $\chi^2 = 3.61$, $df = 2$, $p = 0.166$, *M. r. erubescens*: $\chi^2 = 4.37$, $df = 2$, $p = 0.118$).

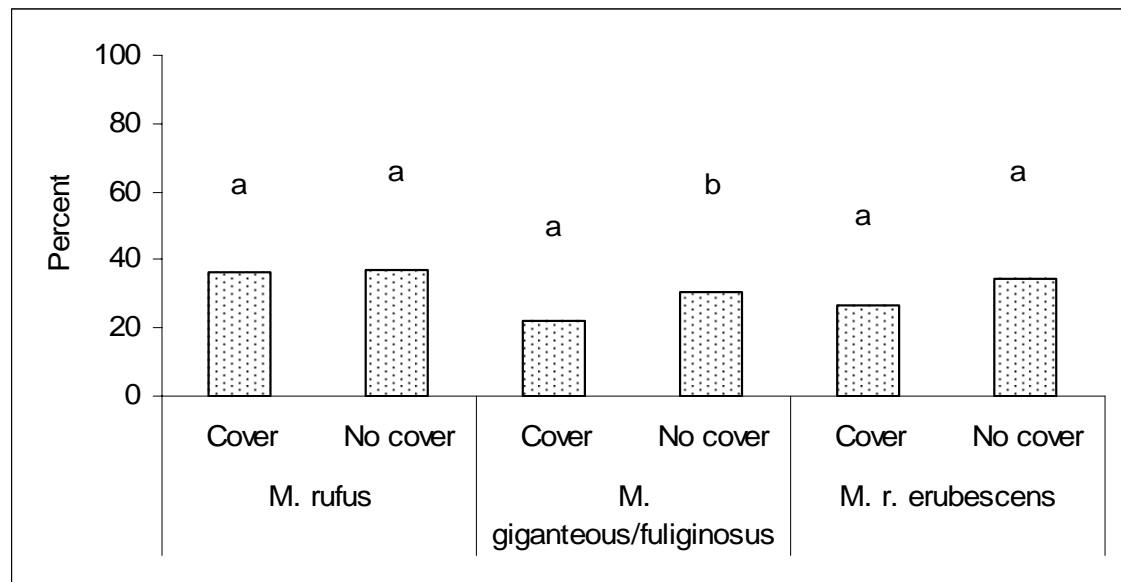


Figure 5.6: Percentage of kangaroos which took flight in two categories of cover for each species. Letters denote significant differences for cover categories predicting flight per species. Results are from separate χ^2 tests per species testing the effect of cover on the probability of flight that followed significant results for species*cover interactions.

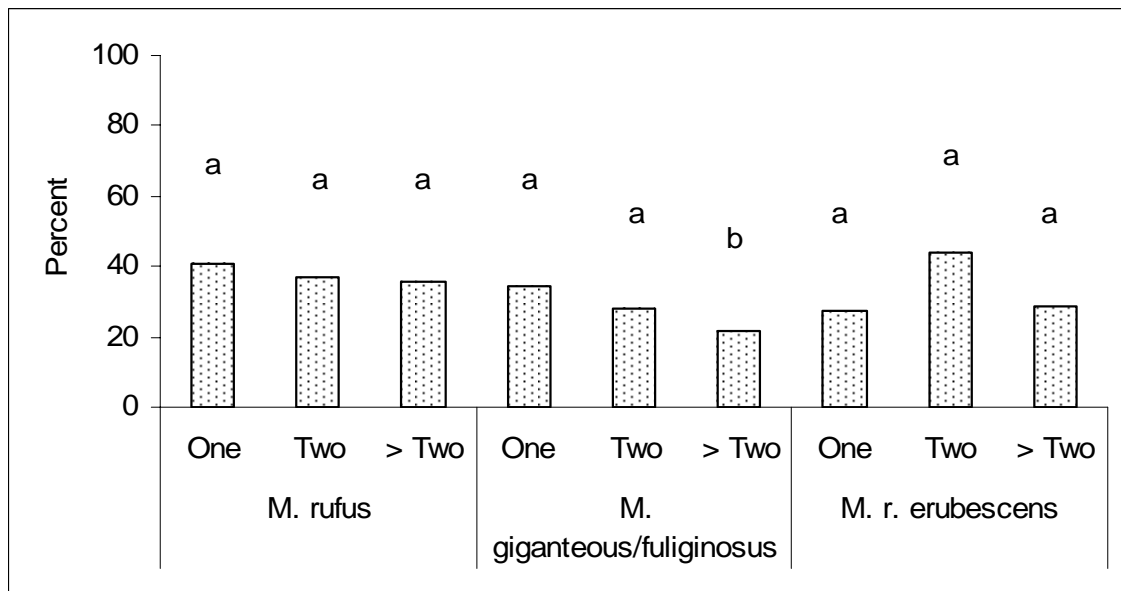


Figure 5.7: Percentage of kangaroos which took flight in three categories of group size for each species. Letters denote significant differences for group size categories predicting flight per species. Results are from separate χ^2 tests per species testing the effect of group size on the probability of flight that followed significant results for species*group size interactions.

5.3.5 Relationship between kangaroo flightiness and roadkill frequency

Both the initial distance to flight and the distance travelled during flight were influenced by species (see Table A5.1 and A5.2 in Appendix 5). Bonferroni tests revealed that *M. rufus* took flight at greater initial distances and travelled further than *M. r. erubescens*, with grey kangaroos intermediate between the two species (Initial distance to flight: *M. rufus* = 152 ± 2 m, n = 2,481; grey kangaroos = 146 ± 4 m, n = 618; *M. r. erubescens* = 77 ± 4 m, n = 181. Distance travelled: *M. rufus* = 107 ± 4 m, n = 692; grey kangaroos = 101 ± 7 m, n = 156; *M. r. erubescens* = 61 ± 8 m, n = 57). These results are consistent with *M. rufus* showing a greater tendency to take flight compared to *M. r. erubescens* and grey kangaroos showing intermediate flight tendencies during the night (section 5.3.5.1), so if there was a relationship between initial distance to flight and roadkill frequency and between distance travelled during flight and roadkill frequency, the same relationship probably held for a kangaroo's tendency to take flight and roadkill frequency.

Kangaroo species with the lowest average initial distance to flight had the lowest kill frequency, while species with higher average initial distances to flight had higher kill frequencies (Figure 5.8). Likewise, kangaroo species with the lowest average distance travelled during flight had the lowest kill frequency, while species with higher average distances travelled during flight had higher kill frequencies (Figure 5.9). Thus, the tendency for kangaroos to take flight compared to exhibit other behaviours probably also relates to kill frequencies in this pattern.

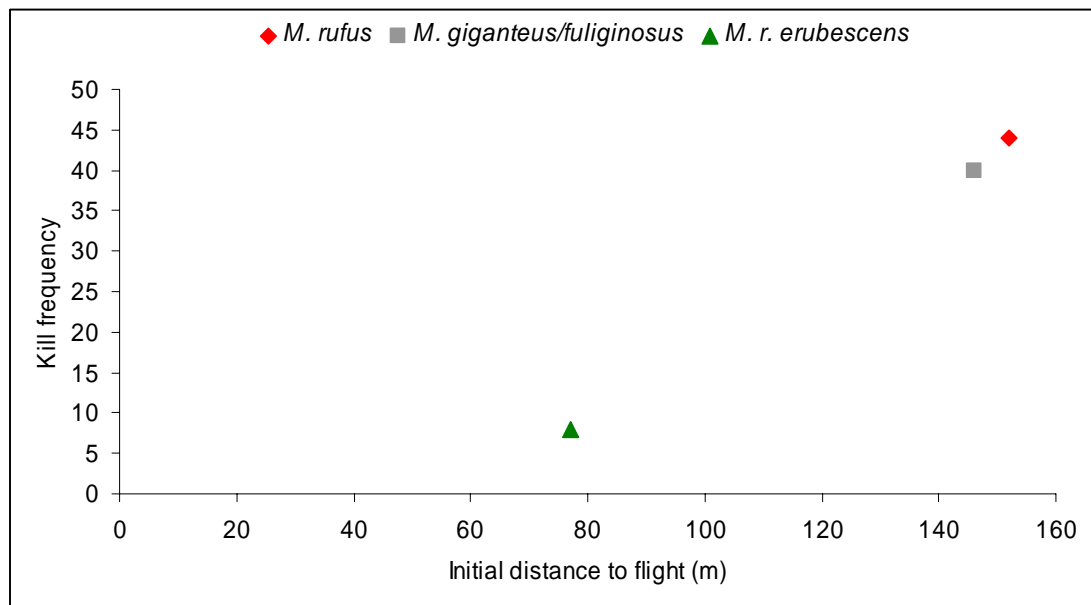


Figure 5.8: Relationship between a kangaroo species' average initial distance to flight (unknown sexes and night-time observations excluded) and kill frequency.

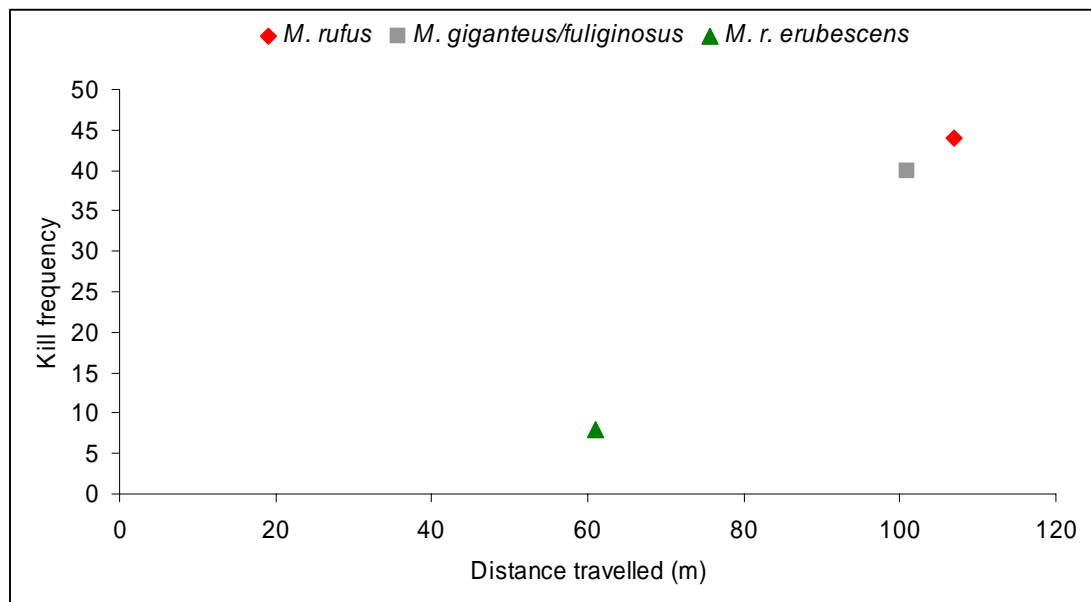


Figure 5.9: Relationship between the average distance travelled by a kangaroo species (unknown sexes and night-time observations excluded) and kill frequency.

5.3.6 Population demographic and community effects of roadkill

Kangaroo species were killed in similar proportions to their estimated proportion of the daytime population in the hills habitat ($\chi^2 = 4.26$, $df = 2$, $p = 0.154$), but fewer grey kangaroos and more *M. rufus* and *M. r. erubescens* were killed than expected in the

floodplains habitat ($\chi^2 = 6.85$, $df = 2$, $p = 0.033$; grey kangaroos: observed: 33, expected: 46; *M. rufus*: observed: 37, expected: 26; *M. r. erubescens*: observed: 2, expected: 0). There were no significant differences in the proportions of species killed to their estimated proportion in the night-time population, although a similar trend for less grey kangaroos and more *M. rufus* killed was again found in the floodplains (hills: $\chi^2 = 0.14$, $df = 2$, $p = 1$; floodplains: $\chi^2 = 6.05$, $df = 2$, $p = 0.079$, grey kangaroos: observed: 33, expected: 19; *M. rufus*: observed: 37, expected: 51; *M. r. erubescens*: observed: 2, expected: 2).

No sex biases were found for *M. rufus* or *M. r. erubescens* when compared to the respective proportions of males and females in the source populations in the hills and floodplains (*M. rufus*: hills: $\chi^2 = 1.53$, $df = 1$, $p = 1$; floodplains: $\chi^2 = 1.68$, $df = 1$, $p = 0.301$; *M. r. erubescens*: hills: $\chi^2 = 3.18$, $df = 1$, $p = 0.455$; floodplains: observed and expected values equal). However, the number of roadkilled male *M. rufus* appeared higher than females in the floodplains habitat, a population that was female-dominated (males: observed = 17, expected = 12; females: observed = 13, expected = 18).

5.4 Discussion

This study showed that roadkill of kangaroos occurred along an arid-zone road at an average rate of 0.007 roadkills $\text{day}^{-1} \text{km}^{-1}$. The study found that spatio-temporal factors, such as the quality of forage at the road edge, areas of dense vegetation along the road, the night-time density of kangaroos in the road vicinity, night-time traffic volume, and some weather variables influenced roadkill, but also clearly revealed that the different flight behaviours of kangaroo species towards an approaching vehicle affected roadkill, especially night-time behaviours when collisions between kangaroos and vehicles generally occurred. As no biases towards any particular species or age/sex class were found in roadkilled animals relative to those in the source population, there was no statistically significant evidence to support the hypotheses that local kangaroo population demographics will be disproportionately skewed, or that the local kangaroo community will change as a result of kangaroo-vehicle collisions. However, data suggested that the behaviour of male *M. rufus* and *M. r. erubescens* that place them at greater risks of collisions than females could potentially skew the population demographics of *M. rufus* and *M. r. erubescens*. Likewise, data implied that *M. rufus* may be killed more often and grey kangaroos less

often than expected from their proportions in the source population, which could possibly impact the composition of the local kangaroo community.

The information obtained from the current study is invaluable to extending current understanding of roadkill along roads in arid ecosystems. The information can lead to the development of more informed management strategies to reduce roadkill frequency along arid-zone roads in the future, and by so doing, prevent any possible population or community changes from occurring as a result of roadkill. Furthermore, information on species' flight behaviour data from this study may be useful in modelling the likelihood of roadkill along roads outside of arid ecosystems; the kangaroo species studied have wide distributions, and information on their flight behaviour towards approaching vehicles can be used wherever these species occur.

5.4.1 Roadkill in an arid ecosystem

The average roadkill rate found in this study fell within the lower range of those of other studies investigating macropod roadkill (0.001 to 0.04 roadkills day⁻¹ km⁻¹; Coulson, 1982; Osawa, 1989; Morrissey, 2003; Lee *et al.*, 2004; Taylor and Goldingay, 2004; Ramp *et al.*, 2005). That the roadkill rate in this study is comparable to those of other studies despite differences in the ecosystems and habitats traversed by study roads, variations in traffic volumes along study roads (the current study had approximately 4 times, 8 times, 50 times, and up to 340 times lower traffic volumes than those of Osawa (1989), Ramp *et al.* (2005), Morrissey (2003), and Taylor and Goldingay (2004), respectively), and variations in macropod population densities along study roads, clearly reinforces the fact that the relative importance of influencing factors for roadkill along different roads vary and ecosystem-specific and species-specific roadkill studies should be undertaken. Obviously, some spatio-temporal factors influencing roadkill will be common along all roads regardless of the ecosystem traversed or species studied, but removing variation between ecosystems and species is an essential step towards better understanding the patterns and causal factors of roadkill.

5.4.2 Spatial factors influencing roadkill

Some of the spatial factors identified as influencing roadkill in this study are in accordance with what was predicted to affect roadkill along an arid-zone road, although a few of the predictions were not substantiated in the current study. One of the more obvious factors that was expected to affect roadkill along an arid-zone road was the availability of high quality forage at roadside areas as high quality forage is limited and patchily distributed in arid areas (Stafford Smith and Morton, 1990) and kangaroos usually select forage that are high in quality and nutritional value (Dawson and Ellis, 1994, 1996; Dawson, 1998). Indeed, roadkill occurred at areas along the road that had higher quality forage (both over the entire 30 m measured from the road edge and at the immediate road edge) than at areas along the road where roadkill did not occur, and was most likely due to kangaroos moving to these areas to harvest available forage. Increased movements to areas along the road with higher quality forage would lead to increases in kangaroo densities in these areas (Chapter 4), which would in turn lead to increased roadkill frequencies as the chances of collisions with vehicles increase when there are more animals present (Mysterud, 2004; Seiler, 2005). In fact, this study also identified night-time densities of kangaroos as the greatest temporal factor influencing the probability of roadkill, with increases in densities increasing the probability of roadkill.

Analyses of forage quality at roadkill areas versus non-roadkill areas were performed on pooled data (for all roadkilled kangaroo species) such that the quality of forage at roadkill sites versus non-roadkill sites per species was not examined. Despite this, the foraging behaviour of the different species could influence the susceptibility of kangaroo species of becoming roadkill and hence partly account for the species composition of roadkill. *Macropus rufus* are more selective feeders than grey kangaroos (Dawson, 1998), with the former species taking in more grass in their diets than browse (Dawson and Ellis, 1994) and the latter group often incorporating browse in their diets (Barker, 1987; Norbury, 1987). Thus, higher densities of *M. rufus* may have been present along the road than grey kangaroos that might place them at a higher risk of being involved in collisions with vehicles. In fact, there was more evidence of *M. rufus* using roadsides as foraging areas compared with grey kangaroos (see Chapter 4), and the probability of *M. rufus* becoming roadkill increased with increasing night-time *M. rufus* densities along the

road, confirming that more *M. rufus* were attracted to the road for forage and were more susceptible than other species to becoming roadkill. *Macropus r. erubescens* are also highly selective feeders (Dawson and Ellis, 1996) so their susceptibility of becoming roadkill might be expected to be high. Apart from during periods of drought when conditions become unfavourable and food sources become scarce, however (where male *M. r. erubescens* may move out of their preferred hilly habitats in search for food; Clancy and Croft, 1992; Lee *et al.*, 2004), *M. r. erubescens* usually remain in small home ranges, so may not have been as susceptible to becoming roadkill as other species in this study.

Another spatial feature that was expected to influence kangaroo roadkill along an arid-zone road was shrubby vegetation lining the road, and this prediction was confirmed in this study. Areas of cover increase roadkill via their effects on increasing animal densities, and the effect of cover on roadkill additionally increases with the proximity of cover to roads and amount of cover in the wider landscape, with less cover in the landscape increasing roadkill frequency compared with more cover (as animals in cover that are already at high densities come into closer proximity to passing vehicles and animals are restricted to limited areas of cover, respectively, Ramp *et al.*, 2005; Seiler, 2005). Arid areas are characterised by heterogeneous distributions of water and nutrients that in turn influence vegetation cover and vegetation type (Stafford Smith and Morton, 1990). As such, vegetation along the road in this study were mostly made up of low shrublands or tussock grasslands, with only very small areas made up of tall open-shrublands or low open-woodlands (see Chapter 2 for more details). Thus, as the areas of cover in the landscape were highly limited and shrubby areas also closely lined the road (sometimes at only 10 m from the road edge) the effect of cover on roadkill frequency in this study was quite pronounced. An additional explanation for the high roadkill frequencies in areas of shrub lining the road may be partly related to grey kangaroo flightiness when cover is present (kangaroos killed in shrubby areas were made up of all species, but grey kangaroos made up approximately 56 % of kills). Grey kangaroos may initially remain vigilant when in cover thereby reducing their likelihood of collisions with vehicles. If vehicles approach to close distances to the cover in which they are sheltering, as in the case where the shrubs closely lined the road, grey kangaroos may react with flight and increase their susceptibility of crossing the path of an oncoming vehicle (see section 5.4.4 for more details).

None of the other spatial features along the road influenced roadkill frequency and this was surprising given that Klöcker (2002) found that water sources and obstructions influenced roadkill at the same study site. Roadkill was expected to be higher at areas along the road where water sources were available given that water is limited in arid ecosystems (Stafford Smith and Morton, 1990), and would likely attract high densities of kangaroos. In addition, roadkill might be higher along areas of the road where obstructions to movement such as road cuttings and stockraces were present as kangaroos that might be harvesting high quality forage at the road might be prevented from escaping from approaching vehicles at these areas. However, unlike Klöcker's (2002) study, which was conducted during an extreme drought period, this study was conducted during a period of less extreme conditions. During drought, water is more limited than during periods of non-drought, so effects on kangaroo densities at water sources may have been greater during drought (see Chapter 4). Furthermore, during drought, more kangaroos are attracted to road areas compared to during non-drought periods (as more kangaroos move to the road to harvest remaining forage in the area, Coulson, 1989; Lee *et al.*, 2004), especially areas along the road that may provide higher quality forage. Areas where obstructions to kangaroo movements occur along the road may provide such high quality forage as obstructions like road cuttings may funnel available water towards the road and promote vegetation growth in these areas (see Chapter 3). During less extreme conditions, forage is less limiting, so kangaroos may not have been as attracted to forage along the road or in dangerous areas along the road (the benefits of harvesting forage at these areas may have been outweighed by the costs of being in the road vicinity, see Chapter 4; Lima and Dill, 1990; Kotler and Blaustein, 1995).

5.4.3 Temporal factors influencing roadkill

Of the temporal factors influencing roadkill, night-time kangaroo densities along the road (discussed above in section 5.4.2), night-time traffic volume along the road, and the weather component (2) associated with windgust (see section 5.4.4) influenced the probability that roadkill would occur (the weather component (1) associated with temperature and humidity also influenced the probability that roadkill of *M. rufus* would occur). Two of these factors (night-time kangaroo densities along the road and weather

component 1) are most likely related to the fact that the study road ran through an arid ecosystem as night-time kangaroo densities were in turn related to the availability of high quality forage and limited presence of cover resources, and arid ecosystems experience extreme temperatures that fauna must cope with. The remaining temporal factors influencing roadkill (night-time traffic volume along the road and weather component 2) are probably more independent of the fact that the road traversed an arid ecosystem as changes in these factors are unaffected by ecosystem type.

Increases in night-time traffic volume and decreases in night-time temperatures increased the likelihood that kills would occur. The positive relationship between traffic volume and roadkill occurrence is in accordance with many other studies that have found traffic parameters to be important predictors of collision risks with fauna (Osawa, 1989; Fahrig *et al.*, 1995; van Langevelde and Jaarsma, 2004; Seiler, 2005). An observation that has been made in some recent studies of the effects of traffic volume is that the effects of traffic volume are not linear and that intensive traffic may repel wildlife from approaching roads, thereby reducing the likelihood of accidents (Clarke *et al.*, 1998; van Langevelde and Jaarsma, 2004; Seiler, 2005; Ramp *et al.*, 2006). This study did not detect this effect, but traffic volumes during the study were most likely too low to induce any avoidance to the road by kangaroos (see Chapter 4).

