# The suitability of habitat for greater bilby (*Macrotis lagotis*) in the Tanami Desert and the relationship with fire

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# Contents

# Abstract

The bilby *Macrotis lagotis* is a threatened species of bandicoot and wild populations are now restricted largely to spinifex grasslands in arid Australia. The species is one of the few medium-sized native mammals (35-5500 g) remaining in the arid zone. Most other species in this size range have become extinct or are now restricted to the more temperate parts of their former range.

In this thesis, I examined the distribution and abundance of the bilby in the Tanami Desert in an area covering 230,000 km$^2$. This desert is similar to other parts of the arid zone dominated by spinifex grasses. The landscape is mostly flat, soils are generally poor and annual rainfall is exceedingly variable. It is sparsely settled by humans and supports little pastoral production and no agriculture. The challenge to manage these areas for conservation is immense because of the difficulties in controlling populations of introduced predators and herbivores and wildfire.

The bilby can be easily bred in captivity and populations have now been established in several predator-proof exclosures on the Australian mainland. This high-intensity form of custodial management has taken much of the attention away for the wild bilby populations. My work aimed to partially redress this situation. I investigated the potential of fire as a form of low-intensity manipulative management to improve the status of wild bilby populations. The use of fire as a management tool was examined because previous research indicated that fire-promoted foods sometimes formed a large component of the bilby diet.

The scarcity of bilbies in the study area posed a number of methodological problems and a number of techniques to collect information on bilby occurrence were trialed. The use of tracking as the principal means to record bilby occurrence provided the opportunity to collect data on a range of other species that occupied habitat concurrently, including feral cats, foxes, dingoes, rabbits and camels. A combination of an aerial survey using a helicopter and a ground-truth plot technique proved to be the most rapid and cost effective means to produce repeatable data on bilby occurrence.

A statistical modelling approach was used to make inferences about the processes that shape distribution and the environmental conditions that provide refugia for the species examined. I used this approach to examine a number of ecological models. Three related to the ecological framework for arid Australia proposed by Stafford Smith and Morton (1990) and the remainder related to the hypothesised causes of medium-sized mammal decline. The proposition that introduced herbivores would be more prevalent on fluvial substrates was supported but there was little support for the proposition that introduced predator species would follow a similar pattern. Foxes and feral cats used a wide variety of habitats and were common on the poorer, sandy substrates. The dingo was the only predator species that showed a strong association with drainage lines.

At a landscape scale, a number of variables were found to associate significantly with bilby prevalence. Proximity to recent fire was a significant variable but only in the central part of Tanami Desert. There was a positive association with lateritic and rock feature substrate, the rainfall gradient and dingo prevalence. None of the hypotheses proposed to explain medium-sized mammal decline was overwhelmingly supported. The positive association between bilby and dingo prevalence indicated that the two species favoured similar habitat and that the dingoes may be providing a rescue effect for bilbies. A substantial part of the dingo diet in the study area was feral cat and foxes were absent in the northern quarter of the study area and on drainage substrates when dingoes were prevalent.

Through dietary analysis I was able to link fire pattern and bilby prevalence. Plant material was the predominant component of the diet in the central part of the study area where bilby prevalence was greatest. Seed from a fire-promoted plant *Yakirra australiense* formed most of the plant material consumed particularly, in close proximity to recently burnt habitat. This provided a strong indication that habitat suitability for the bilby could be improved with fire management.

The factors affecting the production of *Yakirra* and fire recurrence were investigated and a simple decision model was developed to assist managers decide where and when to burn, and amount of *Yakirra* to expect. The information required to run the decision model could be derived from current remotely sensed spatial databases that document monthly rainfall and fire history. *Yakirra* abundance was associated positively with summer rainfall and diminished with time since fire. Fire recurrence was associated with vegetation cover that could be best estimated using the variables of antecedent rainfall since fire and rainfall within a three month period. Fire management to enhance habitat suitability for the bilby would be of most benefit in the northern part of the Tanami Desert where growth rate of vegetation is high and there is little existing fire age heterogeneity.

Based on the extent of occurrence, the distribution of the bilby has changed little in the last 20 years. However, much of the area defined by occurrence is evidently acting as a dispersal sink with widely dispersed, extremely low-density bilby sign and no indication of juvenile production. It is suggested that the bilby status is less secure than previously thought and future assessment should be based on the area of occupancy and not extent of occurrence.

# Declaration

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

A declaration of the contribution made by the co-authors identified on the manuscripts that have been submitted for publication, are in press or published is contained at the end of the thesis

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

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**Date** 13 Oct 2006

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‘Ahrete, ahrete …’ were the last words uttered by T.G.H. Strehlow, the renown linguist before he died in 1978. Ahrete is a name for the greater bilby in Arrernte, one of the main Aboriginal languages in central Australian and the language in which T.G.H. Strehlow amassed a huge quantity of artifacts, myths, songs, photographs, films and sound recordings that are currently stored at the Strehlow Research Centre in Alice Springs. So why should this man’s last words refer to bilbies? According to Justice Michael Kirby, who was with the dying Strehlow, the words were symbolic and indicative of the loss of ceremonies, culture and secrets of traditional Aboriginal people. They, just like the bilby, are now threatened in the Australian landscape.

Bilby tracks on a Tanami Desert sand dune.

A bilby moving quickly towards a burrow.

# Chapter 1

# General Introduction

Questions about the distribution and abundance of species are central to many ecological studies (Begon *et al.* 1996; Krebs 1989). Understanding the relationship between a species and its environment allows us to better predict the species' occurrence and embark upon programs to manage its abundance and distribution (Wiens 2002), either positively or negatively.

The general aim of this study was to examine factors affecting the distribution of the bilby *Macrotis lagotis*, an Australian bandicoot that is considered vulnerable to extinction. More specifically, I aimed to:

- determine the distribution and occurrence of the bilby in the Tanami Desert, a portion of central Australia that covers approximately 200,000 km$^2$,
- define the main environmental variables associated with habitat suitability for the species,
- develop a model to predict the distribution of the bilby based on spatial data,
- evaluate the relationship between bilby prevalence, diet and fire-promoted foods,
- describe the conditions controlling the production of fire-promoted food plants and fire recurrence, and
- assess whether fire management could be used to improve habitat suitability for the bilby.

There has been intense interest in the conservation and appropriate management of fauna in Australia because the continent has one of the worst records of species loss in the world (Burgman and Lindenmayer 1998). Within the last 200 years, 29 mammal species have become extinct, and 43 mammal and 50 bird species are currently listed as endangered or vulnerable. The loss of species has not occurred evenly across Australia, with the arid and semi-arid zone being most severely affected (Woinarski and Braithwaite 1990; Caughley

1994). Roughly one third of the mammal species that inhabited the region have become extinct (Burbidge and McKenzie 1989; Morton 1990).

**Knowledge of Australian arid-zone fauna**

An understanding of the pre-European faunal composition in most of central Australia is relatively poor and is reliant largely on the reports from a few scientific expeditions (Krefft, 1866; Spencer, 1896; Shortridge, 1909), the work of several naturalists (Jones 1924; Finlayson 1961) and the accounts of Aboriginal people (see Burbidge *et al.* 1988). A number of detailed surveys in recent times (eg. Gibson and Cole 1988; McKenzie and Youngson 1983; McKenzie and Robinson 1987; Reid *et al.* 1993) including a comprehensive survey of the Tanami Desert in the period 1982-85 (Gibson 1986) have revealed how dramatically the fauna composition has changed. Gibson (1986) reported that over 30% of the known mammal species had become extinct or were restricted to populations outside the region and seven of the 12 native mammals in the size range 120 - 5400 g had disappeared.

The more recent surveys have also reported the extent to which introduced and naturalised herbivore and predator species have become widespread, and in some parts, abundant in central Australia. In the Tanami Desert, rabbits *Oryctolagus cuniculus*, camels *Camelus dromadarius* and house mice *Mus domesticus* are the most common and widespread introduced herbivores. Cattle *Bos taurus*, horses *Equs equs*, donkeys *Equs asinus* and water buffalo are rare vagrants and goats *Capra hircus* and pigs *Sus scrofa* have not been recorded (Gibson 1986). Among the introduced and naturalised predator species, feral cats *Felis catus* and the dingo *Canis familiaris* were recorded as more widespread than foxes *Vulpes vulpes* (Gibson 1986).

The bilby is one of the few medium-sized mammals that persists in arid Australia (Burbidge and McKenzie 1989; Woinarski and Braithwaite 1990), but its disappearance from the southern part of the continent indicates it is also sensitive to a range of threatening processes (Southgate 1990a). The study of this species in its natural environment provides a rare opportunity to examine the importance of the processes proposed to explain the high historic extinction rate of mammal species in arid Australia. Austin (2002) has argued that an investigation of this sort initially requires a clear articulation of an 'ecological model'. This should identify the primary processes thought to be influencing the species and the assumptions, propositions or hypotheses to be tested. Neglect in providing this framework is a limiting factor in the successful application of statistical modelling.

## Pattern and process in the arid zone

Environments are heterogeneous in time and space and the pattern of this heterogeneity affects the abundance and distribution of organisms (Wiens 1995; Wiens and Milne 1989). A wide range of factors influences heterogeneity including abiotic processes, biologically mediated processes and processes dominated by biotic interactions (Mackey and Lindenmayer 2001). Knowledge of both composition and structure of an ecosystem and an understanding of functional relationships between species and their environment are required to accurately make predictions about the effect of management and natural perturbations (Austin 2002; Holling 1978; Noss 1990).

Stafford Smith and Morton (1990) put forward a set of propositions regarding the main physical patterns and driving forces affecting the distribution of biota in arid Australia and an explanation of why Australian deserts are different from those elsewhere in the world. While low soil fertility and unpredictable climates occur in other desert landscapes throughout the world, they argued that the geographic extent over which these factors co-occur and the fact that the climate is only moderately arid is what makes Australia special (Stafford Smith 1995). The landscape of arid and semi-arid Australia is predominantly flat and dominated by sand desert (dune fields and sand plains) followed by shield desert, upland and piedmont desert, stony desert, and riverine desert and clay plains (Mabbut 1984). These patterns have resulted from the erosion and redistribution of geological features over millions of years. Soils are generally deeply weathered and infertile. Almost all the soils show extreme poverty of phosphorous and nitrogen compared to areas of comparable aridity on other continents. Local soil differentiation and heterogeneity is present within broad landscape types and has resulted from subtle topographic variation and fine-scale redistribution of nutrients. Run-on areas accumulate water and nutrients permitting higher biomass and more frequent growth than would be possible on a totally flat landscape (Ludwig *et al.* 1997).

James *et al.* (1995) ranked the productivity of substrate types in arid Australia. Those of least productivity were associated with sand plains or dune fields because of low fertility and poor water holding ability of sediments, although the swales of dune fields show increased productivity because of the localised redistribution of water and nutrients. The deep red earths, red sandy loams with lateritic content and the skeletal soils associated with outcrops are slightly more productive than sandy substrates. Both the lateritic and skeletal soils mostly occur in slightly elevated situations and consequently inundation is infrequent. However, the small-scale redistribution of water can support more nutritious grasses as well as large woody perennials including mulga *Acacia aneura*. Calcareous earths and cracking clays are more fertile again and support chenopod shrublands and tussock grasslands. The areas regarded as the most productive run-on and deposition zones are represented by riparian woodlands and floodplains and paleodrainage lines. Extensive parts of these areas can be subject to inundation following periods of exceptional rainfall.

Stafford Smith and Morton (1990) described the key driving forces on the biota in central Australia as climate, grazing and fire. Compared to other desert regions of the world, the rainfall in Australian deserts is highly unpredictable in time and spatially variable (Stafford Smith and Morton 1990; Williams and Calaby 1985). The El Nino – Southern Oscillation (ENSO) phenomenon has a marked effect on the rainfall in Australia. The tendency for major droughts in eastern and northern Australia to coincide with ENSO events and extensive wet periods to accompany 'anti-ENSO' events is well documented (Nicholls 1991; Nicholls and Wong 1990). Stafford Smith and Morton (1990) argued that most rainfalls are too small and isolated in time to have a stimulatory effect on plant growth and germination and proposed that big rains structure the environment. Massive incursions of cyclonic and monsoonal depressions occur infrequently but their impact is widespread because the landscape is flat. Periods of exceptional rainfall, when 3-4 times the annual rainfall occur, trigger major biotic changes and a surfeit of surface water in low-lying areas.

The vegetation communities of the fertile and infertile soils of arid Australia are distinctive (Stafford Smith 1995). The more fertile cracking clay soils are dominated by open grasslands such as mitchell grasses *Astrebla* spp. and the calcareous clays are dominated by low chenopod shrubs such as salt bush *Atriplex* spp. and blue bush *Maireana* spp. The infertile soils are dominated by *Acacia* shrubs and spinifex grasses in the genus *Triodia*. Plant production with higher digestibility is restricted largely to the more fertile substrates and medium and large-sized mammals are limited to these areas because of their body plan and physiological constraints (Morton 1990). Hence, grazing pressure can become concentrated on very small areas within the landscape.

Fire is a ubiquitous component in the arid zone of Australia, particularly in the spinifex grasslands because of the high accumulation of biomass in this form of perennial vegetation and slow rates of decomposition on the infertile substrates (Stafford Smith and Morton 1990). Where land is too poor for grazing, fuel build up can result in the occurrence of vast wildfires sometimes exceeding 30,000 km$^2$ in area. In the more productive grazing areas, fires are generally suppressed because of the removal of vegetation by stock and active management of pastoralists. However, even in these areas, fires may occur following a period of exceptional rainfall (Allan and Southgate 2002; Griffin *et al.* 1983).