The effect of higher night-time temperatures decreasing the probability of roadkill occurring for *M. rufus* may have been due to high road temperatures on hot nights, which created an unfavourable microclimate around the road that *M. rufus* may avoid during hot nights. The unfavourable microclimate around the road could lead to decreases in *M. rufus* densities in the road vicinity and hence lower their risks of being involved in collisions. Conversely, the effect of low night-time temperatures increasing the probability of roadkill for *M. rufus* may have been due to their attraction to the warmer road environment during cold nights, leading to increases in *M. rufus* densities. Indeed, high and low ambient temperatures were found to decrease and increase kangaroo densities along the road, respectively (Chapter 4), which lends support to this idea that *M. rufus* avoided unfavourable microclimates and were attracted to favourable ones.

5.4.4 Biological factors influencing roadkill

An important finding of this study was that besides the spatio-temporal factors influencing roadkill, the behaviour of kangaroos towards an approaching vehicle influenced roadkill, with the flightiness of kangaroos in general and the flightiness of different kangaroo species increasing roadkill frequency. These results were inferred from increased roadkill probability with increases in windgust (windgust loaded on weather component 2) as kangaroos often respond to strong winds with increases in flightiness (Croft, 1980; Southwell, 1987; Montague-Drake, 2003) and from the relationships found for the initial distance to flight and the distance travelled by kangaroo species (and hence the tendency to take flight) with roadkill frequency. These results imply that the general behaviour that kangaroos have evolved to deal with perceived high level threats (flight) may not in fact act as an effective defence against the threat of collisions with vehicles (provided that drivers of vehicles do not greatly vary their own behaviours; see further below). Rather, other behaviours which kangaroos have generally evolved to deal with lower perceived threat levels (vigilance: ranging from low, medium to high levels; Colagross and Cockburn, 1993) may be more adaptive against the threat of collisions with vehicles. This result is surprising since, usually, both vigilance and flight are fundamental to a kangaroo's survival as they are performed primarily to minimise a kangaroo's close encounter with predators (Southwell, 1987; Coulson, 1996), and kangaroo flight is more effective an anti-predator behaviour against high level threats than vigilance as kangaroos are usually more able to escape from danger using flight.

A possible reason for why the tendency to take flight may actually increase a kangaroo's susceptibility to becoming roadkill is that kangaroos that take flight have a greater chance of moving into the path of an oncoming vehicle compared to kangaroos that do not take flight. This is especially the case when kangaroos that take flight do so at closer distances to approaching vehicles than those that do not, and across rather than away from the direction of an approaching vehicle. Indeed, the probability of flight in this study was higher when a vehicle approached kangaroos to close distances, and, during the night when kangaroos displayed more flight behaviour than during the day, higher proportions of kangaroos also fled across the path of an oncoming vehicle. Likely reasons for these flight behaviours are that approaching vehicles appear larger and are louder at close distances,

and both large predators or threats, and predators and threats that reach particular threshold distances from animals induce high levels of anti-predator behaviour (Frid and Dill, 2002). In addition, threats can be seen and detected by kangaroos at greater distances during the day compared to during the night when only the headlights of approaching vehicle are seen, so vehicles during the day that could be detected more clearly may have been perceived as less threatening. Moreover, average night-time traffic volume was lower than average daytime traffic along the road (see section 2.2.1.5), and animals often invest higher levels of anti-predator effort in situations where threats are brief and infrequent (Lima and Bednekoff, 1999). More flight across the direction of an approaching vehicle at night compared with during the day may also be related to lower night-time visibility, where kangaroos possibly could not as readily predict the direction of vehicle travel in order to flee away from danger.

Differences in flightiness among the species are most likely related to both the habitat preferences of the kangaroo species and their various responses to predators or perceived risks (note that no species effect was detected in the logistic regression and this was most likely related to the incorporation of other influencing factors in the logistic model. Species is nevertheless considered as a significant factor influencing flight as significant interactions with species were found from the logistic model, and significant species effects were found in the chi-square analysis and GLM for other measures kangaroo flightiness). *Macropus rufus* generally prefer open habitats that have occasional patches of shrubs and shade trees (Priddel, 1988; Croft, 1991a; Dawson, 1998), grey kangaroos prefer habitats with shrub or tree cover (Southwell, 1987; Priddel, 1988; Arnold *et al.*, 1992; Coulson, 1993a and b), and *M. r. erubescens* prefer rough, hilly habitats (Croft, 1981; Croft, 1991b; Clancy and Croft, 1992). As the open habitat preferred by *M. rufus* provides little cover, *M. rufus* are at high risk from being detected by predators (Barry, 2004), so may rely on early flight and long flight distances away from approaching danger, plus their superior speed in open country to escape from predators or situations perceived as risky (Dawson, 1998).

In contrast, the habitat of grey kangaroos provides more cover than that of *M. rufus*, and this cover decreases the likelihood of grey kangaroos being detected by predators. As a first line of defence against predators or risky situations, grey kangaroos may remain

vigilant in cover rather than take flight since their perceived levels of risk while in cover may be low and flight may do little to increase their safety (Frid and Dill, 2002). Indeed, of the kangaroo species, grey kangaroos in this study took flight less often when they were in cover compared to when they were not in cover. If pressed, grey kangaroos in cover may eventually switch to flight, their second line of defence from predators or situations of high risk, as in the case of other animals which flee when predators or approaching disturbance exceed specific threshold distances (Frid and Dill, 2002), but may nevertheless remain in cover, relying on the cover of their preferred habitat and their mobility to escape from predators or risky situations (Dawson, 1998). When not initially in cover, flight behaviours of grey kangaroos may be similar to that of *M. rufus*, although movements will usually be towards cover rather than across open country (Croft, 1989), reflecting their preference for habitats with cover. Besides being related to habitat preferences, flight behaviour in grey kangaroos may also be influenced by group size (Frid and Dill, 2002). The probability of flight for grey kangaroos that were alone or in groups of two was higher than for grey kangaroos in larger groups. This may be due to grey kangaroos in smaller groups having to invest higher levels of anti-predator effort than those in larger groups as the probability of detecting danger in smaller groups is lower (Jarman, 1987; Jarman and Wright, 1993) and the risk of predation is higher for smaller groups (Banks, 2001; Lett *et al.*, 2004). Lastly, *Macropus r. erubescens* can be difficult to detect in their preferred rocky habitats and can avoid detection by predators altogether by remaining still (pers. obs). If detected, flight may occur and the short distances travelled during flight may be related to the rough terrain that may deter predators from pursuit, but pose no movement problems for *M. r. erubescens* (Dawson, 1998).

Since kangaroo roadkill frequency increased with increasing kangaroo flightiness, it would be expected that any other factors increasing kangaroo flightiness in general would also increase roadkill frequency (such as closer distances approached by vehicles; see above). Two factors, the speed of an approaching vehicle, and transect on which the approaching vehicle was travelling (site) influenced the probability of flight for kangaroos. However, an increase in roadkill frequency may not necessarily have occurred in situations where these factors increased the probability of flight (at low speeds and in the hinterland). This is because when travelling at these conditions, drivers of vehicles would be able to

influence the likelihood of collisions by reacting to and avoiding kangaroos before collisions occurred (the time taken to halt a vehicle is shorter when travelling at slow speeds and speeds were slower out of necessity in the hinterland compared to along the road). This clearly illustrates that driver behaviour can also influence roadkill frequency, an observation that has also been made in other studies (Jones, 2000; Dique *et al.*, 2003; van Langevelde and Jaasma, 2004). The current study did not explore the influence of driver behaviour in detail. Plainly, this area of study may be one of importance as it can be targeted as a form of roadkill mitigation and deserves further investigation.

A possible reason for why kangaroos were flightier towards a vehicle travelling at low speed compared to one travelling at high speed may be that kangaroos have learnt to associate the appearance of vehicles with the faster loom rate that occurs once vehicles are closer (Frid and Dill, 2002) (looming is the term given to the accelerated magnification of the form of an approaching object over time; Horejsi, 1981). Increased flightiness towards vehicles is usually associated with those travelling at higher speeds, but Frid and Dill (2002) argue that with repeated exposure to stimulus, increases in flightiness may occur (even at low speeds), and also that slower disturbance stimuli are analogous to a stalking predator so may be perceived as more dangerous to animals than a faster stimulus. Sampling biases may have influenced results though: when travelling at high speeds, it was not as easy to detect kangaroos and subsequently observe their behaviours towards the approaching vehicle, so some kangaroo behaviours at high speeds may have been missed. Differences in the probability of flight in response to vehicles approaching on road and hinterland transects may reflect temporal variations in danger (Lima and Bednekoff, 1999). In this study, traffic volume was low in the hinterland, consisting mainly of motorbikes that traversed the hinterland track infrequently, with traffic volume higher along the road. Animals exposed to brief and infrequent periods of high-risk allocate high levels of anti-predator effort, and those exposed to more prolonged periods of high-risk are forced to decrease their allocation of high level anti-predator effort to allow for feeding time (Lima and Bednekoff, 1999). Thus, the difference in the probability of kangaroo flight in the two areas could be a reflection of responses to brief versus prolonged periods of high risk. Alternatively, differences in the probability of kangaroo flight in the two areas may be due to differences in resource availability. Frid and Dill (2002) argue that if resources are

higher in certain areas, lost benefits of acquiring these resources after fleeing are higher than in areas with lower resources. There was evidence that resources along the road were higher in quality than they were in the hinterland (Chapter 3), so this may indeed have accounted for differences in flight probabilities in the two areas.

Contrary to expectations, the age or sex of kangaroos did not influence two out of three of the measures of kangaroo flightiness so could not account for the large proportion of young kangaroos killed or the slight male bias in roadkilled *M. giganteus* and *M. r. erubescens*. Young-at-foot were expected to be more flighty than adult kangaroos as they represent the most sensitive class to predation (Banks, 2001; Dawson, 1998). Also, as young-at-foot are naïve and unaccustomed to threats they were expected to respond to all threats with similar levels of anti-predator behaviour (presumed to be high levels). Real differences in flightiness between age/sex classes may not have been detected in this study, though. This may have been due to the grouping of age/sex classes into more general categories in analyses to ensure adequate frequencies per category resulting in a loss of power in detecting an effect. Grouping of females belonging to different reproductive states may have been particularly problematic as reproductive females, females with young-at-foot, and females without young behave differently (Croft, 1980; Jarman and Coulson, 1989; Colagross and Cockburn, 1993; Banks, 2001), with reproductive females (those with heavy pouch young) investing more of their time being vigilant (Colagross and Cockburn, 1993).

5.4.5 Effects of roadkill on kangaroo populations and communities

There was no evidence for population demographic effects in this study (no sex biases were found in roadkilled *M. rufus* and *M. r. erubescens* compared to their respective proportions in the source population, and the age structure of roadkilled animals (for *M. rufus* and *M. fuliginosus* at least) reflected the pyramidal age distributions of kangaroo populations (Norbury *et al.*, 1994)), so it would appear that kangaroo populations in this study are not suffering from disproportionate skews towards any particular sex or age group. However, source population data used in sex analyses were populations along the road at immediate risk of being involved in collisions with vehicles, and these populations had higher proportions of males compared to the proportions of males in hinterland populations

(Chapter 4). Moreover, there was a slight trend for more *M. rufus* males killed than females even within the female-dominated road population. This illustrates that male *M. rufus* and *M. r. erubescens* may have been differentially killed based on their tendency to move to roadside areas (Chapter 4), their riskier behaviours compared to females (Arnold *et al.*, 1994; Colagross and Cockburn, 1993), or their wider movement patterns compared to females (*M. rufus*: Norbury *et al.*, 1994; *M. fuliginosus*: Arnold *et al.*, 1992; *M. giganteus*: Jaremovic and Croft, 1991; *M. r. erubescens*: Clancy, 1989), which could potentially skew their population demographics. Other studies of macropod roadkill have also found a male bias in roadkill (Coulson, 1997; Lintermans and Cunningham, 1997) and a bias towards young kangaroos (Klöcker, 2002). Consequences of differential male and juvenile mortality in kangaroos may not necessarily affect the viability and health of kangaroo populations though, even if population demographics are disproportionately skewed. Selective male and juvenile mortality in kangaroo populations may reduce genetic variation and reproductive success if there are fewer males or young individuals left in populations, but males in sexually dimorphic species typically have higher mortality rates and lower life expectancy than females anyway, as do juveniles compared to adults (Clutton-Brock *et al.*, 1985) and there are likely to be surplus breeding males (Clancy and Croft, 1992) and juveniles in kangaroo populations.

No evidence for changes in kangaroo communities as a result of roadkill were found from analyses of the kangaroo species killed compared with their proportions in the source population along the road. There was a slight trend for more *M. rufus* and less grey kangaroos killed in the floodplains habitat, a finding that has also been found in previous investigations in the same area (Lee *et al.*, 2004), reflecting the greater tendency of *M. rufus* to take flight and higher night-time *M. rufus* densities along the road compared to grey kangaroos. This selective mortality could potentially affect the composition of kangaroos in the area as grey kangaroos could become more numerous in relation to other kangaroo species along the road. However, given that *M. rufus* have a greater ability to reproduce in good conditions compared with grey kangaroos (as the more common of the grey kangaroo species in the area, *Macropus fuliginosus*, lacks embryonic diapause, generally breeds on a seasonal basis, and have young-at-foot that remain with their mothers for longer periods of time compared to other kangaroo species; Dawson, 1998), the slight

bias towards *M. rufus* being roadkilled is probably easily offset by the rapid replacement of individuals within their population.

5.4.6 Management options

Although the health of kangaroo populations (if not their population demographics) and the composition of the kangaroo community may have been relatively unaffected by roadkill along the arid-zone study road, findings of this study could be used to develop suitable management strategies to mitigate the frequency of roadkill along arid-zone roads. Kangaroo populations already suffer mortality from other sources (for example, harvesting for human and animal consumption) and added to these sources, mortality of kangaroos by roadkill is possibly quite high (Ramp *et al.*, 2005). Possible approaches for mitigating roadkill on roads traversing arid ecosystems could involve shifting palatable vegetation further away from roadsides, and/or allowing unpalatable vegetation to grow at the road edge since limited food resources of arid areas were a strong influencing factor for kangaroo roadkill. Either approach could decrease a kangaroo's susceptibility to becoming roadkill as in the former situation kangaroos attracted to roadside forage would be placed outside of immediate danger of collisions with vehicles, and in the latter situation there would be no incentive for kangaroos to approach the roadside verge.

The current management practice along the study road of mowing roadside vegetation (carried out to improve safety through improving driver visibility in the road vicinity, see section 2.2.1.5) is not recommended as a management option for reducing roadkill along arid-zone roads. This is because mowing of vegetation along arid-zone roads increases the quality of roadside forage (see Chapter 3) and attracts kangaroos. Fences erected along shrubby areas lining the road could also be used as a mitigation strategy along arid-zone roads to prevent kangaroos from crossing roads running through these areas. However, more research on this approach is needed as fences often funnel fauna attempting to cross roads to areas where the fences terminate, which lead to increased roadkill occurrences at these areas (Clevenger *et al.*, 2001).

There is possibly very little management that can be specifically undertaken to target *M. rufus*' tendency to approach the road vicinity on cool nights or the flight behaviour of kangaroos in order to reduce their susceptibility of colliding with vehicles.

Indirect management could therefore include mitigation strategies that are not specifically aimed at roads traversing arid ecosystems but rather are common to mitigating roadkill along all roads, such as reducing vehicle speeds as drivers can better respond to and avoid possible collisions with kangaroos and reducing night-time traffic volume as the probability of roadkill increased with increasing traffic volume.

5.4.7 Conclusion

In summary, this study showed that spatial, temporal and biological factors that led to higher quality forage at the road edge, areas of dense cover along the road, favourable microclimates around the road, and kangaroo flightiness, along with high traffic volumes, increased roadkill along an arid-zone road, mainly through their effects on increasing kangaroo densities in the road vicinity and increasing the likelihood of kangaroos crossing paths with approaching vehicles. Thus, the road acted as an ecological trap for kangaroos since the behaviours that kangaroos have evolved to deal with both arid conditions and potential threats, which are normally correlated to survival and reproductive success, instead resulted in their mortality (Schlaepfer *et al.*, 2002; Aresco, 2005). There was evidence of skews in kangaroo population demographics and trends for potential changes in the composition of kangaroo species due to roadkill, but the population viability and composition of kangaroo species are unlikely to be affected by roadkill. Nevertheless, arid-zone roads could be managed to reduce the overall frequency of roadkill, with strategies targeting roadside vegetation or driver behaviour most useful for mitigating roadkill frequency. Differences in species flight behaviour may be more difficult to target, but species flight behaviour data can be used in predictive models of roadkill in other ecosystems where these kangaroo species occur.

Chapter 6

Effects of the road on small mammals

6.1 Introduction

The effects of roads and traffic on fauna are many and varied (Andrews, 1990; Trombulak and Frissell, 2000; Spellerberg, 2002; Forman *et al.*, 2003). Some of their more significant effects are their impacts on faunal movements: fauna may change their movement patterns around roads such that their overall abundances decrease or increase in the vicinity of roads relative to the hinterland, and fauna may change their movement patterns across roads such that their frequencies of road crossings decrease or increase (Forman and Alexander, 1998; Spellerberg, 1998). Faunal movement changes around and across roads may impact the health and stability of populations, especially if shifts in movement are disproportionate between ages and sexes: movements away from roads (exacerbated by decreased movements across roads) may result in faunal populations on either side of roads becoming effectively fragmented and increasingly isolated (Reijnen *et al.*, 1995; Vos and Chardon, 1998; Huijser and Bergers, 2000; Dyer *et al.*, 2002), and movements towards roads (exacerbated by increased movements across roads) may result in higher rates of faunal mortality as fauna come into contact with vehicles using roads (Rosen and Lowe, 1994; Fahrig *et al.*, 1995; Aresco, 2005; Boarman and Sazaki, 2006; Ramp *et al.*, 2006). Moreover, altered faunal movements may have community-level impacts as species within communities may have different responses to roads (Meunier *et al.*, 1999a, b; Goosem, 2000, 2001; Vega *et al.*, 2000; Gutzwiller and Barrow, 2003; Lee *et al.*, 2004). These population and community effects are by no means local. Road networks now permeate ecosystems worldwide; thus, faunal movement shifts around and across roads are of global significance and mitigating their negative impacts must occur on larger regional or landscape scales.

Possible causative factors for faunal movements away from, towards and across roads have been identified in previous reviews (Trombulak and Frissell, 2000; Spellerberg, 2002; Forman *et al.*, 2003). For small mammals, movements away from roads (Adam and

Geis, 1983; Goosem, 2000; Huijser and Bergers, 2000) and limited movements across roads (Mader, 1984; Garland and Bradley, 1984; Richardson *et al.*, 1997; Goosem, 2001; Rondinini and Doncaster, 2002) often occur due to the sudden convergence of contrasting microclimates and habitats around roads which represent unfavourable environments for many species (Mader, 1984; Goosem, 2000) (although contrasting habitats around roads can at times attract some small mammal species with preferences for edge habitat; Adams and Geis, 1983; Goosem, 2000). Small mammals also move away from roads or limit road crossings to avoid open spaces near and on roads that increase their risk of predation (Barclay, 2004) and to avoid disturbances from vehicular traffic (volume, noise, movements, and emissions) occurring in broad bands of various distances around roads (disturbed areas may be sub-optimal environments for many species, Mader, 1984; Richardson *et al.*, 1997; Clarke *et al.*, 1998; Kraaijeveld-Smit *et al.*, 2002; Rondinini and Doncaster, 2002; McDonald and St. Claire, 2004). Movements towards and across roads occur if road habitats or habitats across roads provide higher quality resources in comparison to surrounding areas, such as food and shelter (Garland and Bradley, 1984), and if small mammals are dispersing (Burnett, 1992; Goosem, 2001). However, small mammal movements in relation to roads are affected to varying degrees by the scale of microclimate/microhabitat differences around roads, the width of roads, the levels of predation risk and disturbance along roads, the resources available at roadsides and across roads, and the requirements to cross roads (Bennett, 1991; Van Langevelde and Jaarsma, 1995). Some of these factors, such as the scale of microhabitat changes and the availability of resources around and across roads are affected by the ecosystems traversed by roads. This is because roads interact with ecological processes unique to ecosystems and this influences the magnitude of road effects (Gutzwiller and Barrow, 2003; Brooks and Lair, 2005). Because of the influence of ecosystems on road effects that in turn influence small mammal movements, it is essential that the effects of roads on small mammals be investigated on an ecosystem-specific basis. Without this knowledge, mitigating the negative impacts of altered movement patterns around roads can not be undertaken with confidence.

An ecosystem in which small mammal movements are impacted by roads yet remains little studied is an arid ecosystem (Brooks and Lair, 2005; but see Garland and

Bradley, 1984). Roads in arid ecosystems may not be high in density, but arid ecosystems cover up to one third of the earth's land surface (Kinlaw, 1999), so are ecosystems in which the effects of roads should be studied. Arid-zone roads may influence small mammal movements in various ways. Firstly, arid-zone roads may alter vegetation at their edges (Chapter 3; Lightfoot and Whitford, 1991; Lovich and Bainbridge, 1999; Norton and Stafford Smith, 1999; Lee *et al.*, 2004), with vegetation increasing in quality and productivity. This higher quality vegetation may attract invertebrates, and in turn, both the better quality vegetation and potentially higher densities of invertebrate prey may attract small mammals (Southgate and Masters, 1996; Morton, 1978, 1982; Letnic *et al.*, 2004) in an environment where food and shelter resources are patchily distributed (Stafford Smith and Morton, 1990). Secondly, water pooling on roads may attract small mammals (Dickman *et al.*, 1995) as water is limiting in arid ecosystems (Noy-Meir, 1973; Harrington *et al.*, 1984; Stafford Smith and Morton, 1990). Thirdly, higher temperatures radiated from dark, sealed road surfaces compared to natural surfaces of a higher albedo may attract or repel small mammals depending on ambient conditions.

Since arid-zone roads have the capacity to alter small mammal movements around them with potentially serious consequences on populations, the nature of small mammal movements around arid-zone roads should be known. Thus, this study focused on small mammal species present in arid Australia and investigated their use of an arid-zone road. In Australia, the conservation of arid-zone small mammals is of national importance since many small arid-zone mammal species have already become extinct since European settlement (Dickman *et al.*, 1993; Dickman, 1994). Therefore, understanding how threats posed by anthropogenic disturbances such as roads impact small mammals in arid ecosystems, and the collection of baseline information for the development of informed management frameworks for arid-zone roads are of particular relevance in Australia. The aims were: 1) to determine whether small mammal communities near an arid-zone road differed from communities further from the road, 2) to relate small mammal communities with microhabitat variables and food availability, 3) to relate variation in abundance near and away from an arid-zone road for common small mammal species with proximity to the road, microhabitat variables and food availability, 4) to determine whether the sex ratios of common small mammal species near an arid-zone road differed from their respective sex

ratios further from the road, 5) to relate variations of small mammal biomass and richness with proximity to an arid-zone road, microhabitat variables and food availability, and 6) to investigate small mammal movements across an arid-zone road.

6.2 Methods

6.2.1 Monitoring sites

Vegetation and other resources in the arid zone are typically patchy on a heterogeneous landscape. This variation may influence small mammal distributions and abundances so temporal variation in small mammal and invertebrate communities and microhabitat variables are best measured from changes at fixed sites across a range of seasonal conditions rather than a set of randomly selected sites at each sampling period. Therefore, ten permanent replicate sites were established along the study road (see section 2.2 for details of study road) for small mammal surveys and measurements of accompanying invertebrate abundance and richness, and microhabitat variables. Replicate sites were the same as those used for vegetation and soil measurements (five in the hills and five in the floodplains, see section 3.2.1.1 for more detailed site selection methods) and comprised of three monitoring areas based on distance from the road. These were the road edge (located 10 m from the road edge), the fence (located approximately 50 m from the road edge and running parallel to the road), and the hinterland (located 250 m from the road edge) (Figure 6.1). Road edge and hinterland positions were further replicated on either side of the road at each site (Figure 6.1). Distances from the road were chosen on the basis that small mammals in arid areas are able to cover distances up to 200 m as part of their usual foraging/other activities (Read, 1984) (road edge positions at 10 m from the edge were due to restrictions imposed by the NSW Roads and Traffic Authority on placing objects in roadside areas). Hinterland monitoring areas were considered to be far enough from the road to be relatively unaffected by the road since Chapter 3 revealed that the effects of the study road on vegetation and soil variables extended only a short distance from the road (effects were already non-significant from 50 m away from the road). The lack of a greater number of spatial replicates through the monitoring of additional roads is a potential limitation of the study, but many authors such as Oksanen

(2001, 2004) argue that reasonable predictions can nevertheless be made from large-scale studies lacking such replication.

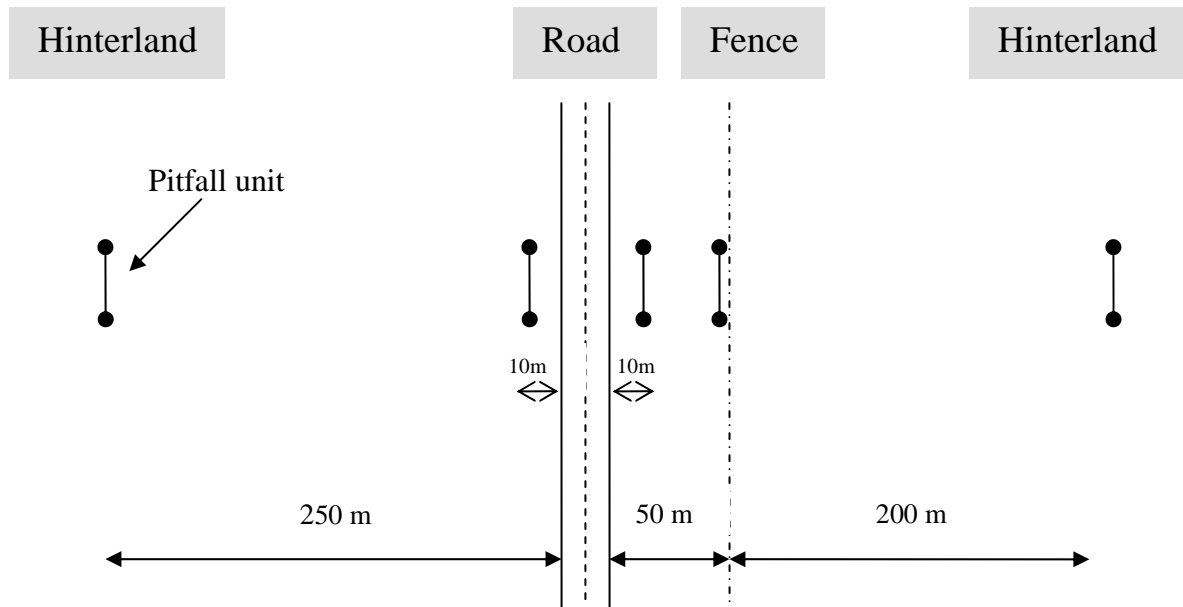


Figure 6.1: Layout of monitoring areas (shaded) and their pitfall units (●) within a site.

6.2.2 Small mammal data

6.2.2.1 Pitfall trapping

Eight seasonal surveys of small mammals were conducted over 2 years between July 2003 and April 2005. Animals were live trapped using pitfall traps located (as pitfall units) in the three monitoring areas within sites (Figure 6.1; total of 50 pitfall units altogether). Pitfall units consisted of two pitfall traps buried flush to the ground that were spaced approximately 10 m apart and linked together by drift fences. Traps were lengths of polyvinyl chloride stormwater pipe, 15 cm in diameter and 60 cm deep, fitted with galvanised steel bases (galvanised steel lids were fitted onto traps when they were not in use), and drift fences were lengths of plastic weed mat that stood approximately 20 cm high after being partially buried into the ground. In each pitfall trap, a small amount of “topstuff” (a synthetic, odourless, and non-absorbent material; moistened in summer) was provided along with a small raft of styrofoam. These items helped captured animals thermoregulate and provided protection from predators, exposure and flash floods.

Trapping was initially conducted for 5 consecutive days and nights per pitfall unit in the winter and spring of 2003 (the number of trapping nights per season actually extended over 10 nights, with pitfall units at sites in the hills open for the first 5 days and nights, and pitfall units at sites in the floodplains open for the next 5 days and nights. Trapping could not occur simultaneously in both landscape types due to time constraints placed on a single researcher checking all traps). However, for the remaining 6 seasons trapping effort was increased to a total of 10 days and nights per pitfall unit to increase the number of small mammal captures. These 10 days and nights were not run consecutively for pitfall units. Instead, pitfall units in the two landscapes were twice alternately opened for 5 days and nights (5 days and nights in the hills followed by 5 days and nights in the floodplains, and repeated again; reasons for splitting trapping in the landscape types as above) to minimise the confounding of small mammal responses to temporal variation in climatic conditions. The total number of trap nights over the study was therefore 7000 (number of trapping nights * number of traps).

Traps were checked twice a day at sunrise and from mid afternoon. Captured animals were identified to species (nomenclature followed Strahan, 1995), weighed to 0.1 g (Jaycar Mini Pocket Scales), sexed, measured (snout-vent length and tail length) and marked to identify re-captured individuals (unique ear-notching). Following measurements, animals were released into the vicinity of the pitfall unit at which they were captured, with care taken to ensure that they did not immediately become re-trapped.

6.2.2.2 Elliott trapping

Supplementary trapping of small mammals along the road was conducted using 50 standard Elliott traps (provisioned with bait and a small handful of “topstuff”) at one monitoring site in the hills where capture numbers were relatively high. This supplementary trapping was conducted in an attempt to increase small mammal capture and re-capture rates at the road edge through both an increase in trapping effort in the area and the provision of bait (a mixture of peanut butter, honey, rolled oats and aniseed essence). Re-capturing individuals at the road edge was important because these data were required to determine whether or not small mammals crossed the road. Traps were placed in two lines lying parallel to the direction of the road and were spaced approximately 4 m apart at areas considered likely for capturing small mammals (for example, under shrubs) at 25 m from

either side of the road edge (traps would have been too exposed if placed any closer to the road edge; 25 traps on each side of the road). Along the trapping lines, traps were alternately oriented perpendicularly and parallel to the direction of the road (Figure 6.2).

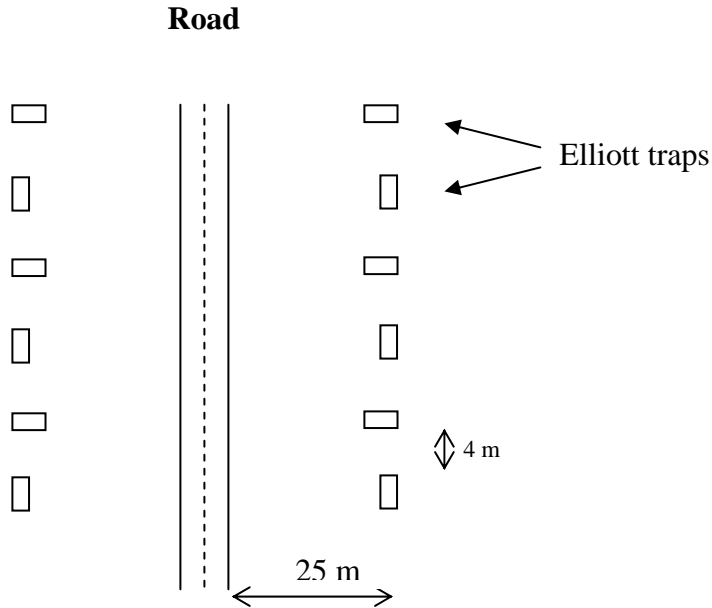


Figure 6.2: Layout of Elliott traps (□) along the road edge. Traps were laid at one monitoring site only. Total number of traps (25 traps on both sides of road) is not shown.

To further test whether small mammals crossed the road, individuals known to be residents on one side of the road were translocated to approximately 10 m away from the road edge on the opposite side of the road (translocated individuals would have to cross the road in order to return to their original locations). Individuals were considered to be residents if they were re-captured one side of the road on at least two occasions (Garland and Bradley, 1984), not three occasions as has been the protocol of other studies (Richardson et al., 1997; Mc Donald and St. Clair, 2004) since capture rate was low in this study. Traps were open during night time hours only (opened in the afternoon and closed after being checked at dawn). As only two *Mus domesticus* and no other mammal species were caught in the Elliott traps, trapping was only conducted for 3 weeks from 26th August 2004 to 16th September 2004 (trapping did not coincide with pitfall trapping as the aim of pitfall trapping was to determine the use of the roadside by small mammals and bait in Elliott traps may have biased results by acting as an attractant).

6.2.3 Invertebrate data

Eight seasonal surveys of invertebrates were conducted over 2 years between July 2003 and April 2005. Surveys were performed at the same time as surveys of small mammals, with invertebrates live-trapped in the same pitfall traps as described above (sometimes with small mammals if they were also trapped). Trapping effort employed per season and the frequency of trap checks were therefore as described above for small mammals. Captured invertebrates were identified to broad taxonomic categories (mostly to Order; ants in the order Hymenoptera were distinguished from other invertebrates in the Hymenoptera as ants can form a large part of small mammal diets; Abensperg-Traun and Steven, 1997) and their numbers were counted before being released into the vicinity of the pitfall unit at which they were captured. While it is acknowledged that invertebrate numbers may have been underestimated due to predation by small mammals captured in the same traps, invertebrate data were nevertheless useful as an index of ordinal diversity and abundance.

6.2.4 Microhabitat data

6.2.4.1 Shrub density

The height, length and width of shrubs within 5 m of pitfall units (Figure 6.3) were measured to the nearest centimetre and multiplied together to obtain estimates for individual shrub densities. Shrubs were distinguished as three main types: flat-leafed chenopods (saltbushes), round leafed chenopods (bluebushes), and other shrubs (mainly bushy groundsels, *Senecio cunninghamii*, and *Senna* species; see Table 3.1 in vegetation chapter for characteristics and descriptions of plants making up flat-leafed and round-leafed chenopod plant groups). Total shrub densities for each pitfall unit were then calculated per shrub type by adding the density values of the shrub types together. Measurements of shrub density were carried out once for each pitfall unit between February 2004 and April 2004 as conditions did not favour recruitment of perennial shrubs throughout the study period.

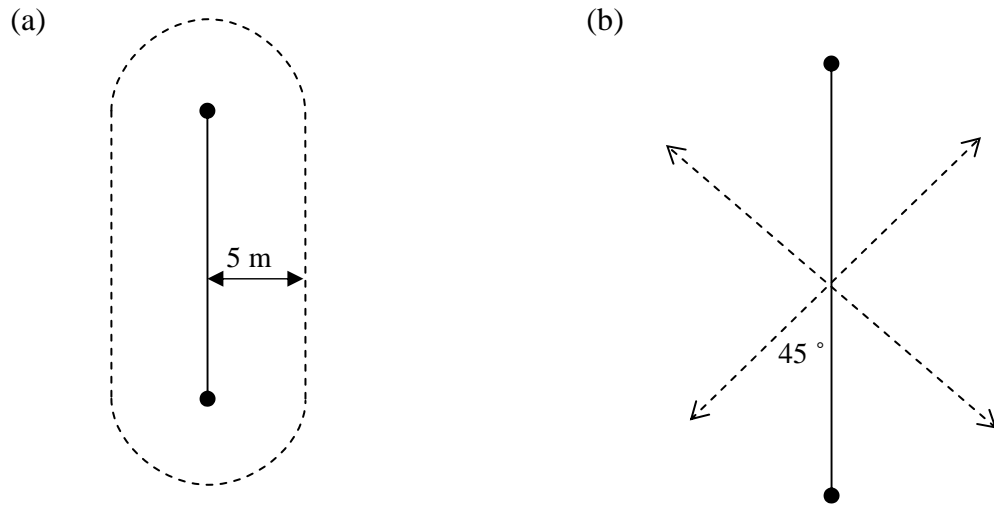


Figure 6.3: Area around pitfall units for which shrub densities were calculated (a), and alignment of 10-m tape for cover measurements and directions of measurements for ground surface temperatures (b).

6.2.4.2 Ground cover

Six seasonal surveys of ground cover around pitfall units were conducted between February 2004 and April 2005. Surveys for the first two seasons (winter 2003 and spring 2003) were not conducted as ground cover data obtained from other vegetation surveys (data collected for vegetation chapter) were being collected during the same time periods and were intended to be used in analyses (for relating various small mammal variables to ground cover). The decision to conduct surveys around pitfall units for the remaining 6 seasons was made as more precise measurements in relation to specific pitfall units were considered necessary.

Ground cover around pitfall units were estimated using a point transect method. At each pitfall unit, a 10-m length of tape was laid at 45° to the drift fence, with the tape crossing the approximate centre of the drift fence (tape laid in two directions with 5 m of tape on either side of the drift fence, Figure 6.3). Ground cover was recorded at each 25 cm interval along the tape according to the broad cover categories outlined in Table 6.1 (see Table 3.1 in vegetation chapter for further detailed descriptions and characteristics of plant groups) and tallied per pitfall unit.

Table 6.1: General description of ground cover categories used around pitfall units.

Category	Description
Bare	Bare ground
Crust	Ground covered with cryptogamic lichen crust
Green grass	Erect green grass
Dry grass	Erect dry and brown grass
Green forb	Erect green forb
Dry forb	Erect dry and brown forb
Green copperburr	Erect green copperburr
Dry copperburr	Erect dry and brown copperburr
Round-leafed chenopod	Green or dry and brown round-leafed chenopod (bluebush)
Flat-leafed chenopod	Green or dry and brown flat-leafed chenopod (saltbush)
Litter	Loose plant material of any plant group
Dung	Animal dung

6.2.4.3 Surface temperature

Six seasonal surveys of surface temperatures around pitfall units were conducted between February 2004 and April 2005. Surveys for the first two seasons (winter 2003 and spring 2003) were not conducted as the decision to make detailed surveys of microhabitat around pitfall units occurred after pitfall trapping began (see section 6.2.4.2). Surveys were conducted at mid-morning and mid-afternoon at each pitfall unit. Two days were required to complete surveys at all pitfall units because approximately one hour was needed to measure temperatures at pitfall units in one landscape type (for each mid-morning and mid-afternoon survey). Thus, to keep temporal variation for mid-morning and mid-afternoon surveys to a minimum, a day was dedicated to measuring surface temperatures at pitfall units per landscape type. To further account for temporal differences, the order in which the landscape types were surveyed as well as the order of pitfall units at replicate sites within landscape types were alternated each season. Surface temperatures were measured using a

non-contact infrared thermometer (Digitech QM7222). Four readings were taken per pitfall unit from the approximate centre of the drift fence by holding the thermometer at eye level and angling it 15 ° from the horizontal (Figure 6.3), and means were calculated to represent surface temperatures per pitfall unit.

6.2.5 Data analysis

6.2.5.1 Dependent variables

Small mammal abundances and biomass were standardised for trapping effort by dividing their values by the number of trapping nights per pitfall unit in each season (standardisation of species richness values did not make biological sense). In one instance, the mass of an individual *Leggadina forresti* was unknown as it escaped prior to weighing. Its mass was therefore estimated as the mean of the all other *L. forresti* individuals for calculation of biomass. After standardisation, values were averaged across seasons per pitfall unit as averages helped to dampen temporal variation in small mammal captures. In addition, the limitations of low capture numbers necessitated using averages as it was not possible to partition captures into seasons and retain statistical power. Average values across 7 seasons rather than 8 were used in analyses (winter 2003 excluded) as captures in winter 2003 were low (only 2 *M. domesticus* caught over 5 nights in 50 pitfall units) and believed to be influenced by the drought of 2002-2003. To check whether taking averages over time per pitfall unit accurately represented dependent variables, the coefficients of variation over seasons (CV) of all dependent variables were examined between landscape types (hills and flats), positions (road, fence and hinterland areas) and landscape type*position interactions (2-factor Anova, conducted in SPSS for Windows V13.0; all assumptions for parametric tests were checked, see section 3.2.3.2 for details of procedures and steps taken if assumptions were violated; Least Significant Differences post hoc test used to determine where differences lay between positions as sample sizes were not equal, Field, 2000). Although values were high, CVs did not differ for dependent variables between landscape types, positions or landscape type*position interactions for small mammals (Table A6.1 in Appendix).

6.2.5.2 Invertebrate variables

Like the data for small mammals, invertebrate abundance data were standardised for trapping effort by dividing their values by the number of trapping nights per pitfall unit in each season. Averages for standardised abundance data and richness data were then calculated across seasons per pitfall unit for 7 seasons (winter 2003 excluded) to be consistent with mean values for small mammal data. Analyses of CVs over time were made for invertebrate variables using 2-factor Anova (factors: landscape type and position, SPSS for Windows V13.0) to check whether averages over time accurately represented variables. The majority of variables showed no differences in variation between landscape types, positions or landscape type*position interactions (Table A6.2 in Appendix).

Principal component analysis (PCA, conducted in SPSS for Windows V13.0) was performed on averaged invertebrate data to reduce the number of invertebrate variables in analyses (see section 3.2.3.3 for details of use of PCAs and conducting PCAs; methods differ from section 3.2.3.3 in that the number of components extracted was based on Kaiser's Criterion as communalities after extraction were greater than 0.7). The 16 variables were reduced to 7 components and these accounted for 75.51 % of total variance. Extraction communalities for all variables indicated that high amounts of variability were accounted for and that the extracted components represented the variables well. Component 1 was positively correlated to silverfish, termite, ant and spider abundance (Thysanura, Isoptera, Hymenoptera and Araneae orders); Component 2 was positively correlated to bug and bee abundance and negatively to beetle abundance (Hemiptera, Hymenoptera and Coleoptera orders); Component 3 was positively correlated to insect larva and scorpion abundance (orders for insect larva unknown, Scorpiones); Component 4 was positively correlated to cockroach and isopod abundance (Blattodea, Isopoda orders); Component 5 was positively correlated to cricket abundance (Order Orthoptera); Component 6 was positively correlated to stick insect abundance (Order Phasmatodea) and invertebrate richness; and Component 7 was positively correlated to moth abundance and negatively to centipede abundance (Order Lepidoptera and Class Chilopoda) (see Table A6.3 in Appendix 6 for correlations between invertebrate variables and extracted components).

6.2.5.3 Microhabitat variables

Averages were calculated across seasons per pitfall unit for the 6 seasons of available ground cover and surface temperature data. Although existing ground cover and surface temperature data only covered 6 rather than 7 seasons (as for small mammal and invertebrate data), analyses of CVs over time for these variables (2-factor Anova for differences between landscape type, position and landscape type*position interactions, SPSS for Windows V13.0) showed minimal variation for the majority of variables (Table A6.4 in Appendix). Therefore, it was assumed that the exclusion of one season of data would not exert too much influence on results.

PCA (SPSS for Windows V13.0) was used on averaged ground cover and surface temperature data and shrub density data to reduce the number of microhabitat variables for analyses. The 18 variables were reduced to 8 components and these accounted for 83.16 % of total variance. Extraction communalities were strong for all variables which indicated that high amounts of variability were accounted for and that the extracted components represented the variables well. Component 1 was positively correlated to dry forb, litter, dry grass, forb and grass cover and morning temperatures and negatively correlated to bare ground and dry copperburr cover; Component 2 was positively correlated to saltbush density and saltbush and dry saltbush cover; Component 3 was positively correlated to bluebush density and bluebush and dry bluebush cover; Component 4 was positively correlated to other shrub and dry other shrub cover; Component 5 was positively correlated to crust cover and the density of other shrubs; Component 6 was positively correlated to copperburr cover; Component 7 was positively correlated to afternoon temperatures; and Component 8 was positively correlated to dung cover (see Table A6.5 in Appendix 6 for correlations between microhabitat variables and extracted components).

6.2.5.4 Statistical analyses

6.2.5.4.1 *Small mammal communities in relation to the road*

Comparisons of small mammal communities between landscape types, positions, and their interactions (2-factor designs) were made using multivariate tests (all mammal species considered simultaneously). Landscape type was examined as a potential factor influencing small mammal communities; however as the aim of the study was to determine

the effects of the road on communities, landscape type was only of interest if it interacted with position. Results will therefore focus on positions and landscape type*position interactions. Because small mammal data contained many zeros, their distributions were not normal and parametric tests (eg. Manova) could not be used. Instead, a multivariate test that is able to partition variance based on any distance measure and generate a multivariate analogue to Fisher's F-ratio, with permutations used to calculate p-values (distance-based multivariate analysis for a linear model, DISTLM 5; McArdle and Anderson, 2001, Anderson, 2004b) was used. This test allowed for unbalanced designs to be analysed ($n = 20$ for road and hinterland positions and $n = 10$ for the fence position), provided that matrices containing the factor designs were coded appropriately (calculations of design matrices were made using XMATRIX, Anderson, 2003a). For all tests, small mammal data were fourth-root transformed to put greater emphasis on intermediate and rarer species, Bray-Curtis distance measures were used, and 9999 permutations (large numbers of permutations increase precision, Anderson, 2001) were performed for generating p-values. Results were considered significant if $p < 0.05$.