My work in Tanami Desert (**Fig. 1.1**) recorded a range of landscape features quantitatively and provided an opportunity to evaluate a number of the propositions relating to the ecology of arid Australia put forward by Stafford Smith and Morton (1990). They made the prediction that localised patches of higher productivity would support persistent consumers such as medium and large herbivores. Therefore, it would be expected that greatest prevalence of camel and rabbit activity would occur on the most continuously productive substrate types and least prevalence on the poorest substrates. The model can be abbreviated as:

*drainage+calcareous>laterite+rock features>sand plain+sand dune*

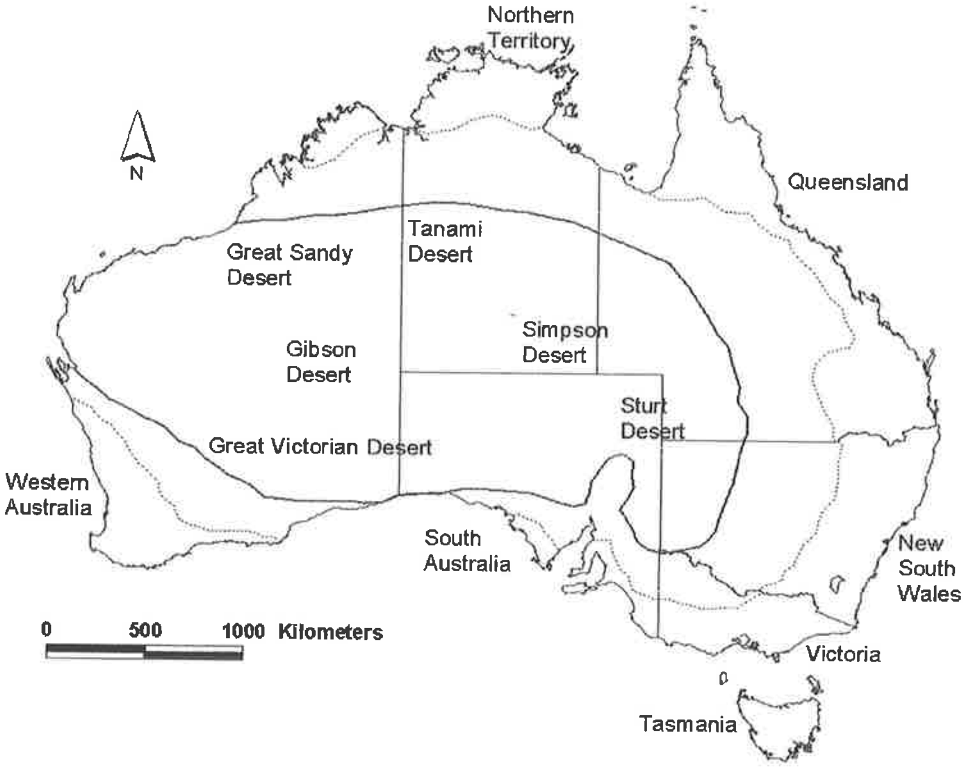


**Fig. 1.1** Map of Australia showing the arid zone (dark stippled line) and semi-arid zone (light dashed line) and the main desert areas, redrawn and slightly modified from Williams and Callaby (1985).

Stafford Smith and Morton (1990) also suggested there would be a trophic cascading effect and that predator richness and abundance would be greater in more productive parts of the arid landscape. Therefore, the greatest prevalence of cat, fox and dingo activity would be expected to occur in the most productive habitats and least in the poorest habitats. The model can be abbreviated as:

*drainage+calcareous>laterite+rock features >sand plain+sand dune*

My work in the Tanami Desert also provided an opportunity to examine a number of hypotheses proposed to explain the decline of native mammal species in the arid zone. Much attention has been directed toward identifying what has decimated populations of medium-sized mammals in Australia (Burbidge and McKenzie 1989; Finlayson 1961; Morton 1990; Newsome 1971; Reid and Fleming 1992; Short and Smith 1994; Smith and Quin 1996) but it is recognised that there is a general lack of empirical data to test hypotheses regarding the decline of Australian arid-zone species (James *et al.* 1995). Three main hypotheses have emerged to explain the decline of these species (Kennedy 1992):

a) Introduced herbivores and refugia

Morton (1990) argued that native mammal herbivores and omnivores would favour the more continuously productive parts of the arid landscape such as riverine channels, paleodrainage lines and runon areas for the same reasons as introduced herbivores like rabbits, camels and stock. He concluded that the degradation of these productive areas by waves of introduced herbivores has been the primary cause of native medium-size mammal decline in arid Australia. The hypothesis is plausible because intensive grazing pressure by stock has compacted soil, changed the soil surface layer, and altered plant species composition and structure (Hobbs and Hopkins 1990). Grazing has been presumed to be partly responsible for the extinction of 34 plant species in Australia and continues to threaten a further 55 (Leigh 1992 in James *et al.* 1995). The effects of introduced herbivores on the native vegetation have been significant and affected both the food availability and the structural form of habitat required by native mammal species for shelter. Moreover, the wide distribution of watering points and the mobility of stock has meant that only a small percentage of the pastoral estate has remained unaffected by grazing (James *et al.* 1999). Conservation areas and sparsely populated Aboriginal lands have not escaped the effect of introduced herbivores because species like rabbits, camels, goats, donkeys and horses have extended beyond the leased pastoral areas (Edwards *et al.* 2004). Overall, the current distribution of the bilby associates well with absence or low density stock and introduced herbivores (Southgate 1990a).

Therefore, it would be expected that bilby prevalence would be greater where introduced herbivore species were least prevalent and a substrate:herbivore interaction would be evident because the bilby would also favour the more productive substrates, abbreviated as:

*low stock-camels-rabbits>low stock+camels-rabbits>stock+camels+rabbits*

I considered rabbits more destructive than camels because rabbits use some important foods of the bilby (Southgate 1990b) and tend to inflate introduced predator abundance (Newsome 1990).

b) Introduced predators and refugia

It has been suggested that added predation pressure from introduced predator species, particularly the feral cat *Felis catus* and the red fox *Vulpes vulpes*, has been the greatest cause of medium size mammal species loss in recent times (Burbidge and McKenzie 1989; Dickman 1996; Johnson *et al.* 1989; Short and Smith 1994). The feral cat now occurs throughout the continent and was reported in central Australia from the late 1800s onwards (Abbott 2002). The fox became established widely by the 1930s and is now distributed in most of Australia except the northern wet tropics. The inclusion of the dingo *Canis domesticus* to the suite of predators would further increase aggregate predation pressure and the three predator species co-occur in a large proportion of central Australia including parts of the Tanami Desert. The dingo is thought to have been introduced only 3000-4000 years ago by Asian travellers and is considered a naturalised species (Corbett 1995).

There is good evidence of the role of foxes and cats in the extinction of remnant and reintroduced native mammal populations on the mainland (Kinnear *et al.* 1988) and islands (Abbott and Burbidge 1995; Burbidge *et al.* 1997) but the role they individually played in the original decline of medium-sized mammals remains unclear (Abbott 2002; May and Norton 1996). All three predator species are known to prey on the bilby (Southgate 1994) but the impact of foxes on medium-sized arid zone mammals, including the bilby, has been reported to be particularly severe (Finlayson 1961; Jones 1924; May and Norton 1996). Bilby populations have co-occurred with cats for over 100 years and dingoes for thousands of years but they disappeared following the arrival of foxes in a region (Abbott 2001; Southgate 1990a). Furthermore, the medium-sized mammal assemblage in the northern tropics has remained reasonably intact in the absence of foxes but with feral cats and dingoes present (Woinarski and Braithwaite 1990).

The overall predation potential is broadened when a number of predator species operate in concert (Begon and Mortimer 1986) especially if the predator species are all generalists, and therefore can prey-switch, and if each has a slightly different hunting technique and habitat preference (Pech *et al.* 1995). Under these circumstances, the possibility of some habitat types acting as refugia becomes diminished and all age classes of a prey species like the bilby become vulnerable to predation. Therefore, it would be expected that greatest prevalence of the bilby would occur in parts of the study area where there was low prevalence of predators, particularly the feral cat and fox. The model can be abbreviated as:

*dingo-cat-fox>dingo+cat-fox>dingo+cat+fox*

Foxes were considered more destructive to bilby populations than feral cats and dingoes.

c) Fire pattern and refugia

It has been suggested that a fine-grain mosaic of fire ages associated with traditional Aboriginal burning was necessary for the production of food and protection of shelter for medium-sized arid zone mammals (Bolton and Latz 1978; Burbidge *et al.* 1988; Johnson *et al.* 1989). Increasingly, Aboriginal people settled in towns and communities from the 1930s onwards and ceased their burning practices. As a result, the fine-grained mosaic of different age burns maintained by Aboriginal burning disappeared and this was replaced by less frequent, larger fires and inevitably, greater homogeneity of the vegetation age structure (Allan and Southgate 2002; Bowman 1998; Burrows and Christensen 1990; Griffin and Friedel 1985).

The hypothesis that an increase in fire size and the loss of a fine-grain diversity of fire ages has resulted in a decline in medium-sized mammals is plausible because fire is known to impact upon a range of arid zone animal species (Friend 1993; Masters 1993; Masters 1996; Woinarski and Recher 1997) and dramatically alter vegetation structure and composition (Griffin 1990). It is likely that the bilby population would be affected by fire because a number of the plant foods used by the bilby are fire-promoted (Southgate 1990b) but unlikely that fire would affect the availability of shelter because of its ability to burrow, unlike many other former co-habitant species of medium-sized mammal. Hence, it would be expected that greater bilby prevalence would occur in closer proximity to recently burn habitat and possibly in parts of the landscape where the variety of age structure in the vegetation was greater because of higher fire age heterogeneity, and abbreviated as:

*recently burnt habitat>long-unburnt habitat*
*high fire age heterogeneity>low fire age heterogeneity*

Other hypotheses put forward to explain why species have declined or disappeared from parts of Australia including disease, overkill by hunting and loss of habitat through clearance of vegetation for agriculture can be dismissed in the arid zone (Kennedy 1992). This is especially the case in the Tanami Desert where pastoralism is largely absent and the human population is sparsely distributed.

**Habitat suitability modelling**

The use of models to examine species-environment relationships is becoming an increasingly important tool in conservation planning and wildlife management (Austin 2002; Guisan and Zimmerman 2000; Manel *et al.* 2001; Pearce and Ferrier 2000; Rushton *et al.* 2004). In the majority of cases, the purpose of the modelling is in to predict species distribution, although the functional relationship between species and the environment may also be examined (MacNally 2000; Vaughan and Ormerod 2003). Empirical models provide a way to derive a construct of the system and examine features affecting distribution at geographic scales that cannot be examined by experimentation (Elith *et al.* 2002; Mackey and Lindenmayer 2001; MacNally 2000; Manel *et al.* 1999).

A common criticism of species-environment models is that most are based on correlations and it is not possible to determine causation (Heglund 2002). This can have serious ramifications if the outcomes of modelling are not evaluated adequately before they are used to devise or implement management. These problems may be overcome by evaluating the predictive performance of the models using independent data (Fielding and Bell 1997; Pearce and Ferrier 2000). The validity of causal mechanisms identified through modelling can be pursued by experimentally examining components of the system, by theoretical analysis, by repeating the study at a different location or through adaptive management (Austin 2002).

In this thesis, I use multilevel regression analysis to examine hypotheses about the key environmental variables affecting a species' distribution and abundance and to develop predictive distribution models.

### Conservation status and management

The assessment of species status and the provision of management are closely linked in the field of conservation biology because the resources available for the management of a species are determined largely by its assigned status. The categories of conservation status set by the IUCN, Federal and State conservation authorities are supported by decision rules that relate generally to extent of occurrence, area of occupancy, abundance, and population history (Burgman and Lindenmayer 1998). Efforts to assess the status of the bilby in the past have depended primarily on opportunistic reports, general fauna surveys and museum records to define the extent of occurrence (Southgate 1990a; Watts 1969). Techniques to assess bilby population abundance are problematic and have not proved satisfactory (Lavery and Kirkpatrick 1997). In the thesis, I focused on collecting data that would provide a better understanding of the extent of occurrence and area of occupancy.

It is widely acknowledged that the problems facing most threatened species can seldom be rectified until the threatening processes or the factors driving the decline have been removed (Caughley and Gunn 1996). Caughley and Sinclair (1994) indicated that wildlife management can be either *manipulative* or *custodial*. Manipulative management does something to a population such as providing food, altering habitat or predator density whereas custodial management is preventative or protective and is aimed at minimising external influences on a population. I argue that it is useful to identify two additional features of management: *high-intensity* and *low-intensity* (**Table 10.1**). With high-intensity management, I mean daily or on-call maintenance of a managed resource and with low-intensity, I mean to the application of management on an annual or less frequent basis. The four categories can be used to define a range of options available for the management of a species and define a series of goals for the overall conservation program.

High-intensity manipulative management may be required to minimise the probability of an endangered target species from becoming extinct. However, it must be realised that high-intensity management is risky and problematic. Firstly, the probability of sustaining the high-intensity of management in the long-term is low because of the vagaries of politics, economics and social attitude. Zoos, fenced wildlife refuges and botanic gardens are examples of high-intensity management programs and most are concentrated in developed countries (Burgman and Lindenmayer 1998). History has shown that these institutions close and conservation programs halt in periods of severe economic and social turmoil (Noss and Murphy 1995). Secondly, a crucial goal in conservation is to ensure a species retains its potential for evolutionary change (Burgman and Lindenmayer 1998; Possingham *et al.* 1993). However, the evolutionary fitness of a species becomes increasingly subjugated with prolonged dependency on intensive management. For example, a species protected from exposure to predators may in the long term lose its ability to respond to threats of predation (McLean *et al.* 1995).

**Table 10.1** Examples of high- and low-intensity forms of manipulative and custodial wildlife management

| | High-intensity management | Low-intensity management |
|---|---|---|
| Manipulative | Predator baiting control | Fire management |
| Custodial | Predator-proof wildlife refuges | Legislative refugia protection |

Conservation problems are best solved by the implementation of low-intensity custodial management of natural resources. Low-intensity manipulative management provides the next best option. There needs to be an explicit goal in conservation programs to move from high-intensity to low-intensity forms of management.

In terms of bilby conservation, a low-intensity custodial program has been developed with the introduction of a bilby population to an island free of dingoes, foxes and feral cats in South Australia. Several high-intensity custodial programs have also been developed on the mainland of Australia where felid and canid predators are excluded with the use of mesh fencing (Pavey 2004). There are few problems with the breeding of bilbies in captivity (Southgate *et al.* 2000) and the bilby populations have grown rapidly when released into predator-free exclosures (Moseby and O'Donnell 2003). To some degree the spectacular success of the high-intensity programs has taken attention away from determining the status of wild populations and exploring the effectiveness of low-intensity custodial or manipulative forms of management.

In this thesis, I aimed redress the issue and determine whether low-intensity custodial and manipulative management could play a role in the conservation of the bilby. For a low-intensity custodial program to be effective, *refugia* must be identified within a species' range. These areas may not represent the most favourable habitats for the species but the habitat least favourable to the agents of decline (Caughley 1994; Mackey *et al.* 2002; Morton *et al.* 1995). They represent areas that could be protected from degrading land use practice through legislation or agreement but without the need for manipulative management. A low-intensity form of manipulative management will be successful if habitat suitability can be improved with broad-scale and infrequent input. I explored the possibility of using fire management to enhance bilby populations because previous studies indicated that some of the key food resources used by the bilby were promoted by fire (Southgate 1990b) and fire was already a conspicuous feature in the Tanami Desert landscape (Allan and Southgate 2002; Griffin 1984). Aboriginal people, who are custodians for the majority of the area, are also comfortable with the use of fire as a management tool (Griffin and Allan 1986). Higher-intensity forms of manupulative management such as the broad-scale predator baiting would be more difficult and costly to implement because of the size, remoteness and relatively inaccessible of the study area.

### The structure of the thesis

The study was conducted in the Tanami Desert (**Fig. 1.1**) where the impacts associated with pastoralism and human settlement are much reduced compared to other parts of Australia. Access to this area was limited by the scarcity of tracks and roads and by restrictions imposed by the Central Land Council. Fieldwork in different parts of the study area was conducted in conjunction with the relevant Aboriginal traditional owners at all times.

The thesis is presented in the chapters following this introduction (**Fig. 1.2**) and the aim has been to prepare and make seven chapters ready for publication. This has resulted in some repetition in the introduction, methods and references among Chapters. The bilbiographic style used in each chapter confoms to the format of the journal to which it has been submitted.

In **Chapter 2**, I provide information on the species' life history and status characteristics relevant to the objectives of the study.

In **Chapter 3**, I compare three monitoring techniques used to collect information on bilby occurrence. Fixed transects, stratified random plots and an aerial survey technique were examined and the presence of tracks or diggings was used on each to determine bilby occurrence. The transects and plots in the study area were also used to collect information on the occurrence of a range of other animal species, collect data on vegetation and to ground-truth remotely-sensed spatial data.

In **Chapter 4**, the adequacy of an ecological model presented by Stafford Smith and Morton (1990) that describes the key elements controlling the biotic structure of the Australian arid zone is considered in relation to the landscape features found within the study area. In doing so, I describe the characteristics of the spatial data that formed the main explanatory variables in the habitat suitability modelling in the following chapters. The accuracy of the remote-sensed data is considered in relation to field-derived data.

**Chapter 5** provides a description of the distribution of introduced herbivores and predators in the Tanami Desert and derives a relationship with spatial landscape data. The proposition made by Stafford Smith and Morton (1990) and Morton (1990) that the prevalence of these species will be greater on more productive substrates is examined. Models predicting the distribution of these species are converted to probability surfaces and the accuracy of each model is evaluated using independently derived data. I later use the probability surface data for each species as explanatory variable in bilby habitat modelling.

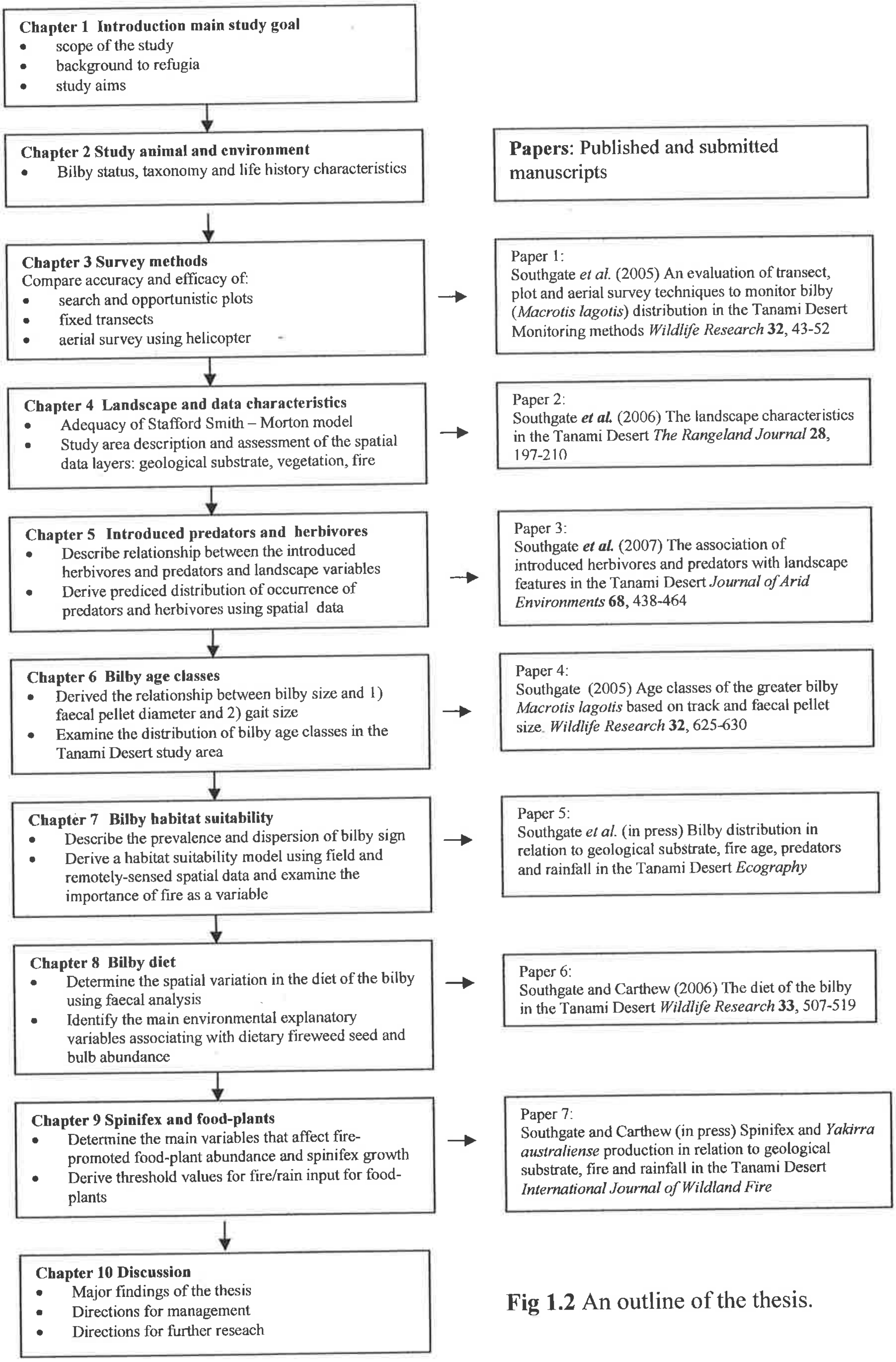
In **Chapter 6**, I derive a relationship between bilby weight and faecal pellet size, and bilby weight and track dimensions using data collected during a previous study. The regression equations are reversed to allow estimation of bilby size based on faecal diameter and track dimensions. The pellet and track measurements that correspond with three age classes of bilby (immature-independent individuals <500g, mature females and small males 500-1200 g, and large males >1700 g) are identified. This allowed me to investigate whether immature individuals and large males were distributed evenly throughout the Tanami Desert based on the measurements of tracks and faecal pellets.

In **Chapter 7**, I investigate the distribution and dispersion of the bilby population and examine the relationship between bilby occurrence and landscape variables. Models of predicted bilby occurrence are derived and evaluated using independent data. The pattern of bilby distribution is examined in relation to the main hypotheses proposed to explain the decline of medium-sized mammals in arid Australia. A key finding was that bilby prevalence associated positively with proximity to recently burnt habitat in the central part of the study area. Substrate, rainfall and dingo distribution were among the other important variables associated with bilby distribution.

In **Chapter 8**, I examine the link between fire, key fire-promoted plants used by the bilby as food and bilby prevalence. Seed from the 'fireweed' *Yakirra australiense* is found to be extremely important in the diet of the bilby. The habitat variables that associate with fire promoted plant foods are derived and compared with the variables associated with bilby habitat occupancy presented in Chapter 7. This approach is used to clarify the effect of fire on altering habitat suitability for the bilby.

In **Chapter 9**, I examine the effect of substrate, fire, competitive vegetation and rainfall on the production of key food plants used by the bilby. The data were derived from repeatedly measured experimental fire plots and from the vegetation transects conducted on random plots and fixed transects. A simple decision tree is developed for managers to determine when to burn habitat and the amount of *Yakirra australiense* to expect in relation to time since fire and rainfall.

In **Chapter 10**, I summarise the key findings and present an outlook for the future and consequences for management.



**Chapter 1 Introduction main study goal**
- scope of the study
- background to refugia
- study aims

**Chapter 2 Study animal and environment**
- Bilby status, taxonomy and life history characteristics

**Papers:** Published and submitted manuscripts

**Chapter 3 Survey methods**
Compare accuracy and efficacy of:
- search and opportunistic plots
- fixed transects
- aerial survey using helicopter

Paper 1:
Southgate *et al.* (2005) An evaluation of transect, plot and aerial survey techniques to monitor bilby (*Macrotis lagotis*) distribution in the Tanami Desert Monitoring methods *Wildlife Research* **32**, 43-52

**Chapter 4 Landscape and data characteristics**
- Adequacy of Stafford Smith – Morton model
- Study area description and assessment of the spatial data layers: geological substrate, vegetation, fire

Paper 2:
Southgate ***et al.*** (2006) The landscape characteristics in the Tanami Desert *The Rangeland Journal* **28**, 197-210

**Chapter 5 Introduced predators and herbivores**
- Describe relationship between the introduced herbivores and predators and landscape variables
- Derive prediced distribution of occurrence of predators and herbivores using spatial data

Paper 3:
Southgate ***et al.*** (2007) The association of introduced herbivores and predators with landscape features in the Tanami Desert *Journal of Arid Environments* **68**, 438-464

**Chapter 6 Bilby age classes**
- Derived the relationship between bilby size and 1) faecal pellet diameter and 2) gait size
- Examine the distribution of bilby age classes in the Tanami Desert study area

Paper 4:
Southgate (2005) Age classes of the greater bilby *Macrotis lagotis* based on track and faecal pellet size. *Wildlife Research* **32**, 625-630

**Chapter 7 Bilby habitat suitability**
- Describe the prevalence and dispersion of bilby sign
- Derive a habitat suitability model using field and remotely-sensed spatial data and examine the importance of fire as a variable

Paper 5:
Southgate *et al.* (in press) Bilby distribution in relation to geological substrate, fire age, predators and rainfall in the Tanami Desert *Ecography*

**Chapter 8 Bilby diet**
- Determine the spatial variation in the diet of the bilby using faecal analysis
- Identify the main environmental explanatory variables associating with dietary fireweed seed and bulb abundance

Paper 6:
Southgate and Carthew (2006) The diet of the bilby in the Tanami Desert *Wildlife Research* **33**, 507-519

**Chapter 9 Spinifex and food-plants**
- Determine the main variables that affect fire-promoted food-plant abundance and spinifex growth
- Derive threshold values for fire/rain input for food-plants

Paper 7:
Southgate and Carthew (in press) Spinifex and *Yakirra australiense* production in relation to geological substrate, fire and rainfall in the Tanami Desert *International Journal of Wildland Fire*

**Chapter 10 Discussion**
- Major findings of the thesis
- Directions for management
- Directions for further reseach

**Fig 1.2** An outline of the thesis.

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# Chapter 2

# The study species

## Taxonomy, distribution and status

Setting priorities for the protection of natural areas and the conservation of taxa not only requires an understanding of the distribution and abundance of individuals and populations making up that taxa but an understanding of the genetic variation within and among these entities and the relationship with other taxa (Burgman and Lindenmayer 1998).

### *Taxonomy*

The greater bilby *Macrotis lagotis* is one of 23 species of bilby and bandicoot currently described. Five genera are represented in Australia and five in New Guinea. Bandicoots fall within the Order Peramelamorphia (Archer 1999) and all have similar life history characteristics (Cockburn 1990; Lee and Cockburn 1985; McCracken 1990). The relationship of bandicoots to other marsupials is interesting because some physiological features such as the presence of alliantic placenta make them *the most eutherian of marsupials* (Gemmell, unpublished data) and their short gestation and pouch life and rapid growth make them *the most marsupial of marsupials* (Cockburn 1990).

The relationship of bilbies to other bandicoots has been controversial. Bilbies were initially treated as highly specialised peramelids, but Bensley (1903) recognised their distinctiveness and placed bilbies in the subfamily Thylacomyinae particularly on the basis of molar morphology. Tate (1948) grouped bilbies with the peramelids but Archer and Kirsch (1977), on the basis of dental structure, basiocranial differences and serological evidence, elevated the taxon to familial status of Thylacomyidae from the Peramelidae. On the basis of skull morphology, Groves and Flannery (1990) considered the New Guinea bandicoots should be given familial status (Peroryctidae) and be separated from the Australian bandicoots (Perameidae) which was considered to also include bilbies. Recent molecular analysis has suggested that bilbies should be given separate familial status and that Thylacomyidae be reinstated (Kirsch *et al.* 1997; Westerman and Krajewski 2000).