In addition to these quantitative multivariate tests, hierarchical agglomerative clustering was performed on small mammal abundance data to examine whether similarities existed for positions relative to the road (conducted in SPSS for Windows V13.0, average abundance values for pitfall units at positions were used). This test was only used in an exploratory manner to identify possible relationships between abundances and position (dendrograms were produced) and was meant to complement the more comprehensive multivariate tests described above. The clustering method and similarity measure used in analyses were Ward's linkage method and the squared Euclidean distance measure respectively as Ward's linkage method produced the greatest gaps in distance coefficients and squared Euclidean distance measures gave meaningful results (usually Bray-Curtis measures are recommended when variables are abundances of different species, Quinn and Keough, 2002).

6.2.5.4.2 Other factors influencing small mammal communities and abundances of common species

To determine if factors other than position relative to the road better accounted for variations in small mammal communities, examinations of the individual contributions of

microhabitat and invertebrate components were made using a variation of DISTLM 5 (distance-based multivariate analysis for a linear model using forward selection, DISTLM *forward*; McArdle and Anderson, 2001, Anderson, 2003b). Transformations of small mammal data, distance measures, number of permutations, and significance levels were as outlined in section 6.2.5.4.1.

To further examine factors potentially influencing small mammal abundances and determine which factors explained most of the variation in abundances (landscape type, positions, their interactions, or microhabitat and invertebrate components), separate analyses were conducted for species that had more than 20 captured individuals using univariate general linear models (GLM, conducted in SPSS for Windows V13.0). Model terms were added into the GLM using a stepwise technique, with all terms and interactions initially entered into the model and dropped if not significant at $p < 0.05$. The final model was that which included terms for which elimination would have reduced the explanatory power of the model (that is, the model which accounted for the most variation; Adjusted R^2 used, Quinn and Keough, 2002). If significant differences were found for factors, Bonferroni corrected post hoc comparisons were used to determine where differences lay (Bonferroni's test controls Type 1 error very well and has good power when the number of comparisons is small, Field, 2000). If variables were found to significantly influence abundances, then the nature of the relationships was determined from the sign of β calculated using regression analysis. All assumptions for GLM were checked (see section 3.2.3.4 for details of procedures and steps taken if assumptions were violated). Reported values and statistics for significant terms were derived from final models and values for non-significant terms were obtained by re-running the final model containing all significant terms with each non-significant term included individually.

6.2.5.4.3 Sex ratios of common small mammal species in relation to the road

Three-factor Anova was used (see section 6.2.5.1) to determine if the sex ratios of common small mammal species differed between positions relative to the road (landscape type was included in models but was only of interest if it interacted with position and sex).

6.2.5.4.4 Stability of small mammal populations in relation to the road

Populations of small mammals may be more stable in particular areas due to the availability of resources in these areas that are necessary for survival (for example, food and shelter) and the aversion to more unfavourable areas that may increase such risks as predation. If individuals were re-captured in particular areas more often than in other areas, it would suggest that areas with higher re-capture frequencies had populations that were more stable than those with lower re-capture frequencies. To make an inference about the stability of populations in certain areas relative to the road, chi-square tests (exact tests with 10, 000 Monte Carlo simulations with the likelihood ratio statistic used to account for the small sample size, SPSS for Windows V13.0) were used (frequencies of re-captured individuals at the road edge, fence and hinterland compared to their frequencies as would be expected by chance). Prior to tests, the frequencies of re-captured individuals at positions were standardised by the number of replicate sites ($n = 20$ for road and hinterland positions and $n = 10$ for fence position). All frequencies were then multiplied by 100 to obtain whole numbers that could be used in analyses.

6.2.5.4.5 Factors influencing small mammal richness and biomass

General linear models were used (see section 6.2.5.4.2) to examine how small mammal richness and biomass varied between landscape types, positions and landscape*position interactions (the latter two of interest), and according to microhabitat and invertebrate components.

6.3 Results

6.3.1 Small mammal captures

A total of 252 small mammals were caught in pitfall traps over the study period (7000 trap nights altogether), with an additional 2 mammals caught in Elliott traps. Seven species of mammal were captured of which *Sminthopsis macroura* was the most abundant followed by *S. crassicaudata*, *Mus domesticus* and *Leggadina forresti* (Table 6.2). The re-capture rate was low (6.75 %) and only occurred for *S. crassicaudata*, *S. macroura* and *M. domesticus* (Table 6.2). Mortality during the study was also low (3 individuals in pitfall traps, accounting for ~ 1 %) with the causes of death unknown.

Table 6.2: Small mammals caught between spring 2003 and summer 2005 and the number of road crossings recorded.

Scientific name	Common name	Number of individuals captured	Number of individuals re-captured	Number of individuals that crossed the road
<i>Sminthopsis crassicaudata</i>	Fat-tailed Dunnart	68	7	1
<i>Sminthopsis macroura</i>	Stripe-faced Dunnart	79	7	0
<i>Planigale tenuirostris</i>	Narrow-nosed Planigale	7	0	0
<i>Planigale gilesi</i>	Giles' Planigale	1	0	0
<i>Leggadina forresti</i>	Forrest's Mouse	35	0	0
<i>Pseudomys hermannsburgensis</i>	Sandy Inland Mouse	2	0	0
<i>Mus domesticus</i>	House Mouse	60	3	2

6.3.2 Small mammal communities in relation to the road

Distance-based multivariate analysis found that differences in small mammal communities existed between positions (only just bordered on significant; $F_{(2,44)} = 2.47$, $p = 0.053$) but found no differences in small mammal communities for landscape type*position interactions ($F_{(2,44)} = 1.31$, $p = 0.298$). Positions relative to the road accounted for only a little over 7 % of variation between small mammal communities. The nature of the differences between positions could not be determined using DISTLM 5, but Figure 6.4 and results from select univariate analyses for mammal species (section 6.3.3) suggested that the small mammal community at the road edge differed from communities at the fence and hinterland areas. The species driving this difference was most likely the most commonly caught species, *S. macroura* (abundances significantly lower at the road edge compared to at fence and hinterland areas; Table 6.4, Figure 6.6), but differences in small mammal communities at the positions were probably also influenced by lower *Leggadina forresti* abundances and higher *M. domesticus* and *S. crassicaudata* abundances at the road edge compared to those in the hinterland (Figure 6.4).

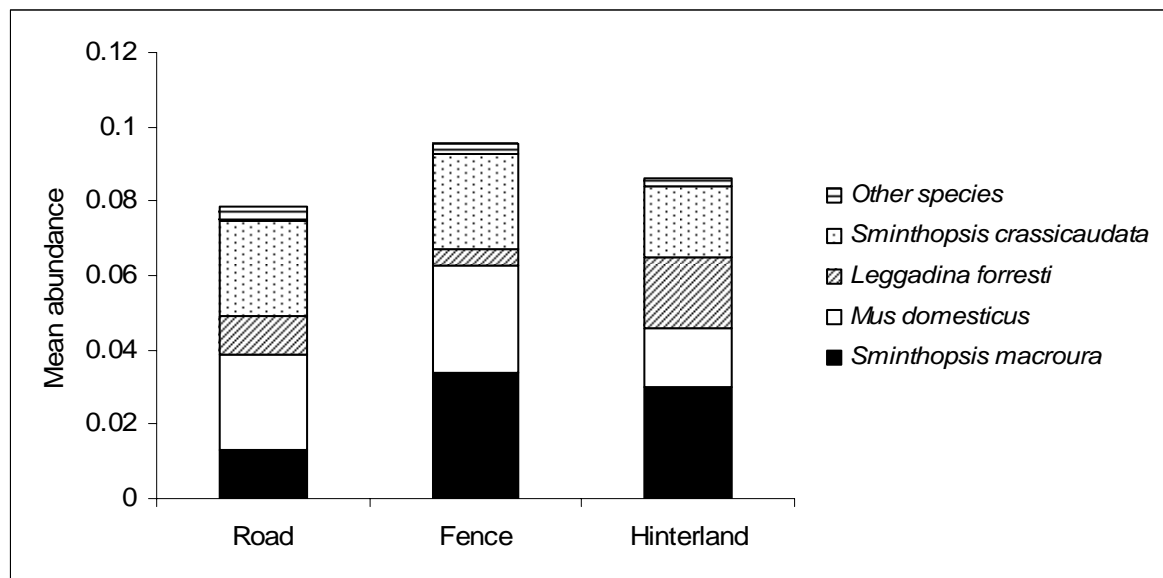


Figure 6.4: Mean abundance of small mammals per sampling night at road, fence and hinterland positions over the study period.

Cluster analysis also indicated that the small mammal community at the road edge were different to communities at other positions, although the clear separation of one of the hinterland replicates suggested that hinterland replicates were not very similar (Figure 6.5). It should be remembered, however, that cluster analyses are prone to inaccuracies due to objects being forced into clusters that cannot be reassessed during the clustering procedure (Quinn and Keough, 2002).

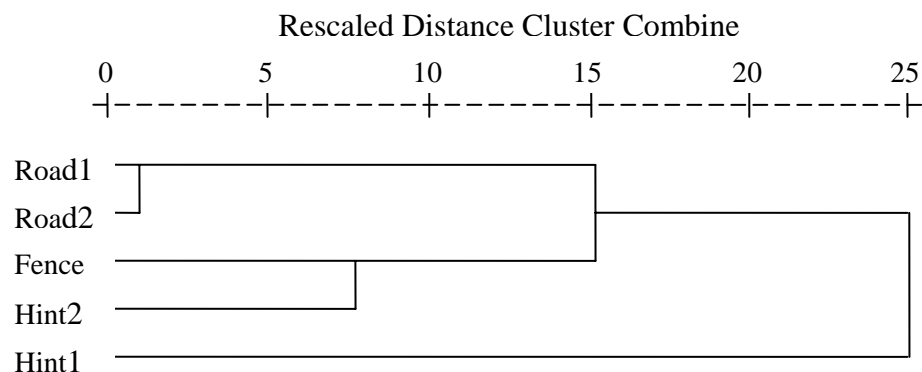


Figure 6.5: Dendrogram from hierarchical cluster analysis on small mammal abundance data. Hint = pitfall units in the hinterland monitoring areas. Numbers in road and hinterland positions refer to replicate pitfall units at these positions.

6.3.3 Other factors influencing small mammal communities and abundances of common species

The stepwise regression procedure for distance-based multivariate analysis revealed that small mammal communities were influenced most by the microhabitat component (1) associated with grass (dry and green), forb (dry and green), litter, copperburr and bare ground cover and morning temperatures (proportion of variance explained = 14 %), and the invertebrates component (1) associated with silverfish, termite, ant and spider abundance (proportion of variance explained = 6 %), with trends for significance found for the invertebrate component (3) associated with insect larva and scorpion abundance (Table 6.3 and Table A6.6 in Appendix 6) (no microhabitat or invertebrate components were correlated to positions relative to the road). Like for differences in small mammal communities relative to the road, the nature of microhabitat and invertebrate influences could not be determined with the multivariate analysis package used. However, examination of relationships between these components and select mammal species indicated that *S. macroura*, *S. crassicaudata*, and *L. forresti* were positively and *M. domesticus* negatively correlated to Component 1 microhabitat, and *S. macroura* and *L. forresti* positively and *S. crassicaudata* and *M. domesticus* negatively correlated to Component 1 invertebrates (*S. macroura*, *S. crassicaudata*, and *L. forresti* were negatively and *M. domesticus* positively correlated to Component 3 invertebrates).

Table 6.3: Results from the stepwise multiple regression for multivariate small mammal abundance (significant results only). F-values are pseudo multivariate F-values analogous to the univariate F statistic and p-values are calculated using permutations. Values for small mammal abundance were fourth-root transformed.

Variable	F-value	P-value	Proportion variance
Component 1 microhabitat ^A	8.06	< 0.001	0.14
Component 1 invertebrates ^B	3.72	0.034	0.06

^A positively correlated to dry forb, litter, dry grass, forb and grass cover and morning temperatures and negatively correlated to bare ground and dry copperburr cover.

^B positively correlated to silverfish, termite, ant and spider abundance.

Separate analysis of model terms influencing the abundance of *S. macroura* revealed that abundances were primarily influenced by proximity to the road, with

abundances significantly lower at the road compared to fence and hinterland areas (Figure 6.6). In addition, abundances were positively influenced by both Component 2 microhabitat (associated with saltbush density and the cover of dry and green saltbush) and Component 8 microhabitat (associated with dung cover) (Figure 6.7 and 6.8, Table 6.4). In addition, there was a trend for Component 1 microhabitat to positively influence *S. macroura* abundances ($F_{(1,44)} = 3.01$, $p = 0.09$; Table A6.7 in Appendix 6) and this is in agreement with the results of the multivariate analysis that also identified Component 1 microhabitat as influencing small mammal communities.

Table 6.4: Results from GLM examining effects of factors and variables on *Sminthopsis macroura* abundance (significant results only). The final model accounted for 32% of variation ($\text{Adj } R^2 = 0.323$, $F_{(4,45)} = 6.83$, $p < 0.001$).

Model Terms	F values	P values
Position	$F_{(2,45)} = 4.86$	$p = 0.012$
Component 2 microhabitat ^A	$F_{(1,45)} = 6.13$	$p = 0.017$
Component 8 microhabitat ^B	$F_{(1,45)} = 6.15$	$p = 0.017$

^A positively correlated to saltbush density and saltbush and dry saltbush cover.

^B positively correlated to dung cover.

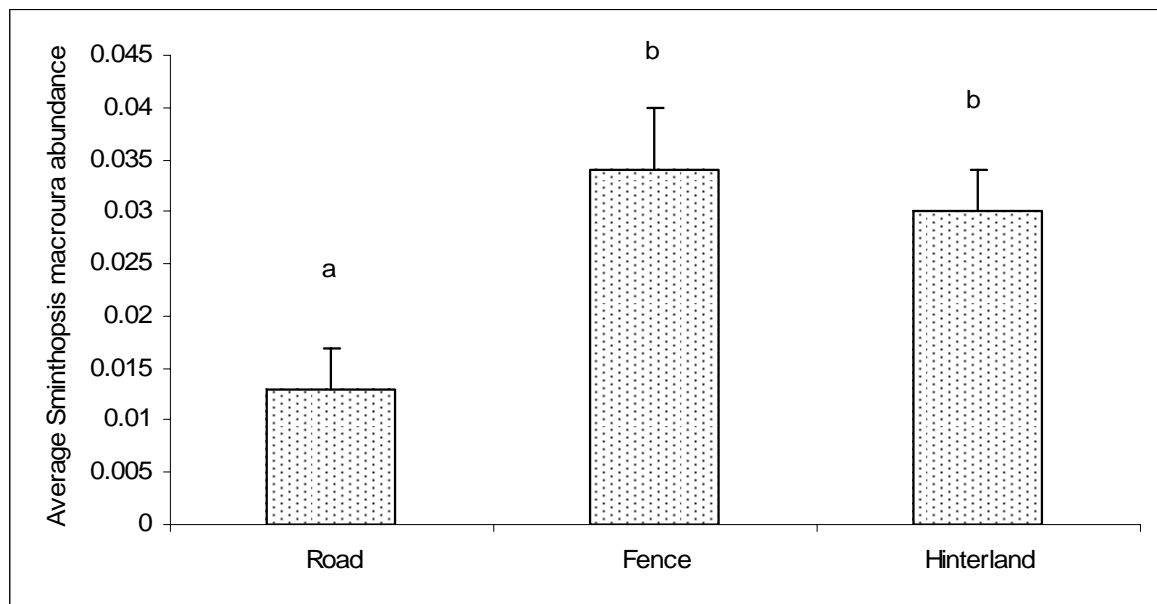


Figure 6.6: Mean *Sminthopsis macroura* abundance per sampling night (+ 1 SE) at road, fence and hinterland positions over the study period. Different letters denotes significant differences between mean abundances at each position.

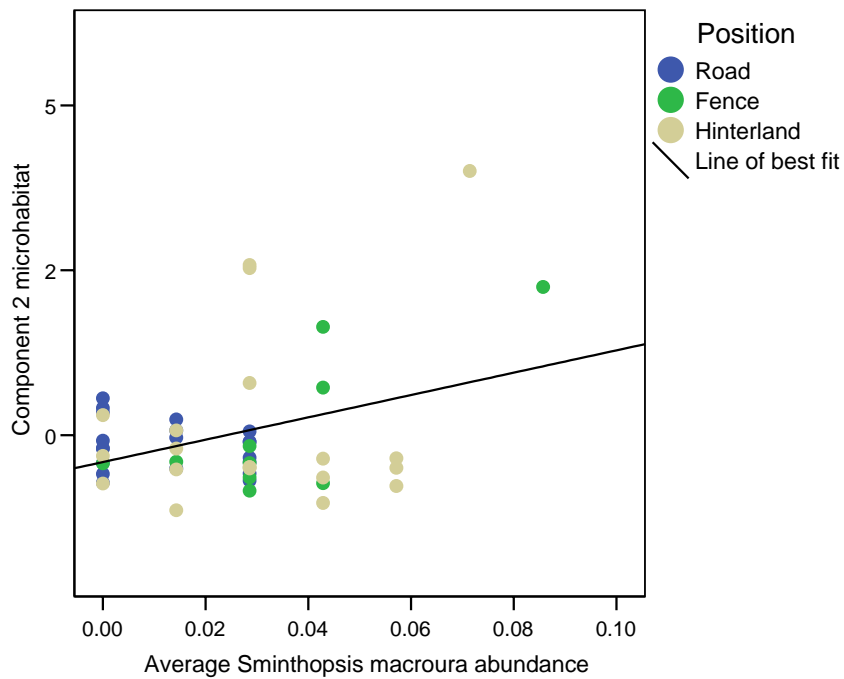


Figure 6.7: Relationship between mean *Sminthopsis macroura* abundance (per sampling night) and Component 2 microhabitat (positively correlated with saltbush density and the cover of dry and green saltbush).

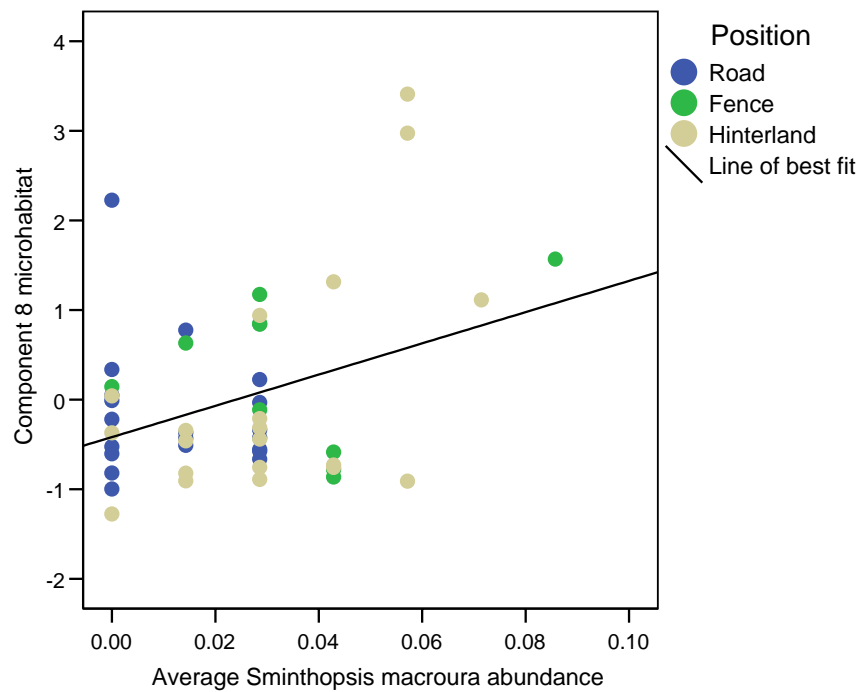


Figure 6.8: Relationship between mean *Sminthopsis macroura* abundance (per sampling night) and Component 8 microhabitat (positively correlated with dung cover).

Analysis of the model terms influencing *M. domesticus* abundance revealed that abundances were influenced most by Component 1 microhabitat (negative relationship) and Component 3 invertebrates (positive relationship), confirming multivariate analysis results for factors influencing small mammal communities (Table 6.5). No significant relationship with position was found (Table A6.8 in Appendix 6).

Table 6.5: Results from GLM examining effects of factors and variables on *Mus domesticus* abundance (significant results only). The final model accounted for 25% of variation (Adj $R^2 = 0.246$, $F_{(2,47)} = 8.99$, $p < 0.001$).

Model Terms	F values	P values
Component 1 microhabitat ^A	$F_{(1,47)} = 12.30$	$p = 0.001$
Component 3 invertebrates ^B	$F_{(1,47)} = 6.71$	$p = 0.013$

^A positively correlated to dry forb, litter, dry grass, forb and grass cover and morning temperatures and negatively correlated to bare ground and dry copperburr cover.

^B positively correlated to insect larva and scorpion abundance.

Analysis of the model terms influencing *L. forresti* abundance revealed that abundances were influenced most by landscape type, with higher abundances occurring in the floodplains compared to in the hills (0.02 ± 0.01 and 0.001 ± 0.01 animals per sampling night, respectively), and Component 5 microhabitat (positive influence; component associated with crust and the density of other shrubs) (Table 6.6). There were no significant relationships with position or landscape type*position interactions (Table A6.9 in Appendix 6). No significant model terms were found to influence *S. crassicaudata* abundance.

Table 6.6: Results from GLM examining effects of factors and variables on *Leggadina forresti* abundance (significant results only). The final model accounted for 50% of variation (Adj $R^2 = 0.495$, $F_{(2,47)} = 24.98$, $p < 0.001$). Values for *Leggadina forresti* abundance were square-root transformed.

Model Terms	F values	P values
Landscape type	$F_{(1,47)} = 39.26$	$p < 0.001$
Component 5 microhabitat ^A	$F_{(1,47)} = 5.61$	$p = 0.022$

^A positively correlated to crust cover and the density of other shrubs.

6.3.4 Sex ratios of common small mammal species in relation to the road

Overall, significantly more females were caught compared to males for *S. macroura*, *M. domesticus*, and *L. forresti* populations (*S. macroura*: $F_{(1,88)} = 4.31$, $p = 0.041$; *M. domesticus*: $F_{(1,88)} = 32.42$, $p < 0.001$; *L. forresti*: $F_{(1,88)} = 16.09$, $p < 0.001$; difference was not significant for *S. crassicaudata*: $F_{(1,88)} = 2.36$, $p = 0.128$). This female dominance was consistent at all positions relative to the road (no position*sex or landscape type*position*sex interactions) for all of the more commonly caught small mammal species (Tables A6.10 to A6.13 in Appendix 6).

6.3.5 Stability of small mammal populations in relation to the road

Significantly less small mammals were re-captured at the road edge while significantly more small mammals were re-captured at the fence position than would be expected by chance. No differences between observed and expected frequencies of re-capture were found in the hinterland ($\chi^2 = 33.48$, $df = 2$, $p < 0.001$). Thus, populations at the road edge may have been less stable than those at the fence position.

6.3.6 Factors influencing small mammal richness and biomass

Only landscape type was found to influence small mammal richness (Adjusted $R^2 = 0.112$, $F_{(1,48)} = 7.19$, $p = 0.010$), with higher values found in the floodplains compared to the hills. Model terms influencing small mammal biomass were Component 2 invertebrates (associated with bug, bee and beetle abundance; positive relationship) and Component 1 invertebrates (positive relationship) (Table 6.7). Position or landscape type*position interactions did not significantly influence small mammal richness or biomass (Tables A6.14 and A6.15 in Appendix 6).

Table 6.7: Results from GLM examining effects of factors and variables on small mammal biomass (significant results only). The final model accounted for 13% of variation (Adj $R^2 = 0.129$, $F_{(2,47)} = 4.64$, $p = 0.015$).

Model Terms	F values	P values
Component 2 invertebrates ^A	$F_{(1,47)} = 5.08$	$p = 0.029$
Component 1 invertebrates ^B	$F_{(1,47)} = 4.19$	$p = 0.046$

^A positively correlated to bug and bee abundance and negatively to beetle abundance.

^B positively correlated to silverfish, termite, ant and spider abundance.

6.3.7 Road crossings

Of the small mammals that were recaptured, only three individuals of two species crossed the road (Table 6.2) (only one *M. domesticus* was translocated). For one of the two *M. domesticus* that crossed and for the single *S. crassicaudata* that crossed, only one record of crossing occurred. For the other *M. domesticus* that crossed, two records of road crossing occurred, and this may have been the result of it being translocated to the opposite side of the road to which it was originally captured (the individual was captured on enough occasions to be considered a resident on one side of the road. It was only ever recaptured on its original side of capture, and this occurred after two separate translocations to the opposite side of the road to original capture). One additional road crossing was recorded for *S. macroura* from personal observation (individual crossed the road after release). Another individual (*S. crassicaudata*) was observed fleeing after release toward the road edge, but did not cross, even though it moved away from and returned to the road edge several times. Of the remaining recaptured individuals that did not cross the road, ten were found at their original pitfall locations. The remaining seven re-captured individuals (5 *S. macroura*, 1 *S. crassicaudata* and 1 *M. musculus*) moved between 100 and 250 m from their original pitfall locations (two of these individuals were originally trapped at the road edge).

6.4 Discussion

This study demonstrated that an arid-zone road impacted the species composition of a small mammal community along its edge and revealed that two threatened small mammal species in NSW, *S. macroura* and *L. forresti*, which are also considered as species of national significance (Dickman *et al.*, 2001), were less abundant at roadside areas compared to areas further from the road (*S. macroura* significantly so). In addition, there was evidence for lower recapture rates for small mammal populations at roadside areas compared to areas further from the road, as well as evidence that the road may have inhibited small mammal movements such that the road acted as a somewhat leaky barrier to small mammal movements across the road. Together, these results suggest that arid-zone roads have the potential to fragment the populations of at least some small mammal species living adjacent to them. However, as position relative to the study road only accounted for a small amount of variation in small mammal communities (just over 7 %) and only

significantly affected the abundance of one species (*S. macroura*); there were no indications of the road also affecting the demographics of small mammal populations; the road did not completely prevent small mammal road crossings; and the areas affected by the road are small relative to the total area of surrounding arid-zone landscapes, the effects of arid-zone roads on small mammal populations are probably not severe and the sustainability of populations are unlikely to be affected unless the density of arid-zone roads increase. Information obtained in this study is a valuable contribution to our understanding of the impacts of arid-zone roads on small mammals. In the event of any increases in the density of arid-zone roads, our knowledge of which populations are vulnerable to fragmentation by arid-zone roads can be used to develop management frameworks for mitigating fragmentation effects for these vulnerable small mammal populations in the future.

6.4.1 Effects of the arid-zone road on small mammals

The influence of position relative to the road on small mammal communities was only just significant ($p = 0.053$). However, that the composition of small mammal communities at roadside positions differed to those at areas further from the road were supported by both cluster analysis results and results for the factors influencing the abundance of the most commonly caught species, *S. macroura*. Limited data prevents firm statements about the nature of the effects of the road on small mammal movements around and across the road as only 17 individuals were recaptured once, which also made translocations of individuals impossible as individuals had to first be recaptured twice (the low recapture rate in this study, 6.75 %, is typical of small mammal studies in the arid zone and reflects the mobility and drifting home-ranges of dasyurids; Dickman *et al.*, 1995, 1999, 2001), and only five road crossings by four individuals were recorded (one from personal observation). Even so, findings that 1) the number of small mammal recaptures at roadside areas was much less than would be expected by chance, 2) a translocated *M. domesticus* only crossed the road when it was moved to the opposite side of the road to its original side of capture, rather than crossing on its own accord, and 3) a *S. crassicaudata* on release from a pitfall trap exhibited a clear reluctance to cross the road when at the road edge and did not subsequently cross the road indicate that the road environment may have been somewhat

unfavourable to small mammals and that the road may have inhibited small mammals from crossing. For the latter, it could be argued that some small mammals might not have been able to cover the distance required to cross the study road (6.5 m wide) so were in fact unable to cross the road, rather than being inhibited from crossing (as suggested by Oxley *et al.*, 1974). Evidence for this argument is weak though. Small mammals in arid Australia can cover great distances (up to 400 m in short-range movements and 14 km in long-range movements, Read, 1984; Dickman *et al.*, 1995) and this is independent of size, age, sex and sexual condition (Dickman *et al.*, 1995), and the seven recaptured small mammals that were trapped in different locations to their original capture locations were recorded up to 250 m from their original capture location.

This study's findings are in accordance with findings of other investigations conducted elsewhere: changes in small mammal community compositions have been found along rainforest roads (Goosem, 2000), roads traversing woody habitats (Adams and Geis, 1983), and roads traversing farmland (Meunier *et al.*, 1999a); road environments have been demonstrated to be unstable environments (Brock and Kelt, 2004) (although these unstable road environments facilitated the dispersal of the endangered Stephen's kangaroo rat, *Diplodomys stephensi*, along dirt roads); and roads have been found to inhibit the movements of small mammals across roads traversing rainforests (Burnett, 1992; Goosem, 2001), forests (Oxley *et al.*, 1974; Mader, 1984; Merriam *et al.*, 1989; Gerlach and Musolf, 2000; McDonald and St. Claire, 2004), temperate grasslands (Kozel and Fleharty, 1979; Wilkins, 1982; Richardson *et al.*, 1997; Clark *et al.*, 2001; McDonald and St. Claire, 2004), and farmland (Swihart and Slade, 1984). The consistency of results among different environments is surprising since it was expected that the effects of roads in arid ecosystems on small mammal communities and movements around and across roads would be different to those in other ecosystems.

Arid-zone roads can increase food resources at their edges in an environment where food resources are limited and patchily distributed (Stafford Smith and Morton, 1990), and this was also demonstrated in the current study (see Chapter 3). Most arid-zone small mammals respond to increases in food availability (Dickman *et al.*, 1999; Letnic *et al.*, 2004), so it was expected that most small mammal species, rather than a select few species, would be attracted to roadside areas, no changes in community compositions would occur

relative to the road, and roadside populations might be relatively stable. In addition, microhabitat changes caused by arid-zone roads relative to surrounding arid landscapes are less obvious than changes caused by roads in other ecosystems as arid landscapes are open and characteristically patterned, with productive vegetated areas scattered in a larger matrix of unproductive open spaces (Stafford Smith and Morton, 1990). The effect of roads on small mammal abundances and road crossings might therefore be expected to have less of an effect in arid ecosystems than in other ecosystems since arid-zone small mammals are adapted to open spaces and traversing open spaces (Dickman *et al.*, 1995). However, small mammals perceive their environments differently to humans (Fox, 1984; Friend and Taylor, 1985) so what might be considered as small microhabitat differences to humans may not be the case from the perspective of small mammals. Furthermore, in many situations presented to fauna, there may have been associated costs involved with being in roadside areas that may have outweighed any benefits of being in these environments for some species (Lima and Dill, 1990; Kotler and Blaustein, 1995). These will be briefly discussed following a discussion on the components that were found to influence small mammal communities, and the most important factors influencing the abundances of common species.

6.4.2 Other factors influencing small mammal communities and the abundances of commonly caught species

The multivariate analysis that was conducted to determine if factors other than position relative to the road better accounted for variations in small mammal communities revealed that microhabitat and invertebrate components affected small mammal communities and accounted for 20 % of variation (position accounted for about 7 %). Of the components, the microhabitat component (1) associated with high forb, grass and litter cover and morning temperatures and low bare ground and dry copperburr cover accounted for most of this variation (14 %), with the remaining 6 % accounted for by the invertebrate component (1) associated with high silverfish, termite, ant and spider abundance. The fact that differences in small mammal communities were influenced most by microhabitat component 1 and that this component explained more variation in small mammal communities than position relative to the road is not surprising. Microhabitat component 1 closely correlated with landscape type (Pearson's correlation = 0.772) and hence much of

what the component measured reflected differences in the hills and floodplains landscape types. As landscape type can influence the amount of food and shelter resources available to small mammals (different habitat structures can enhance food supplies; Frank and Soderquist, 2005), and arid-zone small mammals respond primarily to increases in food availability (Dickman *et al.*, 1999; Letnic *et al.*, 2004) and secondarily to particular habitat structures (Read, 1987), landscape type affects both the occurrence (richness) and abundance of species, which in turn influences their communities. Indeed, when the effect of landscape type was examined on its own, landscape type explained much more of the variation in small mammal communities than position ($F_{(1,44)} = 13.56$, $p < 0.001$, $R^2 = 0.21$) (Landscape type was also the most important factor explaining variations in small mammal richness).

In this study, the effect of landscape type (and components related to landscape types) was not of primary interest and was only included in analyses to determine whether position*landscape type interactions affected small mammals. Nevertheless, the individual relationships shown by common small mammal species with landscape type and the microhabitat and invertebrate components associated with landscape type are generally consistent with our understanding of the habitat and food preferences of these common species. Positive correlations between *S. macroura* abundance and microhabitat component 1 and invertebrate component 1 reflect this species' preference for habitats with high vegetation cover (particularly cover provided by tussock grassland; Dickman *et al.*, 1993; Morton, 1995a) that possibly enhances its food supplies (Frank and Soderquist, 2005), as well as the species' preference for termites (Morton *et al.*, 1983). The positive relationship between *L. forresti* abundance and microhabitat component 1 reflects this species' preference for areas of high vegetation cover, especially grass cover in its preferred habitat of tussock grasslands (Dickman *et al.*, 1993; Reid and Morton, 1995). The negative relationships between *M. domesticus* and microhabitat component 1 and invertebrate component 1 are compatible with this species' tendency to inhabit disturbed areas (Singleton, 1995) or more open areas (Fox and Pople, 1984) that may not support high densities of invertebrates. Relationships between *S. crassicaudata* and microhabitat component 1 and invertebrate component 1 are harder to account for. *Sminthopsis crassicaudata* often forage on bare open areas (Dickman, 1994; Morton, 1995b; Frank and

Soderquist, 2005) and are insectivores (Morton *et al.*, 1983) that respond to changes in food availability (Morton, 1978a, b, 1982), so the positive correlation with microhabitat component 1 and negative correlation with invertebrate component 1 are unexpected. However, *S. crassicaudata* are flexible in their habitat preferences and there have been many instances in the literature for only very weak relationships between *S. crassicaudata* abundances and particular aspects of habitats (Morton *et al.*, 1983; Read, 1987).

When common small mammal species were examined separately to determine which factors influenced their abundances most, only *S. macroura* was significantly influenced by positions relative to the road (position explained 18 % of the total 32 % of variation accounted for). The remaining species examined, which showed trends for increases (*S. crassicaudata* and *M. domesticus*) and decreases (*L. forresti*) in abundances at roadside areas relative to areas further from the road, could not be linked to positions relative to the road (so the significant differences in small mammal communities at roadside areas compared to areas further from the road were most likely driven by significantly lower *S. macroura* abundances at roadside areas), and other variables unrelated to positions were more important in explaining variations in their respective abundances. The factors affecting common small mammal species abundances were not always the same as those found to influence small mammal communities as a whole (although *M. domesticus* and *L. forresti* abundances were still affected most by microhabitat component 1 and landscape type, respectively). A reason for this may lie in the fact that the abundances of arid-zone small mammal species, particularly arid-zone dasyurids are often associated with different independent variables rather than with common variables due to the different species' responses to their surrounding environments (Dickman *et al.*, 2001). For *S. macroura* the microhabitat component (2) associated with saltbush variables also affected abundances and this may be related to the species' preference for areas of cover (Frank and Soderquist, 2005). For *L. forresti*, the variable affecting its abundances after landscape type (41 % of variation explained) was the microhabitat component (5) associated with the cover of cryptogamic crust and the density of shrubs (other than saltbush and bluebush). This variable, however, did not explain a great deal of variation (only 5 % of the total 46 % explained) so may not have actually accounted for variations in *L. forresti* abundance.

6.4.3 Causes behind changes in small mammal communities near the arid-zone road

There was no evidence in this study that microhabitat and invertebrate components played any role in influencing significant differences in small mammal community compositions and abundances of *S. macroura* at roadside areas, unstable populations at roadside areas or road crossings. This is because there were no relationships between positions relative to the road and microhabitat and invertebrate components (Pearson's correlations between positions and microhabitat and invertebrate components were all less than 0.6; indeed, the strongest correlation was 0.361 between positions and microhabitat component 5, and 0.433 between positions and invertebrate component 3). Nevertheless, due to the methodology employed to measure microhabitats and invertebrate abundances, which only included measurements in areas extending to 5 m around pitfall units, it is possible that real microhabitat and invertebrate differences at the roadside compared to areas further from the road may not have been detected and small mammals were in fact affected by microhabitat and invertebrate components.

There is much evidence to suggest that arid-zone roads influence microhabitats (and thus invertebrate abundances) around them (Lightfoot and Whitford, 1991; Norton and Stafford Smith, 1999). Indeed, results from Chapter 3 revealed that the quality of vegetation at roadside areas was higher than vegetation quality further from the road. However, vegetation quality was highest at areas at the immediate road edge (at the first metre from the road edge, Chapter 3) and this area was not covered in measurements around pitfall units at roadside areas. In addition, microhabitat measurements around pitfall units included a combination of vegetation quality and cover measures that Chapter 3 illustrated were not necessarily linked (due to vegetation remaining intact after senescence), and results from Chapter 3 revealed no differences in vegetation cover at table drain areas (which included areas measured around pitfalls in roadside areas) relative to fence and hinterland areas further from the road. Hence, these factors may also have contributed to the lack of correlations between microhabitat components and positions relative to the road. Moreover, there were some elements of microhabitat that were not measured at all (and therefore could not be related to small mammal abundances and use) which may have been important to small mammals. For example, no measurements for soil type and properties were taken but cracking clay soil is known to be an important habitat for arid-zone small mammals

which forage and shelter in the soil cracks (Read, 1987; Moss and Croft, 1988). Chapter 3 showed that soil at roadside areas was less stable at roadside areas in the floodplains compared to in the hills due to higher levels of exchangeable sodium and magnesium in the floodplains causing the soil to flocculate when wet.

Whether or not microhabitats and invertebrate components influenced differences in small mammal communities and the abundances of *S. macroura* at areas relative to the road compared to areas further from the road, however, remains speculative. The study was not designed to test all the potential factors affecting the use of roadside areas by species, rather the aim was to determine whether small mammals were affected by arid-zone roads (with attempts made to relate small mammal variables with microhabitat and invertebrate components), so it is not possible to positively determine what other factors influenced small mammal use of areas around the road or small mammal road crossings. Further studies could be conducted to determine how arid-zone small mammal species are affected by the combination of potentially higher quality vegetation and higher invertebrate abundances at the immediate edges of arid-zone roads, more disturbed soil profiles at roadside areas, higher traffic disturbance levels at roadside areas, road surface properties, and potentially higher levels of predation at roadside areas, which in turn determine their use of particular areas over others (Lima and Dill, 1990; Kotler and Blaustein, 1995).

6.4.4 Effects of the arid-zone road on small mammal populations

While the arid-zone road in this study affected small mammals, the effects were not “severe” and the road probably did not influence the overall sustainability of small mammal populations. The latter conclusion is based on the fact that small mammal populations were female biased at all positions relative to the road for all of the more commonly caught species, and surplus breeding females are more important in increasing small mammal populations than surplus breeding males (most of the animals caught were adults with the capacity to breed based on average masses; *S. macroura*: 81% adults, *S. crassicaudata*: 96 % adults, *M. domesticus*: 98 % adults, *L. forresti*: 77 % adults). In addition, the road surface and breadth did not completely prevent small mammals from crossing it, so populations on either side of the road were not completely isolated.

6.4.5 Conclusion

In summary, this study showed that an arid-zone road affected small mammal communities. In addition, the stability of small mammal populations at roadside areas appeared to be less stable than those at areas further from the road, and the road may have inhibited small mammal road crossings. From a conservation perspective, the effects of arid-zone roads on small mammals may be a concern, particularly for *S. macroura* and *L. forresti* which are threatened in NSW and considered as species of national significance due to their sparse distributions in NSW and across Australia (Dickman et al., 1993), and findings are a useful contribution to our understanding of the impacts of anthropogenic disturbances on arid-zone mammals. However, unless the density of arid-zone roads increases, which would in turn increase the areas affected by roads, arid-zone roads may not represent an immediate threat to the sustainability of small mammals living adjacent to roads.

Chapter 7

General Discussion

7.1 Key findings of the study

Results from this thesis suggest that arid-zone roads have a high overall impact on surrounding landscapes and wildlife. The model road, the Silver City Highway, that I investigated increased vegetation quality (Chapter 3), impacted the physical and chemical properties of soil via increases in soil compaction and water levels and decreases in soil nutrient levels (Chapter 3), influenced the spatial distribution and behaviour of kangaroos, particularly those of *M. rufus* (Chapter 4), affected kangaroo mortality (Chapter 5), affected the population demographics of *M. rufus* and *M. r. erubescens* (Chapter 5), altered the community composition of small mammals, with the threatened species in NSW and species of national significance, *S. macroura*, negatively affected by the road (Chapter 6), and inhibited small mammal movements across its width (Chapter 6). In addition, management of roadside vegetation along the Silver City Highway by mowing increased the quality of roadside vegetation in the floodplains, as well as increased the diversity of vegetation in the hills (Chapter 3). The Silver City Highway also impacted higher-order ecosystem responses (Chapters 5 and 6). However, effects are probably unlikely to compromise the sustainability of populations or the integrity of communities of kangaroos or small mammals (Chapters 5 and 6).

The majority of the impacts of the Silver City Highway on surrounding landscapes were direct consequences of the road interacting with the ecological processes unique to arid ecosystems. Thus, the collection of water at the road edges drove many of the effects since arid ecosystems are driven by water availability and arid-zone flora and fauna are adapted to exploiting limited and patchily distributed resources (Stafford Smith and Morton, 1990). Some immediate impacts were not specific to arid-zone processes but are common causal factors for road effects in general, including mowing which increased roadside vegetation quality in the floodplains, and higher traffic volumes which increased the probability of kangaroo-vehicle collisions. However, subsequent effects of these impacts

were exaggerated due to arid-zone processes. For example, enhanced roadside vegetation caused by mowing attracted kangaroos, which are adapted to seeking out high quality and patchily distributed resources.

Since the effects of the study road were heavily influenced by arid-zone processes, such effects were often interconnected, and some of the underlying mechanisms for similar road effects identified in other ecosystems differed (for example, the mechanism behind enhancing vegetation quality at road edges, see Chapter 3). Thus the findings of this study support the initial hypothesis that the effects of roads are strongly influenced by the ecosystem traversed by roads, and support the idea that a combination of road effects should be examined in investigations of the effects of roads. In addition, as kangaroo populations and small mammal communities were affected by the study road (albeit slightly), the results of this study support the need to investigate the effects of roads on higher-order ecosystem responses in future studies.

7.2 Significance of the study

The acquisition of information on the ecological effects of roads in the context of particular ecosystem types (including information on the effects of roads on higher-order ecosystem responses) and the identification of the factors that govern and modulate these many effects are important first steps in the development of strategic road management frameworks. Such information helps natural resource managers rank road impacts in order of conservation importance in particular ecosystems and thus helps them set management priorities for mitigating the effects of roads. In addition, knowing what factors govern and modulate the effects of roads in particular ecosystems assists conservation managers target road effects. Even so, investigations that provide these types of information are few.

This study has identified a number of key ecological effects of a typical road in an arid ecosystem, an ecosystem in which studies of the effects of roads are few (Brooks and Lair, 2005). Both abiotic and biotic components of an arid ecosystem have been studied. The results from both these components have been integrated in various combinations, and higher-order ecosystem responses to roads identified. Thus, this thesis is a valuable and original contribution to our understanding of at least one exemplar of the effects of arid-zone roads on surrounding arid landscapes and wildlife. Roads in mesic environments have

been viewed as cutting a swathe through dense habitat and causing fission and degradation. This study has shown that the roads in arid zones may actually enrich the immediate landscape with flow-on effects to wildlife accessing the resource rich 'patch' and the addition of another bare area may be a lesser consequence. Furthermore this study has taken advantage of the openness of arid landscapes to investigate some road effects that have previously been ignored in the literature. A key example is the quantification of faunal behaviour towards an approaching vehicle and assessment of how such behaviour relates to roadkill frequency of larger fauna. The development of strategic road management frameworks is an undeniably difficult task for natural resource managers but the outcomes of this study will inform decisions and thus guide future arid-zone road management actions.

7.3 Limitations of the study

There were a number of factors that limited the scope of this study. Firstly, due to time restrictions, this study examined only a small sample of all possible road effects within a relatively short time-frame in a zone of inherently unpredictable climate. Even so, a typical range of environmental conditions were sampled from the temperature extremes of summer and winter, and drought through to some short periods of heavy rain. Furthermore the study targeted abiotic and biotic variables most likely to be directly affected by the operation of a sealed road, and faunal and landscape effects of most significance to wildlife conservation in an arid zone.

Secondly, the study was limited to investigating the effects of a single arid-zone road. The decision was made to investigate one road section in depth rather than several superficially and thus sacrificed some generality to the study. Therefore, to make the most of the use of a single study road, the road section was reasonably long at 20 km in length and traversed two typical habitats of different topography. Furthermore, potential confounding effects of different land tenure were avoided.

Thirdly, causal factors underlying some road effects could not be identified (Chapter 6). The time constraint of the thesis provided limited opportunities for experiment (e.g. mowing and deliberate translocation of small mammals) but the results provide a strategic direction to future experimental research.