At one time there were seven species of bilby recognised (Troughton 1932) but there are now two: *M. lagotis* (Reid, 1836) and *M. leucura* (Finlayson, 1931) (Ride 1970). Electrophoretic and molecular analysis of samples for extant populations of *M. lagotis* suggest there is one broadly distributed species (Moritz *et al.* 1999; Southgate and Adams 1993). The lesser bilby *M. leucura* is now considered extinct (Maxwell *et al.* 1996).

*Distribution and status*

The historic range of the greater bilby covered about 70% of the Australian mainland (**Fig. 2.1**) (Southgate 1990a). Most of the distribution fell within the arid and semiarid (Eyrean) regions of Australia but part extended into the Bassian/Eyrean Interzone bioclimatic area in southern Australia and into the Torresian/ Eyrean Interzone in northern Australia (Nix 1982). The current distribution of the bilby is approximately 20% of the former range or 11% of the Australian mainland. Its distribution in Western Australia is now limited to the Great Sandy and Gibson Deserts (Friend 1990, Abbott 2001). In the Northern Territory, it is now restricted predominantly to the Tanami Desert (Johnson and Southgate 1990) and the Queensland population is limited to brown clay plains between Boulia and Birdsville (Gordon *et al.* 1990).

The decline of the bilby has occurred mostly in the mesotherm and mesotherm-megatherm interzone part of Australia. In general terms this is where the mean air temperatures are less than 24° C but more than 14° C (Nix 1982). The current distribution is most prevalent in parts of Australia that are megatherm dominant or where mean air temperature exceeds 24° C.

The greater bilby is listed nationally as vulnerable to extinction under Schedule 1 of the *Environment Protection and Biodiversity Conservation Act 1999* based primarily on the contraction in range and general scarcity. The species is considered endangered in Queensland, threatened in the Northern Territory and rare or likely to become extinct in Western Australia. Natural wild populations are regarded as extinct in New South Wales and South Australia. It is considered vulnerable by the IUCN/SSC Australasian Marsupial and Monotreme Specialist Group (Maxwell *et al.* 1996).

### Life history characteristics

The selection or development of a method that is suitable to monitor the distribution and abundance of a species requires an understanding of its life history characteristics such as size, the capacity to move or disperse, habitat specificity and fidelity and the potential for population growth. Sampling at an unsuitable spatial and temporal grain may compromise the independence of data and result in problems with pseudoreplication (Hurlbert 1984) and autocorrelation (Legendre *et al.* 2002).

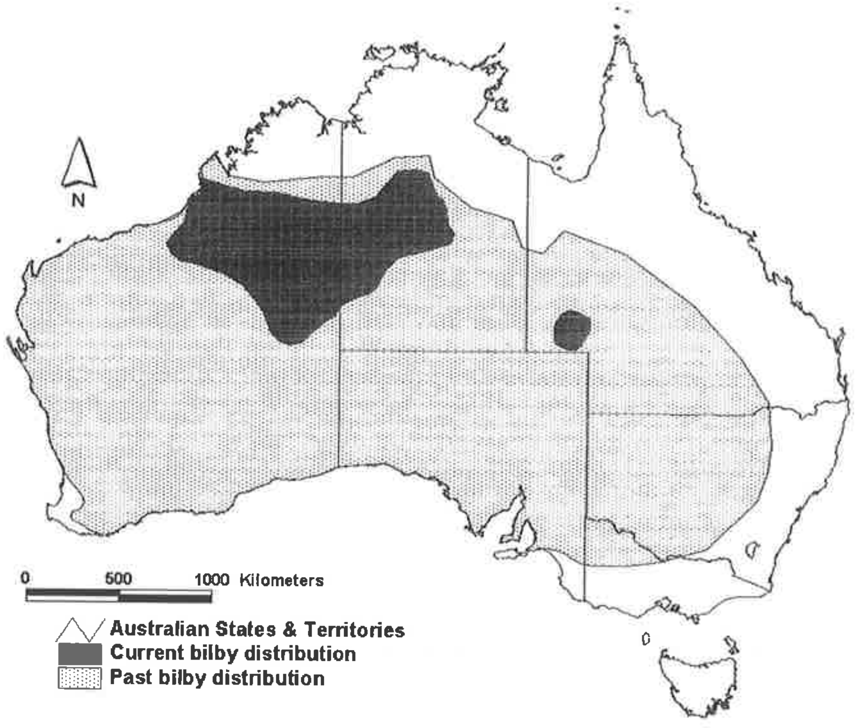

**Fig. 2.1** The historic and current distribution of the bilby *Macrotis lagotis*

*Gestation, fecundity and growth*

Bilbies are sexually dimorphic in size. Males can reach weights of 2500 g while females without pouch young may reach weights of 1200 g. Both female and male bilbies continue to grow to the age of about 540 days. Male and female independent-immature individuals of age 90-180 days have a weight range of 288-493 g (Southgate *et al.* 2000). The size of tracks and faecal pellets of large males (>1800 g) are substantially larger than females (and young males) (500-1200 g) and immature young (<500 g).

The gestation period of 12-14 days for the bilby is similar to the peramelids (McCracken 1990) but other fecundity characteristics are slightly different. Pouch life for the bilby is about 90 days and females reach sexual maturity at about six months of age. Litters may consist of 1-3 young and breeding longevity of males and females may extend to at least 5 years (Southgate and Possingham 1995; Southgate *et al.* 2000). Breeding throughout the year and a mean post partum litter size of 1.88 has been reported under favourable conditions. Up to four litters may be produced in a year (Moseby and O'Donnell 2003; Southgate *et al.* 2000).

Bilbies have less capacity for population growth than other bandicoots because of a slightly longer pouch life and maturation age and smaller litter size. A pouch life of 50-60 days has been reported for *Isoodon obesulus*, *I. macrourus*, *Perameles nasuta* and *P. gunnii* (Gordon and Hulbert 1989). *I. obesulus* and *I. macrourus* may have up to six or seven young with a mean litter size of 3.1 (Gemmell 1989; Gordon 1974).

*Density, home range size and movement*

The bilby is nocturnally active and semi-fossorial, constructing a burrow for rest and refuge. Individuals are shy, secretive and often occur at low densities, making them difficult to observe. Watts (1969) reported that *M. lagotis* burrow of activity near Yuendumu covered areas from 11.3-16.2 ha and Smyth and Philpott (1968) found a similar sized area used by individuals near Warburton in the Gibson Desert. The home range used by reintroduced free-range bilby females with access to supplied food at Watarrka National Park based on burrow occupancy in a 12 month period was 5-16 ha. Males had substantially larger home ranges of 180-340 ha over the same period (Southgate *et al.* 1994). A number of different burrows may be used within an individual's home range. Burrows used by wild female bilbies on consecutive nights have been over 1 km apart and males frequently make use of burrows spaced 2-3 km apart and occasionally distances of over 5 km (Moritz *et al.* 1999; Moseby and O'Donnell 2003). Some *in situ*-bred reintroduced bilby females and males were found to have moved 15 km in a period of a few weeks and a number of satellite colonies were found 5-15 km away from the reintroduction sites, 2.5 years after release at Watarrka National Park (Southgate *et al.* 1994).

Wild bilby populations usually consist of scattered individuals or small groups of individuals (Krefft 1866; Smyth and Philpott 1968; Southgate 1990a; Watts 1969) and bilby density in central Australia is generally much less than 0.001 individuals per ha (Southgate, unpublished). However, conditions do occur that allow the density and abundance of individuals to increase resulting in 'endless mounds' of bilby burrows and feeding activity (Le Souef and Burrell 1926; Southgate 1990a; Spencer and Gillen 1912). In these situations, the density of bilbies has been reported at about 0.08 individuals per ha on the Nullarbor (Le Souef and Burrell 1926) and about 0.12-0.16 individuals per ha in south-west Queensland (Southgate 1987). This is an order of magnitude lower than the densities of 1-2 per ha and sometimes up to 5-8 per ha reported for other peramelids (Gordon and Hulbert 1989; Lobert 1990). There is general agreement that local concentrations of peramelid species in the wild reflect dispersal of food resources rather than social bonding (Lee and Cockburn 1985).

### *Habitat use and diet*

The bilby is catholic in its habitat requirements and capable of occupying most of its current distribution as long as the soils are suitable for burrow construction (Southgate 1990b). Historic reports indicate the species as 'tolerably abundant' over the entire interior grassy districts of Western Australia (Gould 1863), a 'familiar species' in the more fertile portions of South Australia (Jones 1924) and one of the most plentiful and universally distributed of central Australian mammals (Finlayson 1961). There is a high incidence of individuals vacating a location and colonising areas with no previous sign of occupation. For example, half of the 16 sites in the Tanami and Great Sandy Desert revisited after 12 months had no sign of fresh bilby activity (Southgate 1987).

The use of a burrow means the bilby can exploit habitats that have been recently burnt or that have naturally sparse cover. Most peramelids depend on perennial vegetation for nesting/refuge habitat and consequently, suitable vegetative material must be located close to habitat used for foraging (Gordon and Hulbert 1989) although there have been reports of Australian and New Guinea bandicoots using burrows or nesting under rocks (Flannery 1995; Southgate *et al.* 1996).

A wide range of animal, plant and fungi are consumed, indicating the bilby has a generalist dietary strategy (Gibson 2001). Much of the food including termites, ants, larvae, spiders, seed, bulbs and hypogean fungi is foraged on the soil surface or from the soil stratum. The diet of the greater bilby has been found to range from almost complete herbivory (83% identifiable plant material in faecal volume) to insectivory (52% identifiable invertebrate material in faecal volume) depending on location and conditions (Southgate 1987).

The gut morphology and flattened molars of the bilbies are better suited for consumption and processing of plant material than most other bandicoots (Hume 1982). A number of the plant foods used by *M. lagotis* are derived from either fire-promoted or fire-encouraged plants (Southgate 1990b). Other bandicoot species include plant food in their diet but the plant species are generally perennials and not promoted by disturbance. Invertebrates appear to form the main component of peramelid bandicoots (Bradshaw *et al.* 1994; Broughton and Dickman 1991; Heinsohn 1966; Quin 1985; Watts 1974).

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# Chapter 3

# An evaluation of transect, plot and aerial survey techniques to monitor the spatial pattern and status of the bilby (*Macrotis lagotis*) in the Tanami Desert, Northern Territory[1]

*Preamble to Chapter 3*

This chapter describes the three main methods used to monitor bilby occurrence in the study area and examines some of the issues related to the use of animal sign as a means to record occurrence.

The application of three methods concurrently or near concurrently provided an opportunity to compare the accuracy and precision of data provided by each technique and to indicate the costs involved in developing a broad-scale monitoring program for the bilby.

It is suggested that the aerial survey technique combined with ground-truth survey plots would provide the most effective means to accurately determine the occurrence of the bilby in the remote spinifex deserts of central Australia.

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## Introduction

The bilby *Macrotis lagotis* is a species considered vulnerable to extinction (Maxwell *et al.* 1996) based primarily on extent of occurrence data that compares past and present museum and historical records, broad survey and anecdotal information (Watts 1969; Southgate 1990). Population range and size play an important part in most schemes for assessing conservation status (Burgman and Lindenmayer 1998) and preferably, the sampling techniques used to obtain this information need to be relatively unbiased, repeatable and cost effective.

The bilby is medium-sized (1-2.5 kg), nocturnal, semi-fossorial and cryptic. Individuals are mostly solitary and often occur at low densities (<1 $km^{-2}$), are reluctant to enter free-standing baited traps (Southgate *et al.*1995) and are relatively mobile, moving unsystematically between widely scattered burrows some greater than 1 km apart (Moseby and O'Donnell 2003; Southgate, unpublished). Efforts to accurately measure the size of a bilby population at a fine scale by direct measures (i.e. spotlight counts or trapping) and indirect methods (such as burrow counts) have been ineffective (Southgate *et al.* 1995). In parts of Queensland where the terrain is open and the vegetation sparse, burrow counts can be used effectively to map bilby spatial pattern but an accurate measure of bilby abundance has not been obtained because the correlation between the number of burrows and bilbies is poor (Lavery and Kirkpatrick 1997).

Instead of attempting to obtain counts of individuals, the methods proposed here aimed to obtain relative abundance and occurrence data, based on animal sign at a broad scale. Calculation of the frequency of occurrence in relation to specific habitat parameters such as substrate may then be used to determine habitat suitability and assess the area of occupancy (Burgman and Lindenmayer 1998).

Each of the methods outlined in this paper: random plots, fixed transects and aerial survey, involved the observation of footprints or diggings to confirm the presence or absence of the bilby within a sampling unit. Bilbies produce distinctive sets of foot imprints or tracks and characteristic diggings during foraging activity that can be readily identified by an observer traversing sandy substrates. Aboriginal people have traditionally used the imprints and diggings produced by animals as the primary means to secure food in the central parts of Australia. More recently, these track and sign-based techniques have been adopted in wildlife science to estimate the relative abundance for a range of species (Catling and Burt 1994; Allen *et al.* 1996; Catling *et al.* 1997; Mahon *et al.* 1998; Stander 1998; Edwards *et al.* 2000; Paltridge and Southgate 2001, Wilson and Delahay 2001), including bandicoots (Mallick *et al.* 1997; Rees and Paull 2000).

The potential for use of a helicopter to survey bilby diggings from the air was identified by Burbidge and Pearson (1989) during a search for sign of mala *Lagorchestes hirsutus* in Western Australia. No sign of mala were found but they noted that bilby diggings could be confidently distinguished from the air. Fixed-wing aircraft have been used to monitor the spatial pattern of bilby burrow complexes on the brown clay downs in south-west Queensland (Lavery and Kirkpatrick 1997). However, fixed-wing aerial survey is not suitable in areas of higher shrub cover where burrows are more difficult to identify from the air such as areas in the Tanami Desert.

This paper describes and compares three methods of survey that were developed to monitor bilby occurrence at a broad scale in the sandy spinifex deserts of Australia. Their accuracy and precision were assessed after applying each technique to a range of locations and substrates in the Tanami Desert. A description of the relative costs of implementing each method was included to allow a comparison of efficacy and to indicate the costs involved in developing a broad-scale monitoring program.

## Methods

### *Study area*

Bilbies were surveyed in parts of the Tanami Desert located northwest of Alice Springs in the Northern Territory. Much of the landscape was characterised by sandy soils covered with spinifex grasslands (mainly *Triodia basedowii*, *T. pungens* and *T. schinzii*) with an overstorey of low shrub dominated by *Acacia* species. Within this sandy landscape were rocky outcrops, laterite rises and low-lying paleodrainage systems. The paleodrainage channels were characterised by the presence of *Melaleuca* species. Vegetation occurred at a variety of successional stages following various fires throughout the study region (Allan and Southgate 2002).

The study area was divided into four latitudinal zones of approximately 170 km width and referred to as Newcastle Waters (17°-18.5° S), Tennant (18.5° -20° S), the Granites (20° -21.5° S) and Kintore (21.5° -23.5° S) (**Fig. 3.1**). Further description of the study area and climate for the region can be found in Paltridge and Southgate (2001).

*Bilby sign*

The characteristics of fresh bilby tracks and diggings allowed this species to be identified unambiguously during the survey. The gait pattern of the bilby is similar to those of rabbits, dasyurids and other bandicoots but the feet provide distinctive toe imprints allowing differentiation to the level of genera (Southgate 2005) and the greater bilby *M. lagotis* is the only extant species in the genus *Macrotis*. Similarly, the diggings and faecal pellets of the bilby can be distinguished from other species. The distinctive faecal pellets can often be found in the sand apron surrounding digging activity. Extensive diggings associated with bilby feeding activity are sometimes spread over 100 m or more. The diggings, which occasionally reach a depth of 100 mm and a diameter of 200 mm, are made while the animals search for subterranean food such as bulbs, termites and other invertebrates. The rich colour of the recently excavated soil in contrast with the more bleached background allow the diggings to be identified easily. Burrows tend to be less numerous than diggings and, although more soil is displaced, the burrows are often located near logs or under bushes and tend to be inconspicuous.

The four Europeans involved in our survey of bilby sign were familiar with the track, digging and scat characteristics of the species. Traditional Aboriginal people accompanied us on all trips and they also provided expertise on track identification and age. Sign was

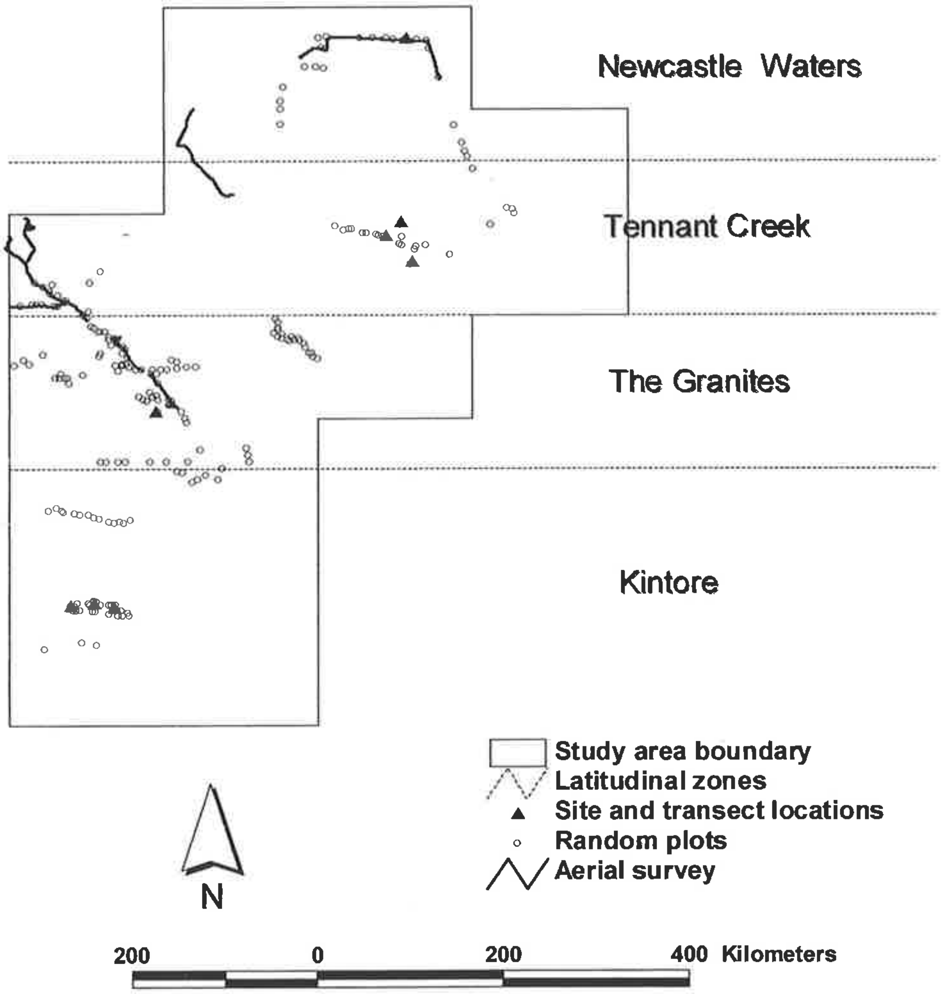

**Fig. 3.1** Location of random plots, site locations for fixed transect locations and aerial survey transects within four latitudinal zones. Inset shows the boundary of the Northern Territory, major towns and some communities.

scored as fresh or old based on the clarity of print definition in the sand surface. The substrate and arid climate conditions frequently allow bilby foot imprints to persist for several days without complete deterioration, and it is often possible to categorise tracks to about 3-4 days old (Southgate, pers. obs.). Tracks up to about three days old were regarded as fresh. Sampling was postponed following periods of rain or high wind.

*Random plots*

Three primary observers (RS, PM and TN) were involved in collecting track information during the random plot survey and all had developed tracking skills with the assistance of Aboriginal people. Plots in the Granites and the Kintore zone were sampled mainly in the period May 1996 to June 1997. Sampling of plots in the northern zones was conducted primarily by RS and concluded by April 1998.

At each plot, the equivalent of one person searched for animal tracks for a period of one hour within a 300 x 200 m (6 ha) quadrat. A 300 point vegetation transect with points spaced 1 m apart using a wheel point apparatus (Griffin 1989) was also conducted. This procedure helped define the dimensions of each plot. Bilbies were recorded as either present or absent based on track identification. Variables likely to affect tracking conditions including the time of day, time of year, wind speed, cloud cover, soil coarse fragment abundance, and standing vegetation cover were recorded at each plot (**Table 3.1**). In all, 208 plots were sampled (**Fig. 3.1**). Restricted stratified random sampling was used in the selection of plots and each plot was separated by at least 4 km. This distance between plots was selected to ensure plot independence and was based on previous research that indicated that the longest axis of bilby nightly home range movements was generally less than 4 km (Southgate and Possingham 1995). The plots were distributed among 15 land units stratified on the basis of fire age and substrate type. Fire age data were merged to form three classifications: recently burnt (<2 years old), intermediate (3-6 years old), and old (>6 years old). These fire age groupings were chosen on the basis of previous studies that examined the recovery of spinifex following fire (Griffin 1990). Geological mapping was used to identify and delineate three substrate classes: drainage line+calcrete, laterite+rock features, sand plain+sand dune.

*Fixed transects*

Two observers (RP and RS) monitored the track activity of bilbies on fixed transects. Three sites spaced about 25 km apart were monitored in the Kintore and Tennant Creek zones, and one site was monitored in the Granites and Newcastle Waters zones (**Fig. 3.1**). Each site consisted of two tracking transects, one located on sand plain/dune substrate and the other on drainage substrate. The exception was the Newcastle Waters zone where both transects were located in sand plain habitat because of the absence of suitable drainage habitat. Each transect was 10 km in length (roughly a 4x1 km rectangle), located 5 km from the other transect and more than 500 m from any permanent vehicular track.

**Table 3.1** The strength of association of bilby sign and tracking condition recorded on random plots

| | Degrees of freedom | Residual degrees of freedom | Residual Deviance | Pr(Chi) |
|---|---|---|---|---|
| NULL | | 153 | 154.67 | |
| Date of tracking | 2 | 152 | 151.97 | 0.10 |
| Time of tracking | 2 | 151 | 152.55 | 0.34 |
| Wind | 2 | 151 | 152.63 | 0.98 |
| Tracker identification | 2 | 151 | 153.03 | 0.44 |
| Soil coarse fragment abundance | 2 | 150 | 125.16 | <0.001 |
| Vegetation cover % | 1 | 152 | 154.64 | 0.85 |
| Surface track visual assessment. | 2 | 150 | 152.30 | 0.50 |
| Cloud | 2 | 151 | 152.63 | 0.98 |

Response and explanatory variables used in the generalised linear modelling

| | |
|---|---|
| Bilby sign | 0=absent; 1=present, logit link function |
| Date of tracking | 1=may-aug; 2=mar-apr, sep-oct; 3=nov-feb |
| Time of tracking | 1=0600-900, 1501-1800; 2=901-1100, 1301-1500; 3=1101-1300 |
| Cloud cover | 1=clear or 1-2/8; 2=partial cloud or 3-4/8; 3=cloudy or 5-8/8 |
| Wind during day prior to sample | 1=calm; 2= breeze; 3=windy |
| Tracker identification | pm=Pip Masters; tn= Theresa Nano; rs=Richard Southgate |
| Coarse fragment abundance | 1=<2%; 2=2-20%; 3=>20% |
| Vegetation cover % | % ground cover derived from a 300 m transect with points 1 m apart |
| Surface track visual assessment | 1=vgood/excellent; 2=ok/good/medium; 3=poor |

The fixed transect method is described further in Paltridge and Southgate (2001). Bilby activity was present on at least one transect at every site when sampling commenced, with the exception of the Kintore zone. Transects were divided into 500 m cells and the presence or absence of the tracks of a species in each cell was recorded. In most cases, transects were sampled for three consecutive mornings (generally 0.5-3 hours after sunrise) while travelling on an All Terrain Vehicle (ATV) at about 10 km $hr^{-1}$. Sampling was conducted every four months between March 1996 and December 1998. The surface of each transect was prepared prior to the first day of sampling and on consecutive days by dragging an iron post and chain behind the ATV. The 1.4 m transect width combined with the 10 km transect length produced a sample unit area of 0.14 ha.

### *Aerial survey*

The aerial survey involved one observer (RS) with two primary ground observers (RP and RS). A Robinson two-seater helicopter was used during the survey. The helicopter was flown at a ground speed of 30-40 knots $hr^{-1}$ (55-74 km $hr^{-1}$) at a height of 15-20 m above the ground. Most of the transects were flown beside vehicle tracks to enable easy ground access. A search strip of about 20 m width was surveyed by the observer on one side of the track. On some occasions different sides of a track were surveyed on an outward and return flight. The observational data and the route of the helicopter were logged with a Magellan Pro Mark X geographic positioning system and down-loaded to a lap-top computer in the field using the Mstar capture program. Two aerial surveys were conducted, one in an area north-west of the Granites to the Western Australian border in May 1999 and the other in an area between Newcastle Waters and Wave Hill Station at the end of August 1999 (**Fig. 3.1**). Overall, 1084 km of transect were flown.

### *Analysis*

Data from each monitoring technique were expressed as the presence or absence of bilby sign observed per sample unit, and as such represented sampling a binomial population. Standard deviation of the binomial probability was derived from the binomial estimate of variance (Zar 1984). The amount of positive sign varied in relation to the latitudinal zone, the type of substrate and the proximity to other records. To assist in the comparison of techniques, bilby records from sand plain, laterite and drainage line substrates were treated separately and data collected at different latitudinal zones were also separated. With the aerial survey, bilby records were combined unless separated by at least 4 km from neighbouring sign along a transect. As the fixed transects and random plots were located at least 4 km apart, no data filtering was necessary. Fixed transect data were presented for sample periods. The aerial survey was conducted in the year following the completion of random plot and the fixed transect sampling. Seasonal conditions did not change significantly between 1998 and 1999, hence it was assumed the frequency occurrence of the bilby sign (and the estimate of variance) within substrate types and zone remained similar during the sample period.

The accuracy of data derived from fixed transects and the random plots was not assessed directly. However, variables likely to affect tracking conditions at the random plots were analysed to determine if they associated with the occurrence of bilby activity. The tracking condition information recorded during the random plot survey was prepared as factorial or continuous data as shown in **Table 3.1** for analysis using generalised linear modelling (S+4.5, Mathsoft). Bilby activity at each plot was used as the response variable with a logit link function. The accuracy of the data collected from the aerial survey was assessed directly by visiting localities on the ground both where no sign was recorded and where bilby sign was recorded from the air. This was used to determine if bilby sign was being overlooked (a false-negative) or non-bilby sign was being recorded as bilby sign (a false-positive). The localities used to determine the occurrence of false-negatives were spaced at least 4 km apart. Some of the plots sampled used to determine false-positive error were located less than 4 km apart. While checking both false-positive and false-negative localities, an area 300 x 100 m was searched for track, burrow and digging activity of bilbies.

Wiegart (1962) proposed that relative variability and relative cost are the two factors of primary importance when selecting among monitoring techniques (as outlined in Krebs 1989). Relative cost may be calculated by estimating the cost of sampling a sample unit using a particular technique and dividing this amount by the cost of unit sampling using the cheapest technique. Similarly, the relative variability may be calculated by dividing the variability obtained using a particular technique by the variability obtained using the least variable technique. The technique with the least (cost)x(variance) product is the technique that offers optimal efficacy.