Finally, the number of re-captures for small mammals was low, so no firm conclusions could be made regarding the influence of an arid-zone road on small mammal road crossings. The study attempted to increase re-capture rate with the use of bait in Elliott traps, but arid-zone small mammals are best caught in pitfall traps. Thus, this limitation could not be overcome in this study as the only way to pick up trends in small mammal crossings and increase confidence in results for arid-zone small mammals using pitfall traps is to conduct long-term studies (Dickman *et al.*, 1999, 2001) beyond the duration of the 2-3 years fieldwork typical of a PhD thesis.

7.4 Future research directions

Natural resource managers face a multitude of challenges when developing strategic management frameworks for most anthropogenic impacts in wildlife conservation. The strategic management of roads is no exception. Two major challenges will be setting management priorities for roads and targeting high-priority impacts for mitigation in the most cost- and time-effective way.

To achieve these two goals, managers will firstly need to gather further information on road effects and the factors governing and modulating road effects in various ecosystems. This study has identified some key impacts of roads in an arid ecosystem but the generality of its findings needs to be tested by further study. In addition, there were a number of other limitations which restricted how much information this study could provide for the effects of arid-zone roads (see section 7.3). Thus, examples of further information that could be obtained for the effects of arid-zone roads are information on the thermal characteristics of the arid-zone roads and the subsequent effects on other animal taxa. A black-tarred road will change the thermal characteristics of the habitat it traverses that may have significant attraction at times to ectotherms like reptiles, which are typically diverse and abundant in arid ecosystems (Pianka, 1986; James and Shine, 2000). If these small animals are killed then scavenging birds like ravens, crows and raptors may be attracted to roads and suffer a secondary impact from vehicles. Likewise, flying insects may settle on roads to warm up and attract insectivorous birds and reptiles which may in turn be killed by vehicle impacts. These thermal effects of roads are by no means exclusive to arid zones but to the extent that ectotherms dominate over endotherms in biomass and

the scavengers and predators from the latter are generalists exploiting any prey opportunity, impacts may be high in this ecosystem. Other examples of further information that could be gathered are information on the effects of roads in other ecosystems, especially those that have not been comprehensively examined. Moreover, information on the influence of road density on the magnitude of road effects could be acquired since some road effects become exacerbated with increases in road densities (Mech *et al.*, 1988; Forman and Alexander, 1998; Vos and Chardon, 1998).

Secondly, after further information has been gathered, natural resource managers will have to weigh up a number of considerations to achieve the two goals of setting management priorities for roads and targeting high-priority impacts for mitigation. Management issues are rarely clear-cut, and opinions of what rank as the most important effects are often divided. In addition, there may be instances where it may not be possible to mitigate one road effect to the exclusion of all other effects and a possible negative impact on a second party. Hence, managers will sometimes have to make some trade-offs during both ranking and mitigation processes. In the case of the ranking procedure, ranking may follow general principles of conservation management (Burgman and Lindenmayer, 1998), such that ranking is guided by knowledge of road effects on higher-level ecosystem responses, the status (threatened or common) of particular species, as well as the integrity of the ecosystems traversed by roads. Even so there may be situations where this ranking system will be circumvented such as usually arise when human needs and concerns are also issues to be addressed. Thus managers may then be under pressure to concentrate mitigation efforts on effects that are not so pressing from a conservation perspective but satisfy human interests such as road safety for drivers.

Natural resource management in relation to roads should be adaptive (Forman *et al.*, 2003) so that attempts are made to mitigate some of the identified negative effects of roads, even before all possible effects of roads are known. Such adaptive management follows the approach that management actions should be taken based on the best current information and then refined or altered if new information indicates better management actions (Burgman and Lindenmayer, 1998). The main reasons for this form of management are that sometimes known effects need to be minimised as soon as possible and that it is impossible to gather complete information sets in complex systems. However, apart from situations

where effects would obviously be considered high priority (for instance, a situation where threatened species are affected by roadkill or habitat fragmentation by roads, Boarman and Sazaki, 2006) where adaptive management would be the best management approach, caution should be exercised against making hasty decisions in every situation. Some mitigation measures have been employed in the past to reduce some negative effects of roads, yet have had limited success. In addition, some mitigation measures employed for one road effect have exacerbated the magnitude of another effect (reviewed by Forman *et al.*, 2003). As some forms of abatement can also be expensive, it may not pay off to install mitigation measures that are ineffective for the intended road effect or exacerbate the harmful nature of another road effect. Therefore, a considered approach for tackling the multitude of road effects, which possibly considers road effects on a case-by-case basis, is advised.

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Appendix 3

Table A3.1: Results from Friedman's tests and overall patterns in vegetation cover (as detected from plots of mean ranks per meter) along 30-m transects at the fence and hinterland monitoring areas (n = 10).

Vegetation		Fence		Hinterland
Pasture	$F_{(1,29)} = 33.44$ $p = 0.260$	Higher along fence line	$F_{(1,29)} = 20.15$ $p = 0.888$	No patterns
Grasses	$F_{(1,29)} = 33.65$ $p = 0.252$	Higher along fence line	$F_{(1,29)} = 21.24$ $p = 0.850$	No patterns
Forbs	$F_{(1,29)} = 28.40$ $p = 0.497$	Higher along fence line	$F_{(1,29)} = 27.47$ $p = 0.546$	No patterns
Copperburrs	$F_{(1,29)} = 36.59$ $p = 0.157$	Higher along fence line	$F_{(1,29)} = 27.05$ $p = 0.569$	No patterns

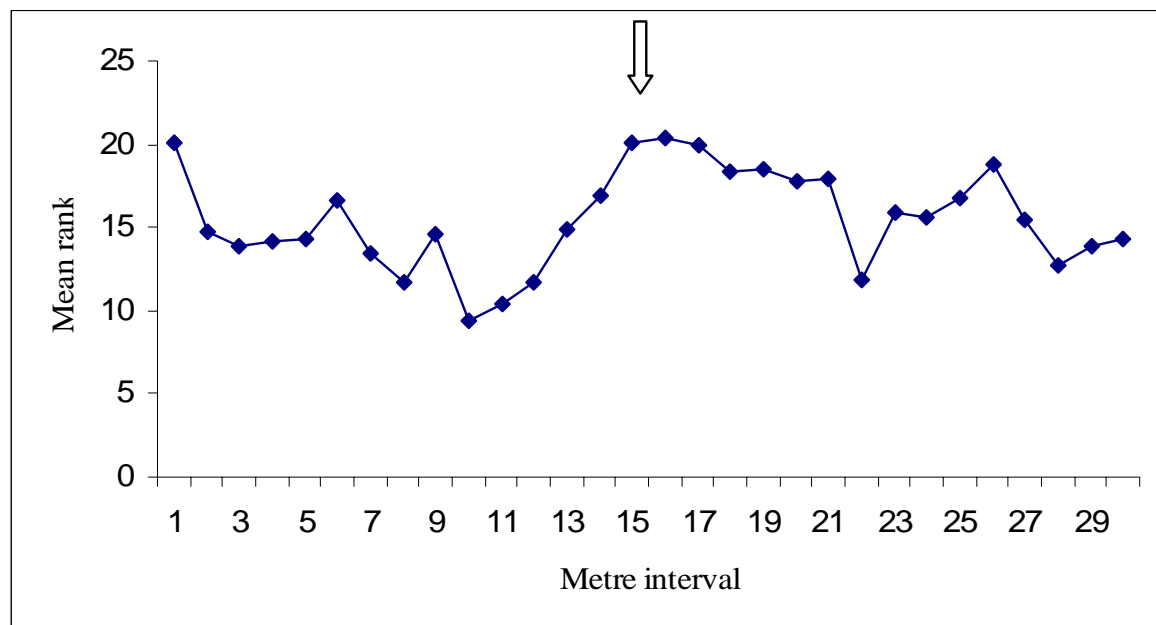


Figure A3.1: Plot of mean ranks per metre interval for pasture cover at the fence. Arrow indicates position of fenceline.

Table A3.2: Results from Friedman's tests and overall patterns in vegetation height (as detected from plots of mean ranks per meter) along 30-m transects at the fence and hinterland monitoring areas (n = 10).

Vegetation	Fence		Hinterland	
Pasture	$F_{(1,29)} = 41.25$ $p = 0.066$	Higher along fence line	$F_{(1,29)} = 17.91$ $p = 0.946$	No patterns
Grasses	$F_{(1,29)} = 33.47$ $p = 0.259$	Higher along fence line	$F_{(1,29)} = 25.88$ $p = 0.632$	No patterns
Forbs	$F_{(1,29)} = 32.75$ $p = 0.288$	Higher along fence line	$F_{(1,29)} = 22.53$ $p = 0.798$	No patterns
Copperburrs	$F_{(1,29)} = 37.06$ $p = 0.145$	Higher along fence line	$F_{(1,29)} = 26.01$ $p = 0.625$	No patterns

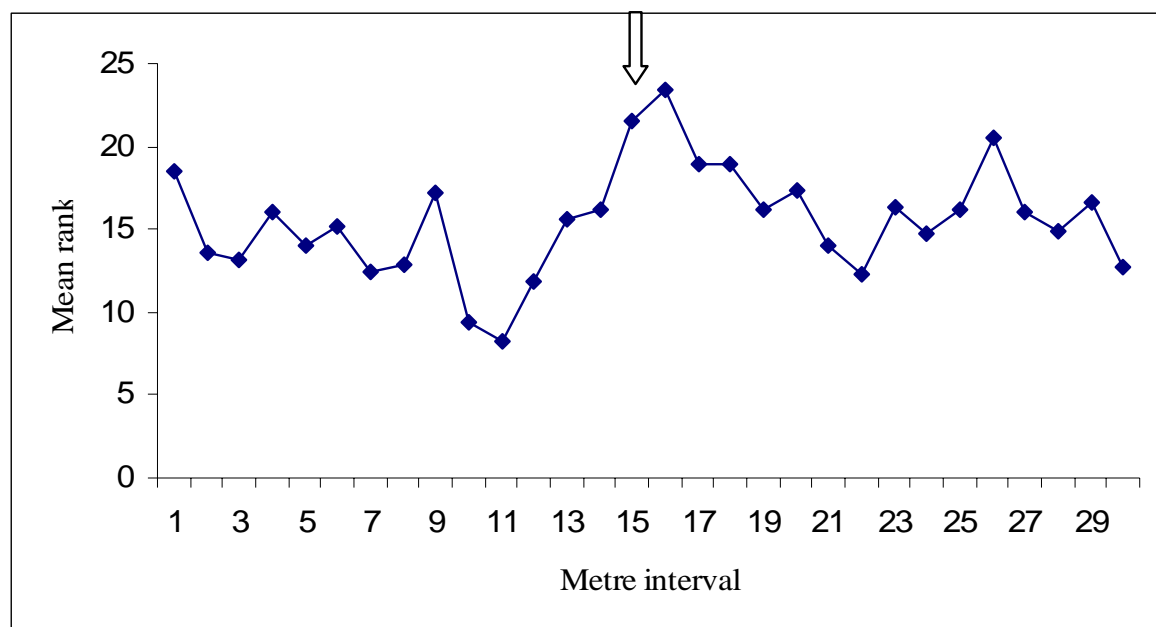


Figure A3.2: Plot of mean ranks per metre interval for pasture height at the fence. Arrow indicates position of fenceline.

Table A3.3: Results from Friedman's tests and overall patterns in vegetation greenness (as detected from plots of mean ranks per meter) along 30-m transects at the fence and hinterland monitoring areas (n = 10).

Vegetation		Fence		Hinterland
Pasture	$F_{(1,29)} = 67.48$ $p < 0.001$	Higher along fence line	$F_{(1,29)} = 26.76$ $p = 0.585$	No patterns
Grasses	$F_{(1,29)} = 36.49$ $p = 0.160$	Higher along fence line	$F_{(1,29)} = 22.81$ $p = 0.785$	No patterns
Forbs	$F_{(1,29)} = 36.39$ $p = 0.163$	Higher along fence line	$F_{(1,29)} = 16.28$ $p = 0.972$	No patterns
Copperburrs	$F_{(1,29)} = 44.91$ $p = 0.03$	Higher along fence line	$F_{(1,29)} = 27.03$ $p = 0.570$	No patterns

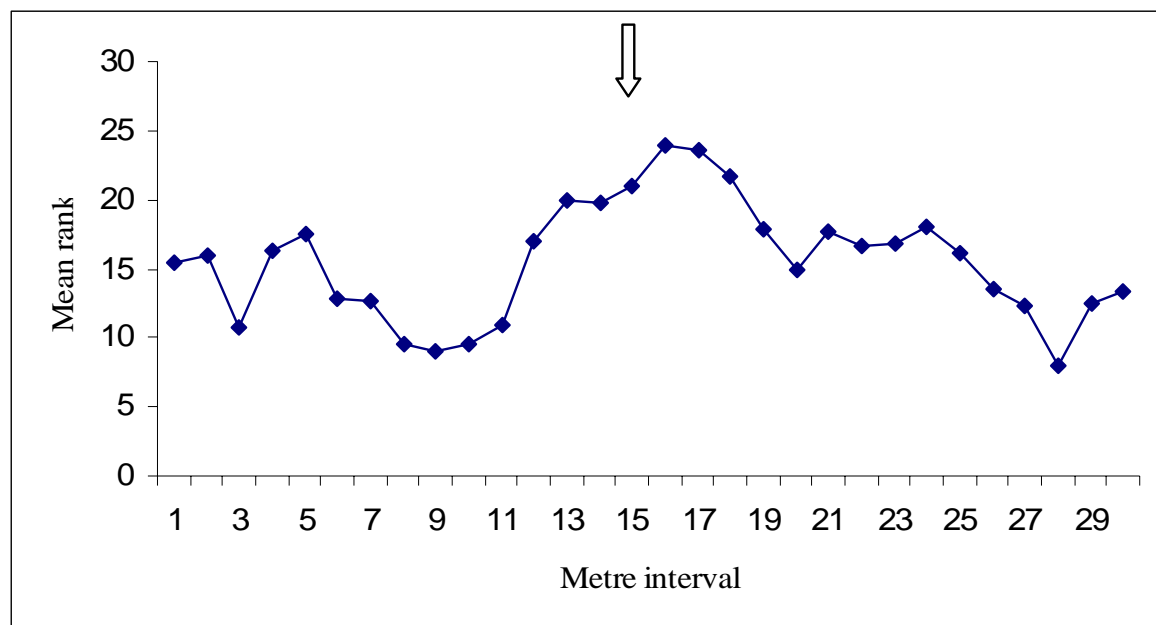


Figure A3.3: Plot of mean ranks per metre interval for pasture greenness at the fence. Arrow indicates position of fenceline.

Table A3.4: Results from 2-factor Anova for CV of pasture cover, height and greenness.

Variable	Landscape type		Position		Landscape type*Position	
Cover	$F_{(1,56)} = 30.94$	$p < 0.001$	$F_{(3,56)} = 4.03$	$p = 0.012$	$F_{(3,56)} = 6.34$	$p = 0.001$
Height	$F_{(1,56)} = 9.88$	$p = 0.003$	$F_{(3,56)} = 7.23$	$p < 0.001$	$F_{(3,56)} = 11.24$	$p < 0.001$
Greenness	$F_{(1,56)} = 17.68$	$p < 0.001$	$F_{(3,56)} = 3.63$	$p = 0.018$	$F_{(3,56)} = 2.88$	$p = 0.044$

Table A3.5: Results from 2-factor Anova for CV of grass cover, height and greenness. Greenness values were square-root transformed.

Variable	Landscape type		Position		Landscape type*Position	
Cover	$F_{(1,56)} = 18.62$	$p < 0.001$	$F_{(3,56)} = 9.29$	$p < 0.001$	$F_{(3,56)} = 13.57$	$p < 0.001$
Height	$F_{(1,56)} = 15.49$	$p < 0.001$	$F_{(3,56)} = 3.47$	$p = 0.022$	$F_{(3,56)} = 9.54$	$p < 0.001$
Greenness	$F_{(1,56)} = 37.91$	$p < 0.001$	$F_{(3,56)} = 13.48$	$p < 0.001$	$F_{(3,56)} = 14.79$	$p < 0.001$

Table A3.6: Results from 2-factor Anova for CV of forb cover, height and greenness. Cover and greenness values were square-root transformed.

Variable	Landscape type		Position		Landscape type*Position	
Cover	$F_{(1,56)} = 60.54$	$p < 0.001$	$F_{(3,56)} = 7.01$	$p < 0.001$	$F_{(3,56)} = 5.80$	$p = 0.002$
Height	$F_{(1,56)} = 70.48$	$p < 0.001$	$F_{(3,56)} = 5.43$	$p = 0.002$	$F_{(3,56)} = 7.04$	$p < 0.001$
Greenness	$F_{(1,56)} = 21.27$	$p < 0.001$	$F_{(3,56)} = 0.32$	$p = 0.808$	$F_{(3,56)} = 0.94$	$p = 0.475$

Table A3.7: Results from 2-factor Anova for CV of copperburr cover, height and greenness. Height values were square-root transformed.

Variable	Landscape type		Position		Landscape type*Position	
Cover	$F_{(1,56)} = 1.65$	$p = 0.205$	$F_{(3,56)} = 3.16$	$p = 0.032$	$F_{(3,56)} = 1.36$	$p = 0.266$
Height	$F_{(1,56)} = 2.55$	$p = 0.116$	$F_{(3,56)} = 1.58$	$p = 0.204$	$F_{(3,56)} = 0.73$	$p = 0.540$
Greenness	$F_{(1,56)} = 3.03$	$p = 0.087$	$F_{(3,56)} = 5.33$	$p = 0.003$	$F_{(3,56)} = 3.01$	$p = 0.038$

Table A3.8: Mean CV values (+ 1 SE) for soil variables at each position. Some soil moisture values at the fence and hinterland positions were estimated using regression estimation.

Variable	Road edge	Table drain	Fence	Hinterland
Exchangeable Ca	18.81 ± 11.35	27.19 ± 13.17	29.38 ± 7.46	32.47 ± 13.35
Exchangeable K	35.04 ± 27.62	28.94 ± 8.22	23.47 ± 1.32	24.21 ± 8.44
Exchangeable Mg	70.96 ± 66.45	18.00 ± 10.75	14.92 ± 7.86	25.34 ± 5.11
Exchangeable Na	99.09 ± 32.07	41.72 ± 8.05	46.57 ± 0.001	46.79 ± 14.98
Active C	29.93 ± 15.85	32.65 ± 13.10	14.83 ± 3.03	20.33 ± 5.15
Available P	41.75 ± 5.20	35.25 ± 5.14	34.43 ± 10.96	32.92 ± 11.60
Nitrate	37.09 ± 2.12	44.34 ± 15.02	22.60 ± 6.47	32.44 ± 8.26
pH	3.49 ± 1.31	3.53 ± 0.50	4.33 ± 0.40	5.87 ± 1.46
EC	41.8 ± 18.62	60.26 ± 49.02	22.68 ± 8.94	48.82 ± 0.02
Compaction	34.95 ± 3.40	33.89 ± 2.72	17.80 ± 6.81	23.00 ± 3.15
Soil moisture	20.45 ± 13.94	15.99 ± 4.67	29.33 ± 24.81	17.21 ± 9.03

Table A3.9: Results from PCA showing correlations between soil variables and extracted components (orthogonal varimax rotated component matrix). Natural-log transformations were used for exchangeable Ca, available P, and EC.

Variable	Component 1	Component 2	Component 3
pH (pH/w)	0.92	-0.02	-0.09
Exchangeable Mg (mg/kg)	0.73	-0.53	-0.10
Exchangeable Na (mg/kg)	0.72	-0.13	0.12
Compaction (Kg/cm ²)	-0.71	0.19	0.45
EC (dS/m)	-0.28	0.91	-0.09
Exchangeable Ca (mg/kg)	0.72	0.85	-0.34
Soil moisture (mm ³ /mm ³)	-0.45	0.73	-0.17
Nitrate (mg/kg)	-0.12	0.06	0.90
Active C (mg/kg)	-0.02	-0.42	0.84
Available P (mg/kg)	-0.46	-0.43	0.70
Exchangeable K (mg/kg)	0.27	-0.43	0.64

Table A3.10: Model equations for relationships between vegetation and soil variables. Square-root transformations were used for copperburr cover, grass height, and grass and forb greenness values and natural-log transformations were used for grass and forb cover, and pasture and forb height values.

Variable	Model
Forb cover	$y = 2.60 - 0.27\text{component } 3$
Copperburr cover	$y = 2.58 + 0.83\text{component } 3$
Forb height	$y = 0.77 - 0.14\text{component } 3$
Copperburr height	$y = 0.68 + 0.25\text{component } 3$
Pasture greenness	$y = 46.74 + 9.83\text{component } 2$
Grass greenness	$y = 3.66 + 0.68\text{component } 2$
Forb greenness	$y = 6.25 - 0.49\text{component } 3 + 0.42\text{component } 2$
Copperburr greenness	$y = 26.09 + 9.73\text{component } 2 + 6.27\text{component } 3 - 6.11\text{component } 1$

Component 1 is positively correlated with pH, and exchangeable Mg and Na, and negatively with compaction.
 Component 2 is positively correlated with EC, exchangeable Ca and soil moisture.
 Component 3 is positively correlated with nitrate, Active C, available P, and exchangeable K.

Table A3.11: Non-significant model terms influencing vegetation variables. Values for copperburr greenness were square-root transformed and values for grass greenness natural-log transformed.