Some costs were fixed regardless of the sampling technique. For all surveys, the payment of two professional officers, two Aboriginal people and travel allowance plus the hire cost for two 4WD vehicles and trailers were standard. This amounted to 8.5 units per day. The cost to establish the fixed transects or prepare the surface prior to the sampling of a fixed transect was not included nor was the cost of travel to the study area. The hire of the Robinson helicopter including fuel amounted to 16.0 units per day and was additional to the fixed field operating costs. The observed variance for a sampling technique was calculated from the number of units on each substrate type for each zone.

About three random plots (2.9) were sampled per day during the survey. This sampling effort could be doubled (5.8) potentially if other activities such as vegetation monitoring and a detailed site description were not conducted. Similarly, although only two transects were sampled per day during the study, four transects could be sampled potentially in the absence of other commitments such as small mammal trapping, vegetation monitoring and bird surveys (Paltridge and Southgate 2001).

Serial correlation was a concern with the fixed transects because each was sampled on successive days. Pooling data collected during a sample period provides a simple remedy to avoid the problems associated with serial correlation, but at the expense of sample precision (Caughley and Gunn 1996). The cost per transect sampled also increases if data from two or three days of monitoring are pooled to produce a result for each sample period, as was the case here.

## Results

No bilby sign was recorded during the fixed transect or random plot sampling in the Kintore zone and no aerial survey was conducted in this region. Consequently, the sampling effort applied in this zone was not included in the comparison of survey techniques. However, the data from plots sampled in the Kintore zone were used in the assessment of factors affecting plot sampling.

### *Random plots*

The search area of a random plot amounted to 6 ha with an edge of about 1 km. Within the Newcastle Waters, Tennant Creek and the Granites zones, 164 plots were sampled and 38 of these had bilby sign. Sampling this number of random plots took 57 days and equated to 27.5, 15.3 and 14.2 sample days for the sand plain, drainage line and laterite substrates, respectively. Greater frequency of occurrence of bilby sign was recorded on laterite compared to other substrates and the least was recorded on sand plain. The mean numbers of bilby records on the sand plain, drainage line and laterite substrates were 11, 10 and 17, respectively and the coefficients of variation were 29%, 26%, and 19%, respectively (**Table 3.2**).

Data from 154 plots located in the Kintore and the Granites zones were used to assess whether bilby activity was associated with variables such as the observer conducting the tracking or the tracking conditions on the plots. Plots from these zones were selected because three observers (RS, PM and TN) sampled simultaneously in the same region over the same period. Generalised linear modelling indicated that bilby activity was not associated with any of the measurements relating to tracking ability. The only significant association was with the amount of soil coarse fragment abundance and this reflected the strong positive association of bilby sign with lateritic soils (**Table 3.1**).

### *Fixed transects*

The search area of a fixed transect amounted to 1.4 ha with an edge of 10 km surrounding a survey area of approximately 4 km$^2$. In the Granites, Tennant and Newcastle Waters zone, fixed transects on sand plain were sampled on 43 separate occasions for a total of

107 days. On sandy substrate, bilby sign was encountered on 11 days. Drainage line substrate was sampled on 31 occasions, for a total of 92 days and resulted in bilby sign being recorded on 23 days (**Table 3.2**). The combined amount of bilby sign recorded per sample period on the sand plain and drainage line substrates was 0.26 and 0.74 respectively, with 26% coefficient of variation for the sand plain transects and 11% for the drainage line transects. If fixed transects were sampled for only one day, approximately 59% of the bilby occurrence from a three day sampling regime would be captured. The second day added 33% to the first day tally and the third added a further 8% to the second day cumulative tally. Bilby sign was recorded every day on only 18% of the sample periods, and two of the three days on 29% of the sample periods.

*Aerial survey*

The aerial transect had a search area of 2 ha per km and an intersection edge of about 1 km for each kilometre surveyed. Eight days of flying for about six hours per day were conducted. This included transect and ferry time between transects. In the Granites zone, transects were sampled along the Tanami Highway south-east of Rabbit Flat in May 1999, which took two days of flying time. The transects flown to the north-west of Rabbit Flat and a sector south-east of Lajamanu took approximately three days to fly and provided data for the Tennant zone. The transects flown between Newcastle Waters and Wave Hill took three days of flying time and contributed data for the Newcastle Waters zone.

Approximately 431 km of transect were flown in the Newcastle Waters zone and 476 km and 177 km in the Tennant and the Granites zone, respectively. This translated to sampling 861 km of sand plain, 106 km of drainage line and 117 km of laterite or, in terms of 4 km cells, 215, 27 and 29, respectively (**Table 3.1**). Bilby sign was recorded in 37 of the 271 cells. Proportionally, 0.26 of the drainage line sample blocks contained putative bilby sign, 0.17 of the blocks with laterite substrate and 0.10 of the sample blocks on sand plain. A similar frequency of sign was seen in the Tennant Creek and the Granites zone which was far greater than that located in the Newcastle Waters zone. The coefficient of variation was the least for the sand plain (17 %) with 35% and 41% recorded from the drainage line and laterite sample blocks, respectively.

**Table 3.2** The amount of bilby sign recorded and the effort used to sample fixed transects, random plots and aerial survey in relation to habitat type and latitudinal zone.

| | Zone | | | |
|---|---|---|---|---|
| | Newcastle Waters | Tennant Creek | The Granites | Total |
| *Fixed transects* | | | | |
| Sand plain & dune | | | | |
| Sites | 1 | 3 | 1 | 5 |
| Sample periods | 12 | 24 | 7 | 43 |
| Sample days | 30 | 72 | 20 | 107 |
| No. days with bilby sign (bdays) | 8 | 3 | 0 | 11 |
| Propn (bdays/period) ±sd (CV%) | 0.67±0.14 (21) | 0.13±0.05 (55) | 0 | 0.26±0.03 (26) |
| Drainage line | | | | |
| Sites | 0 | 3 | 1 | 4 |
| Sample periods | 0 | 24 | 7 | 31 |
| Sample days | 0 | 72 | 20 | 92 |
| No. days with bilby sign (bdays) | - | 18 | 5 | 23 |
| Propn (bdays/period) ±sd (CV%) | - | 0.75±0.05 (12) | 0.71±0.10 (26) | 0.74±0.04 (11) |
| *Random plots* | | | | |
| Sand plain & dune | | | | |
| Plots sampled | 21 | 18 | 40 | 79 |
| Bilby sign | 4 | 3 | 4 | 11 |
| Proportion ±sd (CV%) | 0.19±0.09 (47) | 0.17±0.09 (53) | 0.1±0.05 (50) | 0.14±0.04 (29) |
| Drainage line & calcrete | | | | |
| Plots sampled | 2 | 7 | 35 | 44 |
| Bilby sign | 0 | 1 | 9 | 10 |
| Proportion ±sd (CV%) | 0 | 0.14±0.14 (100) | 0.25±0.07 (28) | 0.23±0.06 (26) |
| Laterite & rock features | | | | |
| Plots sampled | 1 | 17 | 23 | 41 |
| Bilby sign | 0 | 7 | 10 | 17 |
| Proportion ±sd (CV%) | 0 | 0.41±0.12 (29) | 0.43±0.11 (26) | 0.41±0.08 (19) |
| *Aerial survey* | | | | |
| Sand plain & dune | | | | |
| 4 km blocks sampled | 96.8 | 90.7 | 27.7 | 215.3 |
| Bilby sign | 3 | 21 | 1 | 25 |
| Proportion ±sd (CV%) | 0.03±0.02 (67) | 0.23±0.04 (17) | 0.04±0.04 (100) | 0.12±0.02 (17) |
| Drainage line | | | | |
| 4 km blocks sampled | 1.9 | 12.4 | 12.3 | 26.6 |
| Bilby sign | 0 | 2 | 5 | 7 |
| Proportion ±sd (CV%) | 0 | 0.16±0.11 (69) | 0.41±0.15 (37) | 0.26±0.09 (35) |
| Laterite & rock features | | | | |
| 4 km blocks sampled | 9.1 | 15.8 | 4.4 | 29.3 |
| Bilby sign | 0 | 3 | 2 | 5 |
| Proportion ±sd (CV%) | 0 | 0.19±0.1 (53) | 0.46±0.27 (59) | 0.17±0.07 (41) |

Of the 93 plots checked using ground-searches to determine false-negative error, three localities had sign of bilby activity. This represented a false-negative error rate of 3.2%. All the false-negative records were recorded in the Tennant Creek zone where 35 plots were checked. Thirty one plots were checked in the Granites zone and 27 at the Newcastle Waters zone.

Of the 55 plots where putative bilby sign was recorded from the air and checked on the ground, 23 (or 42%) were falsely identified as positive. Most false-positive records were recorded in the Tennant zone (14 from 23) and least in the Granites zone (5 from 25). False positives were recorded in drainage line, laterite and sand plain habitats. Diggings and burrows of rabbits *Oryctolagus cuniculus*, the great desert skink *Egernia kintorei* and goanna *Varanus* spp. were responsible for sign that was mistaken for that produced by the bilby.

*Efficacy*

The cost to monitor one sample unit was calculated using the maximum number of units that could be sampled per day (5.8) for random plots and for fixed transects (4) and three days were required to complete a sample period for a fixed transect. Sampling of one random plot cost 1.46 units, one fixed transect cost 6.37 units and one cell of aerial transect (including some verification on the ground) cost 0.59 units. The relative costs for sampling an aerial transect cell, a random plot and a fixed transect were 1.0, 2.46 and 10.73 respectively. Calculation of the product of the relative cost and the relative variance indicated that the aerial transect monitoring technique was the optimal for sampling most of the substrate types in most of the zones (**Table 3.3**). The random plot technique was better than the aerial survey technique at sampling the drainage and laterite substrates, but only in the Granites zone. The fixed transect approach was the least useful by an order of magnitude or more in capturing bilby sign.

## Discussion

The techniques outlined in this paper were designed to determine the spatial pattern and conservation status of the bilby across a large geographic area. The methods most commonly used for assessing conservation status rely, in part or singly, on estimates of

**Table 3.3** An assessment of the optimal sample technique to capture bilby sign adapted from Wiegart's method. The relative costs were calculated using 5.9 random plots, 4 fixed transects and 41.25 aerial transect cells sampled per day. The fixed transects had a three day sample period. The cost per day for fixed transects and random plots was 8.5 units and 24.5 units for the aerial survey. Comparison among techniques is made within each latitudinal zone and for each substrate type.

| | Zone | | | |
|---|---|---|---|---|
| | Newcastle Waters | Tennant Creek | The Granites | Total |
| ***Fixed transects*** (relative cost=10.73) | | | | |
| Sand plain & dune | | | | |
| Variance | 0.0202 | 0.0047 | - | 0.0045 |
| relative variability | 64.47 | 2.4 | - | 9.46 |
| product | 691.84 | 25.76 | - | 101.57 |
| Drainage line | | | | |
| Variance | - | 0.0081 | 0.034 | 0.0064 |
| relative variability | | 1 | 6.05 | 1 |
| product | | 10.73 | 64.96 | 10.73 |
| ***Random plots*** (relative cost=2.46) | | | | |
| Sand plain & dune | | | | |
| Variance | 0.0077 | 0.0082 | 0.0023 | 0.0016 |
| relative variability | 24.61 | 4.12 | 1.17 | 3.28 |
| product | 60.53 | 10.14 | 4.36 | 8.08 |
| Drainage line & calcrete | | | | |
| Variance | - | 0.0204 | 0.0056 | 0.0041 |
| relative variability | - | 2.5 | 1 | 0.64 |
| product | | 6.15 | 2.46 | 1.57 |
| Laterite & rock features | | | | |
| Variance | - | 0.0151 | 0.0112 | 0.0061 |
| relative variability | - | 1.86 | 1 | 0.95 |
| product | - | 4.56 | 2.46 | 2.34 |
| ***Aerial survey*** (relative cost=1.0) | | | | |
| Sand plain & dune | | | | |
| Variance | 0.0003 | 0.002 | 0.0013 | 0.0005 |
| relative variability | 1 | 1 | 1 | 1 |
| product | 1 | 1 | 1 | 1 |
| Drainage line | | | | |
| Variance | - | 0.01191 | 0.0213 | 0.0076 |
| relative variability | - | 1.46 | 3.8 | 1.19 |
| product | - | 1.46 | 3.8 | 1.19 |
| Laterite & rock features | | | | |
| binomial variance | - | 0.0104 | 0.0735 | 0.005 |
| relative variability | - | 1 | 6.58 | 1 |
| product | - | 1 | 6.58 | 1 |

extent of occurrence, area of occupancy and population size (Burgman and Lindenmayer 1998). The population size of wild or reintroduced bilby populations has proved difficult to estimate because individuals are not easy to spotlight, capture and burrow counts do not reflect the number of individuals accurately (Lavery and Kirkpatrick 1997; Moseby and O'Donnell 2003). In the absence of suitable methods to accurately determine population size, consideration was given to determining an index of abundance or, at least, the extent of occurrence and area of occupancy. The extent of occurrence may be defined as a representation of localities at which a species has been recorded and the area of occupancy defined as a measure of the area within the extent of occurrence that is occupied. The development of a strong statistical relationship between a species occurrence and habitat variables may be used to spatially define the area of occupancy if the habitat variables can be readily mapped (Lindenmayer *et al.* 1995; Burgman and Lindenmayer 1998).

Because of the difficulty in observing bilbies, the three techniques developed all relied on the identification of track or diggings to indicate bilby occurrence. Surveys that sample passive sign overcome many of the problems associated with direct counts and live capture methods (Allen *et al.* 1996; Mahon *et al.* 1998). They can be simple to implement, cost effective and allow simultaneous monitoring of a number of species, and are particularly suited in situations where populations are in low abundance (Caughley 1977; Allen *et al.* 1996; Paltridge and Southgate 2001). Like direct survey techniques, passive survey techniques vary in their ability to procure accurate, precise and cost effective data. Here we refer to accuracy as the closeness of a measured value to its true value, precision as a measure of repeatability and sampling error (Krebs 1989), and efficacy as the product of relative cost and relative sample variance. There is a general aim to maximise precision and accuracy in wildlife ecology but often a trade-off needs to be made between accuracy and precision to answer a particular question (Caughley and Sinclair 1994). Efficacy also pays an important part in technique selection.