Variable	Model terms	F values	P values
Pasture cover	Last rainfall amount	$F_{(1,54)} = 1.53$	$p = 0.222$
	Position	$F_{(3,59)} = 0.50$	$p = 0.686$
Grass cover	Last rainfall amount	$F_{(1,53)} = 1.35$	$p = 0.250$
Forb cover	Last rainfall amount	$F_{(1,60)} = 1.86$	$p = 0.178$
	Landscape type*position	$F_{(3,55)} = 1.66$	$p = 0.187$
	Position	$F_{(3,55)} = 1.16$	$p = 0.335$
Copperburr cover	Landscape type*position	$F_{(3,55)} = 5.03$	$p = 0.029$
	Temperature (3 months)	$F_{(1,57)} = 0.51$	$p = 0.480$
	Last rainfall amount	$F_{(1,57)} = 0.01$	$p = 0.920$
Pasture height	Last rainfall amount	$F_{(1,54)} = 0.18$	$p = 0.675$
	Temperature (1 month)	$F_{(1,54)} = 0.02$	$p = 0.888$
Grass height	Rainfall (3 months)	$F_{(1,55)} = 3.76$	$p = 0.058$
	Temperature (3 months)	$F_{(1,55)} = 0.38$	$p = 0.541$
	Last rainfall amount	$F_{(1,55)} = 0.02$	$p = 0.882$
Forb height	Landscape type*position	$F_{(3,55)} = 2.11$	$p = 0.109$
	Last rainfall amount	$F_{(1,57)} = 0.21$	$p = 0.652$
	Temperature (3 months)	$F_{(1,57)} = 0.20$	$p = 0.658$
Copperburr height	Last rainfall amount	$F_{(1,59)} = 0.06$	$p = 0.802$
	Landscape type*position	$F_{(3,56)} = 0.60$	$p = 0.616$
	Temperature (3 months)	$F_{(1,59)} = 2.39$	$p = 0.128$
	Landscape type	$F_{(1,59)} = 2.46$	$p = 0.122$
	Rainfall (1 month)	$F_{(1,59)} = 2.96$	$p = 0.091$
Pasture greenness	Landscape type	$F_{(1,57)} = 3.76$	$p = 0.058$
	Landscape type*position	$F_{(3,54)} = 2.56$	$p = 0.065$
	Last rainfall amount	$F_{(1,57)} = 0.79$	$p = 0.378$
Grass greenness	Last rainfall amount	$F_{(1,53)} = 2.84$	$p = 0.098$
Forb greenness	Last rainfall amount	$F_{(1,56)} = 1.96$	$p = 0.167$
	Landscape type*position	$F_{(3,54)} = 0.76$	$p = 0.522$
Copperburr greenness	Rainfall (2 weeks)	$F_{(1,54)} = 3.08$	$p = 0.085$
	Position	$F_{(3,59)} = 1.69$	$p = 0.180$
	Last rainfall amount	$F_{(1,54)} = 0.05$	$p = 0.832$

Table A3.12: Non-significant results for comparisons of pasture greenness between mown and unmown quadrats.

Dataset		t-values	Degrees of freedom	P values
All replicates	Entire	1.04	29	0.306
	Hills only	-0.34	14	0.741
	Floodplains only	1.79	14	0.095
Replicate 1	Entire	-0.29	29	0.772
	Hills only	-0.78	14	0.450
	Floodplains only	0.41	14	0.690
Replicate 2	Entire	1.55	29	0.132
	Hills only	0.98	14	0.342
	Floodplains only	1.19	14	0.255
Replicate 3	Entire	1.25	29	0.221
	Hills only	-0.52	14	0.609

Table A3.13: Non-significant results for comparisons of grass greenness between mown and unmown quadrats.

Dataset		t-values	Degrees of freedom	P values
All replicates	Entire	-1.93	22	0.067
	Floodplains only	-0.23	10	0.822
Replicate 1	Entire	-0.94	14	0.361
	Hills only	-1.22	10	0.249
	Floodplains only	1.00	3	0.391
Replicate 2	Entire	-0.70	15	0.493
	Hills only	-0.04	5	0.970
	Floodplains only	-1.16	9	0.278
Replicate 3	Entire	-0.64	8	0.539
	Hills only	-1.97	3	0.144
	Floodplains only	1.26	4	0.277

Table A3.14: Non-significant results for comparisons of forb greenness between mown and unmown quadrats.

Dataset		t-values	Degrees of freedom	P values
All replicates	Entire	0.54	26	0.596
	Hills only	-0.53	12	0.605
	Floodplains only	1.37	13	0.195
Replicate 1	Entire	-0.14	18	0.894
	Hills only	-0.37	11	0.717
	Floodplains only	0.17	6	0.870
Replicate 2	Entire	0.96	21	0.349
	Hills only	0.18	7	0.863
	Floodplains only	0.99	13	0.340
Replicate 3	Entire	0.97	21	0.344
	Hills only	-0.35	8	0.065
	Floodplains only	2.03	12	0.738

Table A3.15: Non-significant results for comparisons of copperburr greenness between mown and unmown quadrats.

Dataset		t-values	Degrees of freedom	P values
All replicates	Entire	0.17	12	0.870
	Hills only	0.95	8	0.369
	Floodplains only	-0.69	3	0.539
Replicate 1	Entire	-0.52	10	0.616
	Hills only	0.14	7	0.890
	Floodplains only	-2.85	2	0.104
Replicate 2	Entire	0.66	10	0.522
	Hills only	1.05	6	0.336
	Floodplains only	-1.96	3	0.144
Replicate 3	Entire	-0.14	7	0.890
	Hills only	0.90	3	0.437
	Floodplains only	-1.45	3	0.243

Table A3.16: List of plant species found in mown and unmown quadrats.

Scientific name	Common name
<i>Abutilon halophilum</i>	Plains lantern bush
<i>Aristida</i> spp.	No common name (grass)
<i>Atriplex limbata</i>	Spreading saltbush
<i>Atriplex vesicaria</i>	Bladder saltbush
<i>Atriplex</i> spp.	No common name (saltbush)
<i>Boerhavia dominii</i>	Tar vine
<i>Brachyscome ciliaris</i>	Variable daisy
<i>Centaurea melitensis</i>	Maltese cockspur
<i>Chamaesyce drummondii</i>	Caustic weed
<i>Convolvulus remotus</i>	*No common name
<i>Dissocarpus biflorus</i>	Twin-horned copperburr
<i>Dissocarpus</i> spp.	No common name (copperburr)
<i>Enchylaena tomentosa</i>	Ruby saltbush
<i>Enneapogon avenaceus</i>	Common bottle washer
<i>Enneapogon intermedius</i>	Tall bottlewasher
<i>Enneapogon nigricans</i>	Niggerhead
<i>Enneapogon</i> spp.	No common name (grass)
<i>Eragrostis dielsii</i>	Mulka
<i>Ixiochlamys cuneifolia</i>	Silverton daisy
<i>Ixiolaena leptolepis</i>	Stalked plover-daisy
<i>Maireana pyramidata</i>	Black bluebush
<i>Maireana</i> spp.	No common name (bluebush)
<i>Malvastrum americanum</i>	Malvastrum
<i>Minuria cunninghamii</i>	Bush minuria
<i>Minuria leptophylla</i>	Minnie daisy
<i>Osteocarpum acropterum</i>	Water weed
<i>Panicum decompositum</i>	Native millet
<i>Portulaca oleracea</i>	Common pigweed
<i>Pterocaulon sphacelatum</i>	Fruit-salad plant

Scientific name	Common name
<i>Rhagodia spinescens</i>	Thorny saltbush
<i>Sclerolaena brachyptera</i>	Short-winged copperburr
<i>Sclerolaena decurrens</i>	Green copperburr
<i>Sclerolaena diacantha</i>	Grey copperburr
<i>Sclerolaena divaricata</i>	Pale poverty-bush
<i>Sclerolaena lanicuspis</i>	Woolly copperburr
<i>Sclerolaena limbata</i>	Pearl copperburr
<i>Sclerolaena muricata</i>	Black roly-poly
<i>Sclerolaena tricuspis</i>	Streaked poverty bush
<i>Sclerolaena spp.</i>	No common name (copperburr)
<i>Senecio cunninghamii</i>	Bushy groundsel
<i>Sida ammophila</i>	Sand sida
<i>Sida filiformis</i>	Fine sida
<i>Sida intricata</i>	Twiggy sida
<i>Solanum esuriale</i>	Quena
<i>Swainsona spp.</i>	No common name (forb – pea)
<i>Teucrium racemosum</i>	Grey germander
<i>Themeda australis</i>	Kangaroo grass
<i>Vittadinia cuneata</i>	Fuzzweed
<i>Wahlenburgia spp.</i>	No common name (forb – bluebell)
Unknown aromatic species	
Unknown daisy species	

Table A3.17: Simpson's diversity indices for mown and unmown quadrats and non-significant results for diversity comparisons between mown and unmown quadrats.

Dataset		Mown	Unmown	P values
All replicates	Entire	29.35	23.92	0.288
	Hills only	21.25	17.27	0.298
	Floodplains only	20.47	16.07	0.363
Replicate 1	Entire	16.5	17.82	0.768
	Hills only	12.55	11.45	0.731
	Floodplains only	8.12	9.76	0.749
Replicate 2	Entire	24.22	18.82	0.186
	Hills only	13.26	11.92	0.612
	Floodplains only	15.98	11.56	0.297
Replicate 3	Floodplains only	14.39	12.54	0.591

Appendix 4

Table A4.1: Weeks and corresponding dates that kangaroo surveys were conducted. ✓ indicates surveys, and ✕ indicates no surveys.

Week	Date	Road (day)	Road (night)	Hinterland (day)	Hinterland (night)
1	03/03/03 to 09/03/03	✓	✓	✓	✓
2	10/03/03 to 16/03/03	✓	✓	✓	✓
3	17/03/03 to 23/03/03	✓	✓	✓	✓
4	24/03/03 to 30/03/03	✓	✓	✓	✓
5	31/03/03 to 06/04/03	✓	✓	✓	✓
6	07/04/03 to 13/04/03	✓	✓	✓	✓
7	14/04/03 to 20/04/03	✓	✓	✓	✓
8	21/04/03 to 27/04/03	✓	✓	✓	✓
9	28/04/03 to 04/05/03	✓	✓	✓	✓
10	05/05/03 to 11/05/03	✓	✓	✓	✓
11	12/05/03 to 18/05/03	✓	✓	✓	✓
12	19/05/03 to 25/05/03	✓	✓	✓	✓
13	26/05/03 to 01/06/03	✓	✓	✓	✓
14	02/06/03 to 08/06/03	✓	✓	✓	✓
15	09/06/03 to 15/06/03	✓	✓	✓	✓
16	16/06/03 to 22/06/03	✓	✓	✓	✓
17	23/06/03 to 29/06/03	✓	✓	✓	✓
18	30/06/03 to 06/07/03	✓	✓	✓	✓
19	07/07/03 to 13/07/03	✓	✓	✓	✓
20	14/07/03 to 20/07/03	✓	✓	✓	✓
21	21/07/03 to 27/07/03	✓	✓	✕	✕
22	28/07/03 to 03/08/03	✓	✓	✓	✓
23	04/08/03 to 10/08/03	✕	✕	✕	✕
24	11/08/03 to 17/08/03	✓	✓	✕	✕
25	18/08/03 to 24/08/03	✓	✓	✕	✕
26	25/08/03 to 31/08/03	✓	✓	✓	✓
27	01/09/03 to 07/09/03	✓	✓	✓	✓
28	08/09/03 to 14/09/03	✓	✓	✓	✓
29	15/09/03 to 21/09/03	✓	✓	✓	✓
30	22/09/03 to 28/09/03	✓	✓	✓	✓
31	29/09/03 to 05/10/03	✓	✓	✓	✓
32	06/10/03 to 12/10/03	✓	✓	✓	✓
33	13/10/03 to 19/10/03	✓	✓	✓	✓
34	20/10/03 to 26/10/03	✓	✓	✓	✓
35	27/10/03 to 02/11/03	✓	✓	✓	✓
36	03/11/03 to 09/11/03	✓	✓	✓	✓
37	10/11/03 to 16/11/03	✓	✓	✓	✓
38	17/11/03 to 23/11/03	✓	✓	✓	✓
39	24/11/03 to 30/11/03	✓	✓	✓	✓
40	01/12/03 to 07/12/03	✕	✕	✕	✕
41	08/12/03 to 14/12/03	✓	✓	✓	✓
42	15/12/03 to 21/12/03	✓	✓	✓	✓

Week	Date	Road (day)	Road (night)	Hinterland (day)	Hinterland (night)
43	22/12/03 to 28/12/03	✓	✓	✓	✓
44	29/12/03 to 04/01/04	✓	✓	✓	✓
45	05/01/04 to 11/01/04	✓	✓	✓	✓
46	12/01/04 to 18/01/04	✓	✓	✓	✓
47	19/01/04 to 25/01/04	✓	✓	✓	✓
48	26/01/04 to 01/02/04	✓	✓	✓	✓
49	02/02/04 to 08/02/04	✓	✓	✓	✓
50	09/02/04 to 15/02/04	✓	✓	✓	✓
51	16/02/04 to 22/02/04	✓	✓	✓	✓
52	23/02/04 to 29/02/04	✓	✓	✓	✓
53	01/03/04 to 07/03/04	✓	✓	✓	✓
54	08/03/04 to 14/03/04	✓	✓	✓	✓
55	15/03/04 to 21/03/04	✓	✓	✓	✓
56	22/03/04 to 28/03/04	x	x	x	x
57	29/03/04 to 04/04/04	x	x	x	x
58	05/04/04 to 11/04/04	✓	✓	✓	✓
59	12/04/04 to 18/04/04	✓	✓	✓	✓
60	19/04/04 to 25/04/04	✓	✓	✓	✓
61	26/04/04 to 02/05/04	✓	✓	✓	✓
62	03/05/04 to 09/05/04	✓	✓	✓	✓
63	10/05/04 to 16/05/04	✓	✓	✓	✓
64	17/05/04 to 23/05/04	✓	✓	✓	✓
65	24/05/04 to 30/05/04	✓	✓	✓	✓
66	31/05/04 to 06/06/04	✓	✓	x	x
67	07/06/04 to 13/06/04	✓	✓	✓	x
68	14/06/04 to 20/06/04	x	x	x	x
69	21/06/04 to 27/06/04	✓	✓	✓	✓
70	28/06/04 to 04/07/04	✓	✓	✓	✓
71	05/07/04 to 11/07/04	✓	✓	✓	✓
72	12/07/04 to 18/07/04	✓	✓	✓	✓
73	19/07/04 to 25/07/04	x	x	x	x
74	26/07/04 to 01/08/04	✓	✓	✓	✓
75	02/08/04 to 08/08/04	✓	✓	✓	✓
76	09/08/04 to 15/08/04	✓	✓	✓	✓
77	16/08/04 to 22/08/04	✓	✓	✓	✓
78	23/08/04 to 29/08/04	✓	✓	✓	✓
79	30/08/04 to 05/09/04	✓	✓	✓	✓
80	06/09/04 to 12/09/04	✓	✓	✓	✓
81	13/09/04 to 19/09/04	✓	✓	✓	✓
82	20/09/04 to 26/09/04	✓	✓	✓	✓
83	27/09/04 to 03/10/04	✓	✓	x	x
84	04/10/04 to 10/10/04	✓	✓	✓	✓
85	11/10/04 to 17/10/04	✓	✓	✓	✓
86	18/10/04 to 24/10/04	✓	✓	✓	✓
87	25/10/04 to 31/10/04	✓	✓	✓	✓
88	01/11/04 to 07/11/04	✓	✓	✓	✓
89	08/11/04 to 14/11/04	✓	✓	✓	✓

Table A4.2: Results from PCA showing correlations between weather variables and extracted components (orthogonal varimax rotated component matrix).

Variable	Component 1	Component 2	Component 3
Maximum humidity	-0.93	-0.24	0.23
Maximum temperature	0.88	0.40	0.15
Minimum humidity	-0.85	-0.37	0.32
Maximum heat index	0.85	0.30	0.08
Minimum temperature	0.85	0.37	0.34
Minimum windchill	0.83	0.16	0.41
Minimum barometric pressure	-0.29	-0.91	-0.20
Maximum wind gust	0.28	0.82	-0.03
Maximum barometric pressure	-0.40	-0.82	-0.26
Minimum dewpoint	-0.09	0.01	0.94
Maximum dewpoint	0.20	0.30	0.83

Table A4.3: Results from PCA showing correlations between “daytime” weather variables (from original Component 1) and extracted components.

Variable	Component
Maximum temperature	0.96
Minimum humidity	-0.94
Maximum heat index	0.94

Table A4.4: Results from PCA showing correlations between “night-time” weather variables (from original Component 1) and extracted components.

Variable	Component
Minimum temperature	0.97
Minimum windchill	0.94
Maximum humidity	-0.90

Appendix 5

Table A5.1: Results from GLM examining effects of various factors and variables on the initial distance to flight when flight was taken (biologically meaningful factor interactions were examined but were not significant). The final model accounted for 22 % of variation ($\text{Adj } R^2 = 0.223$, $F_{(12,3263)} = 79.51$, $p < 0.001$). Values for initial distance were square-root transformed. Significant model terms are shown in **bold**.

Model Terms	F values	P values
Time of day	$F_{(1,3262)} = 0.60$	$p = 0.438$
Site	$F_{(1,3263)} = 96.91$	$p < 0.001$
Speed of approaching vehicle	$F_{(1,3263)} = 315.33$	$p < 0.001$
Species	$F_{(2,3263)} = 36.61$	$p < 0.001$
Age/sex	$F_{(2,3263)} = 14.12$	$p < 0.001$
Group size	$F_{(2,3263)} = 50.02$	$p < 0.001$
Cover	$F_{(1,3263)} = 116.21$	$p < 0.001$
Season	$F_{(3,3263)} = 11.23$	$p < 0.001$

Table A5.2: Results from GLM examining effects of various factors and variables on the distances travelled by kangaroos (biologically meaningful factor interactions were examined but were not significant). The final model accounted for 6 % of variation ($\text{Adj } R^2 = 0.059$, $F_{(4,900)} = 15.11$, $p < 0.001$). Values for distance travelled were natural-log transformed. Significant model terms are shown in **bold**.

Model Terms	F values	P values
Time of day	$F_{(1,900)} = 19.23$	$p < 0.001$
Site	$F_{(1,899)} = 0.15$	$p = 0.703$
Speed of approaching vehicle	$F_{(1,899)} = 0.83$	$p = 0.363$
Distance from approaching vehicle	$F_{(1,900)} = 28.55$	$p < 0.001$
Species	$F_{(2,900)} = 3.69$	$p = 0.025$
Age/sex	$F_{(2,898)} = 0.34$	$p = 0.713$
Group size	$F_{(2,898)} = 2.13$	$p = 0.119$
Cover	$F_{(1,899)} = 0.50$	$p = 0.481$
Season	$F_{(3,897)} = 2.58$	$p = 0.053$

Appendix 6

Table A6.1: Results from 2-factor Anova for CV of small mammal variables over time.

Variable	Habitat		Position		Habitat*Position	
Total abundance	$F_{(1,44)} = 3.00$	$p = 0.090$	$F_{(2,44)} = 0.10$	$p = 0.909$	$F_{(2,44)} = 0.40$	$p = 0.670$
Biomass	$F_{(1,44)} = 2.54$	$p = 0.118$	$F_{(2,44)} = 0.08$	$p = 0.927$	$F_{(2,44)} = 1.12$	$p = 0.334$
Richness	$F_{(1,44)} = 1.98$	$p = 0.167$	$F_{(2,44)} = 0.04$	$p = 0.965$	$F_{(2,44)} = 0.25$	$p = 0.778$

Table A6.2: Results from 2-factor Anova for CV of invertebrate variables over time. Values for larva were square-root transformed. * indicates significant differences.

Variable	Habitat		Position		Habitat*Position	
Ants	$F_{(1,44)} = 0.11$	$p = 0.743$	$F_{(2,44)} = 0.14$	$p = 0.870$	$F_{(2,44)} = 0.71$	$p = 0.499$
Termites	$F_{(1,44)} = 21.71$	$p < 0.001^*$	$F_{(2,44)} = 1.04$	$p = 0.361$	$F_{(2,44)} = 1.04$	$p = 0.361$
Bees	$F_{(1,44)} = 5.97$	$p = 0.019^*$	$F_{(2,44)} = 1.00$	$p = 0.378$	$F_{(2,44)} = 0.92$	$p = 0.408$
Beetles	$F_{(1,44)} = 0.54$	$p = 0.466$	$F_{(2,44)} = 2.05$	$p = 0.141$	$F_{(2,44)} = 0.68$	$p = 0.510$
Bugs	$F_{(1,44)} = 10.41$	$p = 0.002^*$	$F_{(2,44)} = 1.84$	$p = 0.172$	$F_{(2,44)} = 0.10$	$p = 0.905$
Moths	$F_{(1,44)} = 0.92$	$p = 0.344$	$F_{(2,44)} = 0.08$	$p = 0.925$	$F_{(2,44)} = 0.75$	$p = 0.478$
Centipedes	$F_{(1,44)} = 3.12$	$p = 0.084$	$F_{(2,44)} = 0.37$	$p = 0.695$	$F_{(2,44)} = 3.24$	$p = 0.049^*$
Cockroaches	$F_{(1,44)} = 2.16$	$p = 0.149$	$F_{(2,44)} = 1.22$	$p = 0.306$	$F_{(2,44)} = 5.61$	$p = 0.007^*$
Crickets	$F_{(1,44)} = 6.35$	$p = 0.015^*$	$F_{(2,44)} = 1.28$	$p = 0.289$	$F_{(2,44)} = 1.35$	$p = 0.271$
Isopods	$F_{(1,44)} = 0.001$	$p = 0.972$	$F_{(2,44)} = 1.33$	$p = 0.274$	$F_{(2,44)} = 2.64$	$p = 0.083$
Larva	$F_{(1,44)} = 0.38$	$p = 0.539$	$F_{(2,44)} = 4.16$	$p = 0.022^*$	$F_{(2,44)} = 0.89$	$p = 0.417$
Scorpions	$F_{(1,44)} = 0.06$	$p = 0.807$	$F_{(2,44)} = 0.13$	$p = 0.883$	$F_{(2,44)} = 0.30$	$p = 0.742$
Silverfish	$F_{(1,44)} = 0.46$	$p = 0.504$	$F_{(2,44)} = 5.07$	$p = 0.010^*$	$F_{(2,44)} = 3.49$	$p = 0.039^*$
Spiders	$F_{(1,44)} = 2.54$	$p = 0.118$	$F_{(2,44)} = 0.56$	$p = 0.577$	$F_{(2,44)} = 1.02$	$p = 0.368$
Stick insects	$F_{(1,44)} = 1.11$	$p = 0.297$	$F_{(2,44)} = 4.24$	$p = 0.021^*$	$F_{(2,44)} = 0.28$	$p = 0.759$
Richness	$F_{(1,44)} = 12.49$	$p = 0.001^*$	$F_{(2,44)} = 0.10$	$p = 0.902$	$F_{(2,44)} = 0.09$	$p = 0.912$

Table A6.3: Results from PCA showing correlations between invertebrate variables and extracted components (orthogonal varimax rotated component matrix). Values for crickets were natural-log transformed and values for isopods were square-root transformed.

Variable	1	2	3	4	5	6	7
Silverfish	0.764	0.140	0.118	-0.035	-0.369	0.141	-0.175
Termites	0.757	0.166	-0.066	-0.100	0.100	0.012	0.142
Ants	0.662	-0.316	-0.132	0.213	0.068	-0.322	0.095
Spiders	0.568	-0.010	-0.348	0.201	0.301	0.063	-0.292
Bugs	0.035	0.842	-0.051	0.184	-0.155	-0.127	-0.083
Bees	0.276	0.686	0.017	0.018	0.513	-0.028	0.184
Beetles	0.106	-0.629	0.463	0.132	-0.125	-0.233	-0.044
Larvae	-0.101	-0.070	0.852	-0.097	-0.063	-0.014	-0.105
Scorpions	-0.217	-0.382	0.558	-0.123	0.124	-0.082	0.305
Cockroaches	-0.035	0.154	-0.129	0.870	-0.171	-0.107	0.089
Isopods	0.083	-0.033	0.018	0.803	0.392	0.084	-0.021
Crickets	-0.028	0.005	-0.029	0.066	0.913	-0.109	-0.043
Stick insects	-0.138	-0.127	-0.216	-0.091	-0.167	0.761	0.050
Richness	0.300	0.202	0.493	0.227	0.043	0.649	-0.023
Moths	0.125	0.055	-0.004	-0.013	0.058	0.319	0.785
Centipedes	0.131	0.062	0.030	-0.128	0.094	0.392	-0.703

Table A6.4: Results from 2-factor Anova for CV of microhabitat variables over time. * indicates significant differences.

Variable	Habitat		Position		Habitat*Position	
Bare	$F_{(1,44)} = 15.96$	$p < 0.001^*$	$F_{(2,44)} = 1.02$	$p = 0.368$	$F_{(2,44)} = 0.08$	$p = 0.926$
Crust	$F_{(1,44)} = 1.28$	$p = 0.264$	$F_{(2,44)} = 7.15$	$p = 0.002^*$	$F_{(2,44)} = 3.67$	$p = 0.034^*$
Dry Bluebush	$F_{(1,44)} = 7.30$	$p = 0.010^*$	$F_{(2,44)} = 0.02$	$p = 0.982$	$F_{(2,44)} = 0.29$	$p = 0.751$
Bluebush	$F_{(1,44)} = 1.63$	$p = 0.208$	$F_{(2,44)} = 0.77$	$p = 0.470$	$F_{(2,44)} = 0.29$	$p = 0.747$
Dry Forb	$F_{(1,44)} = 11.10$	$p = 0.002^*$	$F_{(2,44)} = 3.11$	$p = 0.055$	$F_{(2,44)} = 0.80$	$p = 0.455$
Forb	$F_{(1,44)} = 1.22$	$p = 0.275$	$F_{(2,44)} = 1.30$	$p = 0.282$	$F_{(2,44)} = 0.71$	$p = 0.496$
Dry Grass	$F_{(1,44)} = 5.86$	$p = 0.020^*$	$F_{(2,44)} = 0.64$	$p = 0.534$	$F_{(2,44)} = 1.85$	$p = 0.169$
Grass	$F_{(1,44)} = 5.73$	$p = 0.021^*$	$F_{(2,44)} = 0.38$	$p = 0.685$	$F_{(2,44)} = 0.96$	$p = 0.393$
Dry Saltbush	$F_{(1,44)} = 0.44$	$p = 0.511$	$F_{(2,44)} = 0.75$	$p = 0.480$	$F_{(2,44)} = 1.04$	$p = 0.364$
Saltbush	$F_{(1,44)} = 0.61$	$p = 0.440$	$F_{(2,44)} = 1.12$	$p = 0.337$	$F_{(2,44)} = 0.20$	$p = 0.817$
Dry Copperburr	$F_{(1,44)} = 6.77$	$p = 0.013^*$	$F_{(2,44)} = 0.30$	$p = 0.743$	$F_{(2,44)} = 1.77$	$p = 0.183$
Copperburr	$F_{(1,44)} = 2.10$	$p = 0.154$	$F_{(2,44)} = 0.24$	$p = 0.791$	$F_{(2,44)} = 3.90$	$p = 0.028^*$
Dung	$F_{(1,44)} = 2.24$	$p = 0.142$	$F_{(2,44)} = 2.34$	$p = 0.108$	$F_{(2,44)} = 0.40$	$p = 0.675$
Litter	$F_{(1,44)} = 15.17$	$p < 0.001^*$	$F_{(2,44)} = 1.75$	$p = 0.185$	$F_{(2,44)} = 1.77$	$p = 0.182$
Dry Shrub	$F_{(1,44)} = 0.61$	$p = 0.439$	$F_{(2,44)} = 0.73$	$p = 0.486$	$F_{(2,44)} = 0.73$	$p = 0.486$
Shrub	$F_{(1,44)} = 0.24$	$p = 0.629$	$F_{(2,44)} = 1.18$	$p = 0.316$	$F_{(2,44)} = 0.29$	$p = 0.754$
Morning temperature	$F_{(1,44)} = 12.71$	$p = 0.001^*$	$F_{(2,44)} = 1.58$	$p = 0.217$	$F_{(2,44)} = 1.16$	$p = 0.324$
Afternoon temperature	$F_{(1,44)} = 33.26$	$p < 0.001^*$	$F_{(2,44)} = 2.42$	$p = 0.101$	$F_{(2,44)} = 1.26$	$p = 0.293$

Table A6.5: Results from PCA showing correlations between microhabitat variables and extracted components (orthogonal varimax rotated component matrix).

Variable	1	2	3	4	5	6	7	8
Dry Forb cover	0.837	-0.232	-0.190	-0.002	-0.076	-0.119	0.214	-0.058
Litter cover	0.828	-0.043	-0.099	0.076	-0.016	0.261	-0.186	0.162
Dry Grass cover	0.819	-0.247	0.093	-0.103	-0.027	-0.153	0.052	0.030
Bare cover	-0.807	-0.383	0.069	-0.095	-0.178	-0.293	-0.012	-0.195
Morning temperature	0.801	-0.385	-0.032	0.093	-0.026	-0.012	-0.227	0.080
Forb cover	0.773	-0.173	-0.157	0.019	-0.189	-0.116	0.078	-0.127
Grass cover	0.704	-0.138	-0.110	-0.056	0.123	-0.400	0.312	0.077
Dry Copperburr cover	-0.487	0.056	-0.125	0.339	-0.081	0.450	-0.078	0.407
Saltbush density	-0.211	0.933	-0.020	-0.042	0.061	-0.047	-0.126	0.008
Dry Saltbush cover	-0.159	0.919	-0.092	0.007	0.094	0.049	-0.095	-0.031
Saltbush cover	-0.165	0.822	-0.131	0.050	-0.118	-0.076	0.076	0.013
Bluebush density	-0.285	-0.089	0.874	-0.009	-0.020	-0.078	-0.076	-0.061
Bluebush cover	-0.248	-0.041	0.824	-0.019	-0.022	0.053	0.136	0.094
Dry Bluebush cover	0.198	-0.107	0.726	-0.038	-0.050	-0.018	-0.184	-0.046
Dry Other shrub cover	-0.064	-0.012	-0.031	0.920	0.042	0.057	-0.146	0.007
Other Shrub cover	0.117	0.024	-0.017	0.917	-0.019	-0.065	0.057	-0.090
Crust cover	-0.042	0.185	0.024	-0.162	0.878	0.021	-0.085	0.087
Other shrub density	-0.035	-0.152	-0.112	0.184	0.838	-0.002	0.093	-0.105
Copperburr cover	-0.033	-0.087	-0.018	-0.046	0.037	0.903	0.078	-0.068
Afternoon temp	0.069	-0.092	-0.093	-0.079	0.000	0.057	0.937	-0.004
Dung cover	0.142	-0.022	0.006	-0.099	-0.005	-0.065	0.007	0.927

Table A6.6: Non-significant results from the stepwise multiple regression for multivariate small mammal abundance.

Variable	F values	P values	Proportion variance
Component 3 invertebrates ^A	3.08	0.061	0.05
Component 2 microhabitat ^B	1.88	0.195	0.03
Component 4 invertebrates ^C	2.06	0.164	0.03
Component 7 invertebrates ^D	1.10	0.369	0.02
Component 5 invertebrates ^E	0.96	0.417	0.01
Component 8 microhabitat ^F	0.40	0.642	0.006
Component 6 invertebrates ^G	0.16	0.764	0.003
Component 4 microhabitat ^H	0.19	0.754	0.003

^A positively correlated to insect larva and scorpion abundance.

^B positively correlated to saltbush density and saltbush and dry saltbush cover.

^C positively correlated to cockroach and isopod abundance.

^D positively correlated to moth abundance and negatively to centipede abundance.

^E positively correlated to cricket abundance.

^F positively correlated to dung cover.

^G positively correlated to stick insect abundance and invertebrate richness.

^H positively correlated to other shrub and dry other shrub cover.

Table A6.7: Non-significant results from GLM examining effects of factors and variables on *Sminthopsis macroura* abundance. No interactions are shown as landscape type was removed as a predictor (due to correlations with Component 1 microhabitat) and only landscape type*position interactions were of interest.

Model Terms	F values	P values
Component 1 microhabitat ^A	$F_{(1,44)} = 3.01$	$p = 0.090$
Component 3 microhabitat ^B	$F_{(1,44)} = 0.17$	$p = 0.681$
Component 4 microhabitat ^C	$F_{(1,44)} = 1.07$	$p = 0.306$
Component 5 microhabitat ^D	$F_{(1,44)} = 0.64$	$p = 0.427$
Component 6 microhabitat ^E	$F_{(1,44)} = 0.37$	$p = 0.545$
Component 7 microhabitat ^F	$F_{(1,44)} = 0.67$	$p = 0.418$
Component 1 invertebrates ^G	$F_{(1,44)} = 2.38$	$p = 0.130$
Component 2 invertebrates ^H	$F_{(1,44)} = 0.12$	$p = 0.732$
Component 3 invertebrates ^I	$F_{(1,44)} = 0.05$	$p = 0.819$
Component 4 invertebrates ^J	$F_{(1,44)} = 0.15$	$p = 0.703$
Component 5 invertebrates ^K	$F_{(1,44)} = 2.29$	$p = 0.137$
Component 6 invertebrates ^L	$F_{(1,44)} = 0.39$	$p = 0.535$
Component 7 invertebrates ^M	$F_{(1,44)} = 0.35$	$p = 0.558$

^A positively correlated to dry forb, litter, dry grass, forb and grass cover and morning temperatures and negatively correlated to bare ground and dry copperburr cover.

^B positively correlated to bluebush density and bluebush and dry bluebush cover.

^C positively correlated to other shrub and dry other shrub cover.

^D positively correlated to crust cover and the density of other shrubs.

^E positively correlated to copperburr cover.

^F positively correlated to afternoon temperatures.

^G positively correlated to silverfish, termite, ant and spider abundance.

^H positively correlated to bug and bee abundance and negatively to beetle abundance.

^I positively correlated to insect larva and scorpion abundance.

^J positively correlated to cockroach and isopod abundance.

^K positively correlated to cricket abundance.

^L positively correlated to stick insect abundance and invertebrate richness.

^M positively correlated to moth abundance and negatively to centipede abundance.

Table A6.8: Non-significant results from GLM examining effects of factors and variables on *Mus domesticus* abundance. No interactions are shown as landscape type was removed as a predictor (due to correlations with Component 1 microhabitat) and only landscape type*position interactions were of interest.

Model Terms	F values	P values
Position	$F_{(2,45)} = 1.88$	$p = 0.164$
Component 2 microhabitat ^A	$F_{(1,46)} = 0.09$	$p = 0.761$
Component 3 microhabitat ^B	$F_{(1,46)} = 0.03$	$p = 0.864$
Component 4 microhabitat ^C	$F_{(1,46)} = 3.05$	$p = 0.087$
Component 5 microhabitat ^D	$F_{(1,46)} = 0.24$	$p = 0.630$
Component 6 microhabitat ^E	$F_{(1,46)} = 0.03$	$p = 0.865$
Component 7 microhabitat ^F	$F_{(1,46)} = 0.19$	$p = 0.662$
Component 8 microhabitat ^G	$F_{(1,46)} = 0.08$	$p = 0.780$
Component 1 invertebrates ^H	$F_{(1,46)} = 0.06$	$p = 0.804$
Component 2 invertebrates ^I	$F_{(1,46)} = 0.07$	$p = 0.792$
Component 4 invertebrates ^J	$F_{(1,46)} = 0.42$	$p = 0.520$
Component 5 invertebrates ^K	$F_{(1,46)} = 2.59$	$p = 0.114$
Component 6 invertebrates ^L	$F_{(1,46)} = 0.04$	$p = 0.846$
Component 7 invertebrates ^M	$F_{(1,46)} = 2.94$	$p = 0.093$

^A positively correlated to saltbush density and saltbush and dry saltbush cover.

^B positively correlated to bluebush density and bluebush and dry bluebush cover.

^C positively correlated to other shrub and dry other shrub cover.

^D positively correlated to crust cover and the density of other shrubs.

^E positively correlated to copperburr cover.

^F positively correlated to afternoon temperatures.

^G positively correlated to dung cover.

^H positively correlated to silverfish, termite, ant and spider abundance.

^I positively correlated to bug and bee abundance and negatively to beetle abundance.

^J positively correlated to cockroach and isopod abundance.

^K positively correlated to cricket abundance.

^L positively correlated to stick insect abundance and invertebrate richness.

^M positively correlated to moth abundance and negatively to centipede abundance.

Table A6.9: Non-significant results from GLM examining effects of factors and variables on *Leggadina forresti* abundance. Only landscape type*position interactions are shown. Values for *Leggadina forresti* abundance were square-root transformed.

Model Terms	F values	P values
Position	$F_{(2,45)} = 1.07$	$p = 0.350$
Landscape type*position	$F_{(4,43)} = 1.41$	$p = 0.246$
Component 2 microhabitat ^A	$F_{(1,46)} = 0.91$	$p = 0.345$
Component 3 microhabitat ^B	$F_{(1,46)} = 0.74$	$p = 0.395$
Component 4 microhabitat ^C	$F_{(1,46)} = 0.05$	$p = 0.817$
Component 6 microhabitat ^D	$F_{(1,46)} = 0.03$	$p = 0.870$
Component 7 microhabitat ^E	$F_{(1,46)} = 0.03$	$p = 0.874$
Component 8 microhabitat ^F	$F_{(1,46)} = 1.05$	$p = 0.310$
Component 1 invertebrates ^G	$F_{(1,46)} = 0.03$	$p = 0.864$
Component 2 invertebrates ^H	$F_{(1,46)} = 1.49$	$p = 0.228$
Component 3 invertebrates ^I	$F_{(1,46)} = 0.45$	$p = 0.507$
Component 4 invertebrates ^J	$F_{(1,46)} = 0.005$	$p = 0.943$
Component 5 invertebrates ^K	$F_{(1,46)} = 1.29$	$p = 0.261$
Component 6 invertebrates ^L	$F_{(1,46)} = 0.08$	$p = 0.774$
Component 7 invertebrates ^M	$F_{(1,46)} = 2.07$	$p = 0.157$

^A positively correlated to saltbush density and saltbush and dry saltbush cover.

^B positively correlated to bluebush density and bluebush and dry bluebush cover.

^C positively correlated to other shrub and dry other shrub cover.

^D positively correlated to copperburr cover.

^E positively correlated to afternoon temperatures.

^F positively correlated to dung cover.

^G positively correlated to silverfish, termite, ant and spider abundance.

^H positively correlated to bug and bee abundance and negatively to beetle abundance.

^I positively correlated to insect larva and scorpion abundance.

^J positively correlated to cockroach and isopod abundance.

^K positively correlated to cricket abundance.

^L positively correlated to stick insect abundance and invertebrate richness.

^M positively correlated to moth abundance and negatively to centipede abundance.

Table A6.10: Results from 3-factor Anova for abundance of *Sminthopsis macroura*. * indicates significant differences.

Model Terms	F values	P values
Landscape type	$F_{(1,88)} = 0.56$	$p = 0.457$
Position	$F_{(2,88)} = 5.75$	$p = 0.004$ *
Sex	$F_{(1,88)} = 4.31$	$p = 0.041$ *
Landscape type*Position	$F_{(2,88)} = 1.34$	$p = 0.266$
Landscape type*Sex	$F_{(1,88)} = 1.99$	$p = 0.161$
Position*Sex	$F_{(2,88)} = 0.79$	$p = 0.456$
Landscape type*Position*Sex	$F_{(2,88)} = 0.10$	$p = 0.908$

Table A6.11: Results from 3-factor Anova for abundance of *Sminthopsis crassicaudata*

Model Terms	F values	P values
Landscape type	$F_{(1,88)} = 2.86$	$p = 0.095$
Position	$F_{(2,88)} = 0.71$	$p = 0.495$
Sex	$F_{(1,88)} = 2.36$	$p = 0.128$
Landscape type*Position	$F_{(2,88)} = 0.82$	$p = 0.443$
Landscape type*Sex	$F_{(1,88)} = 3.40$	$p = 0.069$
Position*Sex	$F_{(2,88)} = 0.47$	$p = 0.625$
Landscape type*Position*Sex	$F_{(2,88)} = 0$	$p = 1.000$

Table A6.12: Results from 3-factor Anova for abundance of *Mus domesticus*. * indicates significant differences.

Model Terms	F values	P values
Landscape type	$F_{(1,88)} = 12.93$	$p = 0.001$ *
Position	$F_{(2,88)} = 1.64$	$p = 0.199$
Sex	$F_{(1,88)} = 32.42$	$p < 0.001$ *
Landscape type*Position	$F_{(2,88)} = 2.08$	$p = 0.131$
Landscape type*Sex	$F_{(1,88)} = 14.03$	$p < 0.001$ *
Position*Sex	$F_{(2,88)} = 1.89$	$p = 0.158$
Landscape type*Position*Sex	$F_{(2,88)} = 2.36$	$p = 0.100$

Table A6.13: Results from 3-factor Anova for abundance of *Leggadina forresti*. Values for *Leggadina forresti* were square-root transformed. * indicates significant differences.

Model Terms	F values	P values
Landscape type	$F_{(1,88)} = 26.08$	$p < 0.001$ *
Position	$F_{(2,88)} = 1.42$	$p = 0.247$
Sex	$F_{(1,88)} = 16.09$	$p < 0.001$ *
Landscape type*Position	$F_{(2,88)} = 1.85$	$p = 0.163$
Landscape type*Sex	$F_{(1,88)} = 12.22$	$p = 0.001$ *
Position*Sex	$F_{(2,88)} = 0.20$	$p = 0.819$
Landscape type*Position*Sex	$F_{(2,88)} = 0.05$	$p = 0.949$

Table A6.14: Non-significant results from GLM examining effects of factors and variables on small mammal richness. Only landscape type*position interactions are shown.

Model Terms	F values	P values
Position	$F_{(2,46)} = 0.23$	$p = 0.792$
Landscape type*position	$F_{(4,44)} = 0.35$	$p = 0.844$
Component 2 microhabitat ^A	$F_{(1,47)} = 0.004$	$p = 0.947$
Component 3 microhabitat ^B	$F_{(1,47)} = 0.44$	$p = 0.513$
Component 4 microhabitat ^C	$F_{(1,47)} = 0.58$	$p = 0.449$
Component 5 microhabitat ^D	$F_{(1,47)} = 0.20$	$p = 0.655$
Component 6 microhabitat ^E	$F_{(1,47)} < 0.001$	$p = 0.992$
Component 7 microhabitat ^F	$F_{(1,47)} = 0.37$	$p = 0.544$
Component 8 microhabitat ^G	$F_{(1,47)} = 1.64$	$p = 0.206$
Component 1 invertebrates ^H	$F_{(1,47)} = 0.01$	$p = 0.923$
Component 2 invertebrates ^I	$F_{(1,47)} = 0.05$	$p = 0.833$
Component 3 invertebrates ^J	$F_{(1,47)} = 0.15$	$p = 0.697$
Component 4 invertebrates ^K	$F_{(1,47)} = 1.48$	$p = 0.230$
Component 5 invertebrates ^L	$F_{(1,47)} = 0.42$	$p = 0.523$
Component 6 invertebrates ^M	$F_{(1,47)} = 0.53$	$p = 0.472$
Component 7 invertebrates ^N	$F_{(1,47)} = 2.15$	$p = 0.149$

^A positively correlated to saltbush density and saltbush and dry saltbush cover.

^B positively correlated to bluebush density and bluebush and dry bluebush cover.

^C positively correlated to other shrub and dry other shrub cover.

^D positively correlated to crust cover and the density of other shrubs.

^E positively correlated to copperburr cover.

^F positively correlated to afternoon temperatures.

^G positively correlated to dung cover.

^H positively correlated to silverfish, termite, ant and spider abundance.

^I positively correlated to bug and bee abundance and negatively to beetle abundance.

^J positively correlated to insect larva and scorpion abundance.

^K positively correlated to cockroach and isopod abundance.

^L positively correlated to cricket abundance.

^M positively correlated to stick insect abundance and invertebrate richness.

^N positively correlated to moth abundance and negatively to centipede abundance.

Table A6.15: Non-significant results from GLM examining effects of factors and variables on small mammal biomass. Only landscape type*position interactions are shown.

Model Terms	F values	P values
Landscape type	$F_{(1,46)} = 0.14$	$p = 0.709$
Position	$F_{(2,45)} = 0.67$	$p = 0.517$
Landscape type*position	$F_{(5,42)} = 0.71$	$p = 0.622$
Component 2 microhabitat ^A	$F_{(1,46)} = 0.03$	$p = 0.865$
Component 3 microhabitat ^B	$F_{(1,46)} = 0.11$	$p = 0.747$
Component 4 microhabitat ^C	$F_{(1,46)} = 0.58$	$p = 0.450$
Component 5 microhabitat ^D	$F_{(1,46)} = 1.22$	$p = 0.275$
Component 6 microhabitat ^E	$F_{(1,46)} = 0.01$	$p = 0.905$
Component 7 microhabitat ^F	$F_{(1,46)} = 0.46$	$p = 0.501$
Component 8 microhabitat ^G	$F_{(1,46)} = 2.60$	$p = 0.114$
Component 3 invertebrates ^H	$F_{(1,46)} = 0.01$	$p = 0.921$
Component 4 invertebrates ^I	$F_{(1,46)} = 0.20$	$p = 0.657$
Component 5 invertebrates ^J	$F_{(1,46)} = 0.34$	$p = 0.565$
Component 6 invertebrates ^K	$F_{(1,46)} = 1.64$	$p = 0.207$
Component 7 invertebrates ^L	$F_{(1,46)} = 0.24$	$p = 0.623$

^A positively correlated to saltbush density and saltbush and dry saltbush cover.

^B positively correlated to bluebush density and bluebush and dry bluebush cover.

^C positively correlated to other shrub and dry other shrub cover.

^D positively correlated to crust cover and the density of other shrubs.

^E positively correlated to copperburr cover.

^F positively correlated to afternoon temperatures.

^G positively correlated to dung cover.

^H positively correlated to insect larva and scorpion abundance.

^I positively correlated to cockroach and isopod abundance.

^J positively correlated to cricket abundance.

^K positively correlated to stick insect abundance and invertebrate richness.

^L positively correlated to moth abundance and negatively to centipede abundance.