The three techniques applied different spatial and temporal strategies to capture bilby sign. The fixed transect technique was designed to examine the effect of substrate type and seasonal conditions on the abundance of the bilby. It relied on the expectation that a number of bilby individuals conducting normal activities such as foraging or dispersal would intersect a thin transect with a long edge. The amount of time a transect was exposed to bilby activity was regulated and restricted to three days. The tally for the amount of sign encountered each day was pooled to avoid serial correlation (Caughley and Gunn 1996). A substantial amount of effort was invested initially in clearing the transect and the time taken to clear and monitor each transect restricted the number of substrate types that could be examined. Bilby sign was sparse and not recorded on the majority of transects.

With fixed transects, either the distance of separation between sign along the transect or the characteristics of specific tracks (eg. size) may be used to identify a minimum number of 'individuals'. Alternatively, the proportion of a transect covered by a species' tracks or the occurrence on a transect can be used to infer relative abundance in terms of sign encountered per sample. A number of issues that affect the reliability of each approach need to be considered. The separation of sign is dependent upon the knowledge of the size of daily home range movements in the study area (Edwards *et al.* 2000). Feral cat tracks separated by 500 m were used by Edwards *et al.* (2002) to identify different feral cat individuals at a study site in central Australia based on the size of a daily home range of 20 ha. There is little information available on the daily home range size for wild bilbies except the burrows used on consecutive days can be 1 km apart for females and 3 km apart for males (Moseby and O'Donnell 2003; Southgate, unpublished). The 10 km transect used in our study was probably an appropriate length to monitor bilbies however, the need to close the transect loop for logistic and safety reasons reduced ability to capture activity. Transects longer than 10 km (and about one hour sampling duration) would most likely result in increased observer fatigue and counting error.

The use of the characteristics and size of tracks to identify individuals or classes of individual is not limited to the fixed transect technique and could have been applied to plot sampling. Such methods have been used to accurately identify individuals and estimate group size of lions, leopards and wild dogs (Stander 1998). With the bilby, measurement of track and faecal pellet characteristics can be used to identify three size classes of individual (Southgate 2005).

In the absence of data on 'individuals', the amount of track activity has been used as an indirect measure of species' abundance for a variety of species. However, situations arise where track density may become a poor predictor of true density. For example, the amount of track activity produced by an individual can be affected by a range of factors including seasonal changes in behaviour, the presence of competing species and the actual density of the population (Edwards *et al.* 2000). The relationship between track density and actual density is generally linear when actual density is extremely low (Caughley 1977). The fixed transect technique has been applied to determine relative abundance/activity of a range of species including predators, macropod spp., *Varanid* spp. and the bilby using the fixed transect technique in the Tanami Desert (Paltridge and Southgate 2001).

The random plot technique was developed primarily as a means to investigate the extent of bilby occurrence and the relationship with range of habitat variables. The size of the plot (200x300 m) was selected on the basis that it could be traversed and monitored within about an hour. The time each plot was exposed to capture bilby sign was subjectively fixed at less than 4 days. The period was based on the knowledge that 1-3 day old bilby tracks could generally be identified and a more restricted capture-window (eg. scoring only very fresh, one day old tracks) would probably result in a large proportion of plots with bilby sign being rejected. While a broader capture-window increased the chance of capture of bilby sign, it also increased the chance that older tracks would not be recognised and result in an elevated level of false-negative error. Without the need to clear or prepare a tracking surface, more plots and a greater number of habitat types could be sampled. This resulted in the importance of laterite and rock feature substrates being identified.

The aerial transect technique was developed primarily to estimate the dispersion of bilby occurrence directly but also determine bilby occurrence in relation to habitat variables using a non-stratified approach. The technique relied upon the observation of bilby diggings along a 20 m strip from a helicopter at a height of about 15-20 m to identify occurrence. The amount of time each transect cell was exposed to capture bilby sign was unrestricted and the occurrence of bilby activity was assigned subjectively based on the extent and freshness of diggings and soil disturbance. There was an opportunity for the ground-support team members to simultaneously conduct plot sampling to verify the observations made from the helicopter, while an aerial transect was being conducted.

The aim of the study was to provide a description of the techniques, the limitations of the data produced and costs associated with applying each technique. A direct comparison of techniques was not appropriate because there was poor spatial overlap and non-contemporaneous sampling among techniques. Nevertheless, each technique provided data that showed consistent differences in bilby occurrence among substrate type. Greater frequency of bilby sign occurred on drainage and lateritic substrates compared to sand plain and dune fields. However, the frequency of sign produced by the techniques was not consistent among latitudes. This may have been a reflection of the unbalanced sampling effort among zones and substrate types or changes in the population size over the sampling period. A discussion of these issues and the factors affecting bilby spatial pattern will be reported in more detail elsewhere. Our study focused on comparing the variability of data produced by techniques applied to a broad range of bilby densities and habitat conditions encountered in the Tanami Desert. This type of information is generally required before an informed decision can be made about the best technique and sample size requirements to answer any biological question (Krebs 1989; Caughley and Sinclair 1994). The fixed transect placed on drainage substrate provided the most precise data but the technique performed no better than random plot or the aerial survey techniques when placed on sandy substrates. The aerial transect and random plot techniques produced similarly precise data.

### *Factors affecting accuracy*

There was little indication that different observers were producing significant bias by sampling at different times of the day, from weather conditions or types of substrate using random plots. As demonstrated by the sampling of the fixed transects, the amount of time a sample unit was exposed to capture sign had a marked effect on the capture success. Hence it is important to record the estimated age of tracks encountered when using the plot technique. This provides an opportunity to examine retrospectively the effect of window breadth on the amount of data captured.

A single day of fixed transect sampling risked overlooking about 40% of activity at a locality whereas two days of sampling overlooked only 8% of the sign captured by three days of sampling. If fresh bilby tracks were noticed opportunistically in the vicinity of a transect, this activity was most often captured by the fixed transect some time over the three day sampling period (Southgate pers. obs). With the aerial survey, the false-negative error of less than 4% meant that little bilby sign was being overlooked. However, the false-positive error of 42% indicated that putative bilby sign could not be separated with confidence from digging and burrowing activity produced by other species such as rabbits and goannas. Verification of bilby digging activity may be achieved by follow-up visitation of localities under the flight path where putative sign was recorded, or by periodic set-downs.

Techniques that use tracks and diggings are vulnerable to bias from a range of factors (Wilson and Delahay 2001). False-positives can arise if sign from another species is misidentified as belonging to the target species. Hence, the skill and experience of the observer plays an important part in producing unbiased data. False-negatives can occur when the clarity of sign has been degraded unknowingly by disturbance from other animals, rain and wind, or sign is overlooked or misidentified. For clear imprints showing details of foot structure and gait, the ground surface needs to be firm, sandy and relatively free of litter and vegetation cover. Track imprints can be most clearly seen if illuminated by direct, low-angle sunlight with the tracks located between the observer and the light source. Hence, time of day, time of year and direction of travel can potentially affect the identification of a species from footprints. Imprints can also be misidentified or missed if the speed travelling by the observer is inappropriate, a factor that significantly affects aerial survey (Caughley 1977). The alignment of the fixed transect sections often forced the observer to search for tracks when the sun-angle was unfavourable and the constant speed travelled on the ATV tended to inhibit the observer from stopping when unclear prints needed to be examined more carefully. With the random plots, monitoring on foot facilitated viewing unclear prints from different angles and thus reduced the chance of making a false record. Compared to foot imprints, the diggings produced by bilby foraging activity provide a longer-lasting indication of bilby occurrence. The size and shape of the diggings make them more resilient to disturbance and weather, and their identification less dependent on sun-angle than foot imprints.

### *Factors affecting precision*

Precision may be increased by increasing sample size, improving sample tally and by rigid standardisation of sampling method (Eberhardt 1978; Krebs 1989; Caughley and Sinclair 1994). Pooling fixed transect data had the effect of reducing sample size but increasing sample tally. The aerial survey and the random plot techniques also produced pooled data because sign that had accumulated over a number of days was included in the tally. However, unlike fixed transects there was no opportunity to directly control the quality of the tracking surface or the period for which it was exposed to animal traffic before sampling. The aerial and random plot techniques were also vulnerable to other biases that could affect precision relating mainly uneven sample effort. Consequently, the fixed transect technique best allowed standardisation of procedures and was most suited to produce fine-grained data for the estimation of population abundance and changes over time or season, but this depended upon the sign being relatively abundant. The scarcity of sign encountered during our study resulted in the information collected for each transect approaching presence/absence data. With this scenario, it was more advantageous to adopt a method that was designed to capture occurrence with a low cost per unit structure to facilitate the collection of many samples.

### *Efficacy*

Taking into account the cost of applying a technique and the variability of data, the fixed transect was the least effective in capturing bilby data and the aerial technique was generally the most effective. The effectiveness of the fixed transects would be further diminished if the costs associated with their establishment, preparation time prior to sampling, and ATV running costs were included. In contrast, the random plots required no site preparation and the smaller edge:area ratio enabled people to sample the area on foot without needing to venture too far from the relative safety of a vehicle, an important aspect while working in the remote parts of central Australia.

Both ground-based survey techniques provided an opportunity to collect relatively accurate information on the spatial pattern and relative abundance of a number of other mammal and bird species simultaneously (Paltridge and Southgate 2001). In contrast, the aerial survey technique in isolation was limited to the collection of putative bilby sign that often included sign from other species that dig and burrow. The advantage of the aerial survey technique however, was the opportunity to sample habitat away from roads and tracks, to effectively locate bilby activity when sparsely distributed and to directly estimate the dispersion of bilby occurrence. However, it became clear that the inclusion of a ground-based component would be important to allow verification of sign and assessment of false-positive and false-negative error when implementing an aerial survey. We suggest that a combination of an aerial survey and ground-truth plots would be the most cost effective means to provide repeatable baseline data to monitor future trends in bilby status in the spinifex deserts of central Australia.

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# Chapter 4

## An examination of the Stafford Smith/ Morton ecological model: a case study in the Tanami Desert, Australia[1]

*Preamble to Chapter 4*

This chapter outlines the substrate, climate, vegetation and fire characteristics present in the Tanami Desert. These spatial data are used as explanatory variables in the development of statistical models throughout the rest of the thesis. The accuracy of spatial data is also examined.

In presenting these data, I also examine whether the composition and extent of key landscape features are consistent with the general pattern described in the framework for the ecology for arid Australia proposed by Stafford Smith and Morton (1990). I assess whether their 'ecological model' adequately identifies the environmental variables likely to be important in the prediction of medium-size mammal distribution in the Tanami Desert.

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## Introduction

Profound changes in the biota of Australia have occurred in just over two hundred years of colonisation by Europeans. The arid parts of Australia have exhibited little resilience to modification of habitat from introduced herbivores such as sheep, cattle and rabbits and eutherian predators such as feral cats and foxes and changes in fire regime despite carrying the smallest and least dense human population, globally (Morton 1990; Woinarski and Recher 1997). Losses from the native bird and mammal species have been substantial and indicative of the damage to biodiversity and production. Austin (2002) has argued that effective examination of the causes of decline and detection of the functional relationship between species and environment requires three components: an *ecological model* that incorporates key variables driving and shaping the system, a *data model* concerning the collection, measurement and nature of data used to represent the key environmental variables or predictors, and a suitable *statistical model* to detect the strength of association among response and predictor variables. An inadequate ecological model may result in the omission of important environmental predictors or the selection of inappropriate ones. It is desirable to predict the distribution of a biotic entity on the basis of parameters that are believed to be the causal, driving forces (Guisan and Zimmerman 2000). The development of a robust relationship will be further confounded if the data model includes key explanatory variables at an inappropriate resolution and with locational inaccuracies.

This paper considers the adequacy of an ecological model that has been developed for arid Australia and whether available spatial data may be used to describe accurately some of the key physical components of this model. Stafford Smith and Morton (1990) proposed a framework for the functioning of Australia's arid lands in which they argued why certain groups of consumers are likely to be limited spatially and more vulnerable to disturbance than others. They began by identifying a set of special characteristics in the physical environment relating to rainfall predictability and soil fertility and argued that the uniqueness of Australia' arid lands spring from a combination of the characters over vast geographic areas. From this they developed broader concepts and ideas relating to diversity, distribution and persistence of plants and animals within arid Australia.

Stafford Smith and Morton (1990) postulated that rainfall unpredictability and infrequent but exceptionally large rainfall events were the principal driving forces in the arid zone of Australia. The infrequent incursions of rain-bearing cyclonic and monsoonal depressions punctuate long periods of average or below average rainfall and have far-reaching and widespread effects because of the flat landscape. Stafford Smith and Morton (1990) also described inland Australia as an ancient flat landscape in which soils are highly weathered and unusually poor in nutrients. They suggested that areas with relatively higher nutrients and water availability are limited, often isolated and tend to be where runoff is concentrated. They identified drainage lines and paleodrainage channels as not necessarily the most productive substrates but areas with continuous and reliable water supplies. Calcareous earths and cracking clay soils were considered relatively fertile but with a low reliability of moisture. The red earths and skeletal soils were considered slightly more productive than sand plain and dune fields. It was postulated that these attributes have resulted in highly patterned plant production in the landscape and this has had a cascading effect on the distribution of higher-order consumers. They suggested much of arid Australia was innately difficult for native herbivorous and omnivorous mammals to inhabit because plant production is unreliable or mostly indigestible.

Our study focuses on the Tanami Desert, one of the six major deserts in Australia and we describe and quantify the general pattern of rainfall, substrate, vegetation and fire derived from spatial data and compare these with those outlined in the Stafford Smith - Morton model. In the Tanami Desert, we would expect to find evidence of broad-scale deviations in rainfall among years that would severely perturb perennial vegetation during periods of deficit and enhance production following big rains. The fire frequency and extent within the region should largely be a reflection of rainfall pattern. We further expect the landscape to be dominated by sand plain and dunes, with little contribution (in area) by drainage and paleodrainage lines and red earths, skeletal soils, calcareous earths and clays. Vegetation communities with distinct characteristics would associate and reflect these substrate types. For example, spinifex (*Triodia* spp.) would be dominant and most strongly associated with lower productivity substrates and tea-tree *Melaleuca* spp. would be largely restricted to drainage and paleodrainage channels.

We investigate here whether the composition and extent of key spatial data are consistent with general patterns described in the Stafford Smith-Morton model and whether other important environmental attributes should be considered. Substantial discrepancies would indicate that either the ecological model is inadequate or the region is atypical. Alternatively, the spatial data may be highly inaccurate. Hence, we also consider whether the accuracy of several broadly mapped environmental variables, which necessarily have been collated at a small geographic scale (~1:250,000 or less), is adequate to test broad-scale hypotheses about the ecology of arid Australia.

## Methods

### *The study area*

The study area was located in the Northern Territory and includes large parts of the Tanami Desert, Great Sandy Desert and Sturt Plateau Bioregions (Thackway and Cresswell 1995). Smaller areas of the Ord-Victoria, Mitchell Grass, Burt Plain and the MacDonnell Range Bioregions are also included. The extreme boundary of the study area ranges from $129^{O}$-$134^{O}$E and $17^{O}$-$23.5^{O}$S, respectively. The pastoral leases on the northern, eastern and south-eastern edges were excluded leaving a core study area of approximately 236,800 $km^2$ (**Fig. 4.1**). There were no major towns within the core of the study area and the largest community was Yuendumu with approximately 800 people. The main highway linking Alice Springs with Darwin was outside the core study area to the east and the most substantial road within the study area was the non-bitumised Tanami Highway.

The core study area was mostly Aboriginal Freehold land, including the Lake Mackay, Mala, Central Desert, Mangkururrpa, Karlantijpa (North & South) and Yiningarra Land Trusts, with major land uses comprising mineral exploration and mining, and a limited area being utilised by pastoral activities. Some of Aboriginal Land parcels under freehold title such as former Tanami Downs, Yuendumu, Mt Allan and Willowra were being managed as cattle stations at the time of the study. Supplejack Station (an existing pastoral lease) and Tanami Downs were located within and were included as part of study area core. There was substantial gold mining activity in the vicinity of the Granites and Rabbit Flat.

The study area was divided into four latitudinal zones of at least 170 km width; Newcastle Waters ($17^{0}$-$18.5^{0}$ S), Tennant ($18.5^{0}$-$20^{0}$ S), the Granites ($20^{0}$-$21.5^{0}$ S) and Kintore ($21.5^{0}$-$23.5^{0}$ S) (**Fig. 4.1**).

*Field data*

A form of gradsect sampling described by Austin and Heyligers (1989) was used in the selection of plot locations. Gradsect sampling aims to cost-effectively sample the steepest environmental gradients within a region. The latitudinal zones were chosen to ensure adequate sampling occurred in distinct geographic regions and in relation to the rainfall gradient. Substrate and fire age categories were also used to stratify sampling intensity. Six substrate types (calcareous, paleodrainage/drainage, laterite, rock (skeletal) features, sand plain/dune field and salt pan/black earth) and three fire ages (<2 yrs, 3-6 yrs, >6 yrs) were identified. No sampling was conducted on salt pan and black earth substrates, thus leaving five substrate classes. Within each fire/substrate category and prior to sampling, the location of plots was chosen randomly although spatially constrained to the vicinity of existing roads and tracks. Plots were spaced at least 4 km apart. At least 5 plots were sampled in each of the 15 fire/substrate categories throughout the study area and at least 24 plots were sampled within each latitudinal zone.

Field data collected from the plots describing substrate, fire age, vegetation cover and composition were compared with data derived from spatial databases for the same point localities. Congalton (1988) indicated that stratified random sampling provides a satisfactory means of selecting samples for a point/pattern error assessment.

Each plot comprised a 300 x 200 m quadrat that was traversed to record fire age, substrate and vegetation characteristics. A wheel point apparatus (Griffin 1989) was used to sample a 300 m point- intersect transect where plant species and aerial cover of vegetation was recorded at 1 m intervals. The type of ground vegetation (<0.5 m) was categorised as spinifex (*Triodia* spp.), non-spinifex, or bare ground plus flat litter. The cover of shrubs or trees in the overstorey (>0.5 m) was recorded as a separate layer. The presence of *Melaleuca glomerata* and *M. lasiandra* was noted because it is restricted to drainage and calcrete substrates (Jessop 1981; Latz 1995) and therefore, indicative of areas where runoff and nutrients are concentrated. Substrate type was also recorded at points along the transect. Sign of recent fire (<2 yrs) was based on the presence of ash or the small size of spinifex plants (<20 cm), while old fire age (> 6yrs) was based on features such as mature shrubs and trees and large, senescent spinifex hummocks. A total of 227 plots were sampled between May 1996 and April 1998 (**Fig. 4.1**). The plots were grouped for convenience of access and the groups were distributed broadly, although the distribution of the groups was skewed diagonally across the study area from south-west to north-east.

### Spatial database

#### *Climate*

The mean annual rainfall (meanrain), mean minimum temperature (mintemp) and mean maximum temperature (maxtemp) for the study area were derived from the Australian Natural Resource Data library. This splined data surface was a spatial grid at 0.05$^{O}$ resolution derived from data for the period January1980–December 1999. The digital elevation model (dem), originally calculated at a 0.025$^{O}$ resolution, was also obtained from the Australian Natural Resource Data library.

Average and median annual rainfall range and the upper and lower decile values were obtained for localities within or surrounding the study area from the Bureau of Meteorology (BOM). To overcome the scarcity of rainfall stations in the vicinity of the search plots, monthly gridded rainfall data for the study region were obtained from the BOM. These data were provided as a spatial grid at 0.25$^{O}$ resolution (roughly 25 km) and were derived using the Barnes successive correlation technique that links designated weather stations across Australia (Jones and Weymouth 1997). The average 'random' station spacing was approximately 70 km and ranging from 10-100 km. The number of

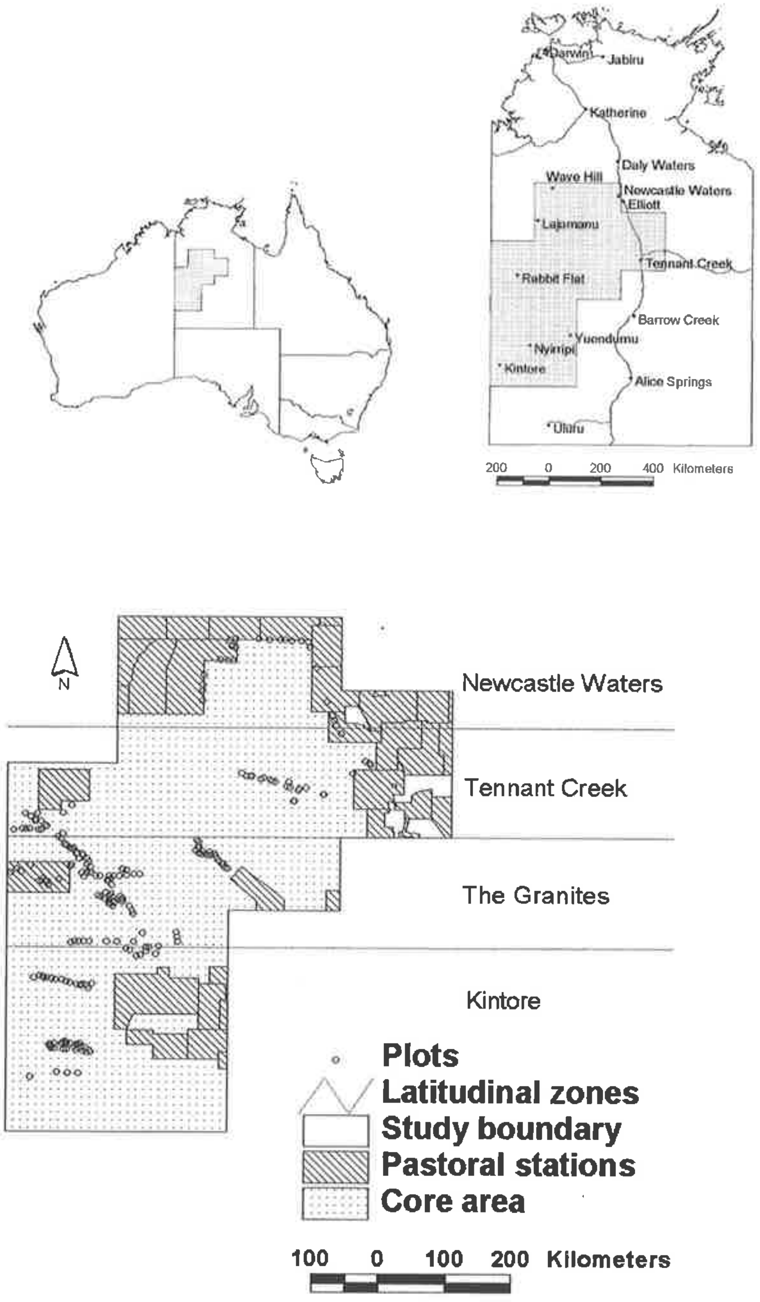


**Fig. 4.1** Location of the study area, core of the study area, pastoral leases and sample plots and sites

stations contributing to the data varied considerably with time from about 3000 in the 1890s to a peak of 7000 during the 1970s.

Rain-years (of August-July) were used instead of calendar years to correspond with summer dominated rainfall. The coordinates of each plot or fixed site were intersected with the gridded rainfall data set and this was used to derive antecedent cumulative rainfall and residual rainfall for a particular grid cell or locality.

*Substrate*

Geological mapping in digital vector format was purchased from the Australian Geological Survey Office (AGSO). This mapping, based on aerial photography, radiomagnetic survey, helicopter and ground traverses, provides complete coverage of the arid zone at a scale of 1: 250 000, although the reliability and currency of the surveys vary within and among map sheets.

Geological units were merged to produce six substrate categories: calcareous (c), paleodrainage/drainage (d), laterite (l), rock (skeletal) features (r), sand plain and dune (s), and black soil and salt lakes (bsl). The classification scheme used to produce the substrate categories is presented in **Appendix 4.1**. The boundaries separating sand dune and sand plain communities were taken from the Northern Territory vegetation map (Wilson *et al.* 1990). These substrate classes correspond approximately with the seven physiographic zones identified by Gibson (1986). The grain-size of substrate types was approximately 0.2 km based on the diameter of the smallest mapped vector. Data were converted to raster format with a spatial grid resolution of 0.002 $^{\circ}$ (roughly 0.2 km). The most notable discrepancy in the substrate classification scheme involved calcareous geological units from the Wave Hill map sheet that were not of Tertiary origin and did not have the vegetation characteristics associated with paleodrainage lines and lower lying depositional zones. The vegetation associated with the problematic units was more similar to those included in the sand plain category and was placed in this category accordingly. A neighbourhood analysis was performed to determine the variety of substrate classes in the vicinity of each cell centroid at different sized radii (1, 2.5, 5,10 and 25 km).

*Vegetation and fire*

The extent of communities with dominant ground cover of spinifex and *Melaleuca* identified in the Vegetation Survey of the Northern Territory (Wilson *et al.* 1990) compiled from 1:500,000 Landsat imagery were compared with vegetation data collected during field surveys. The annual extent of fire 1984-1998 in the Tanami region was derived from the Central Australian fire history database (Allan and Southgate 2002). Prior to 1986, fire history was mapped by visual interpretation of multi-temporal Landsat images and aerial photographs (Allan 1993). The fire history for the period 1986 to 1996 for the Tanami was mapped from Advanced Very High Resolution Radiometer (AVHRR) National Oceanic and Atmospheric Administration (NOAA) satellite imagery at a resolution of approximately 1 km (Allan 1993). Fire history mapping from 1997-1999 was provided by Western Australian Department of Land Assessment (DOLA) using the same form of satellite imagery. Areas burnt prior to 1984 were included in the >16 years category.

Fire data were stored in vector format with a separate coverage for each year from 1995 onwards. Data were merged to produce three classifications: recently burnt (1-2 years old), intermediate (3-6 years old) and old (greater than 6 years old). This age classification was chosen on the basis of previous studies that examined the recovery of spinifex following fire (Griffin 1992). A neighbourhood analysis was performed to determine the variety of fire age classes in the vicinity of each cell centroid at different sized radii (1, 2.5, 5,10 and 25 km). The effect of substrate on the amount of area burnt was examined by comparing the observed amount of area burnt within a substrate class for separate years (1997-1999) with the expected amount burnt based on the proportional area of each substrate class.

*Analysis*

The proportion of the study area with a particular substrate or fire age class was calculated using ArcView GIS software. The accuracy of the mapped data was determined using an error matrix (Congalton and Green 1999). **Table 4.1** identifies the parameters examined and the method of comparison used.

**Table 4.1** Methods used to compare the point data with spatial data sets.

| Parameter | Comparison |
|---|---|
| Substrate | Direct comparison of observational data from field plots (n=227) with mapped values from spatial data (1:250,000 geological mapping) |
| Climate | Descriptive comparison of regional climate data, especially the pattern of rainfall derived from splined rainfall coverage at 0.25 degree resolution and maximum and minimum temperature at a 0.05 degree resolution |
| Vegetation | Direct comparison of observational data from field plots (n=227) with spinifex (*Triodia* spp.) and *Melaleuca* cover with mapped values from spatial data (1:1,000,000 Northern Territory vegetation mapping) |
| Fire | Direct comparison of observational data from field plots (n=227) with fire history mapping derived from satellite imagery at a approximate resolution of 1 km |

## Results

### *Rainfall, elevation and temperature*

Substantial interannual and spatial variation in rainfall occurred in the Tanami Desert. Large rainfall events (sometimes of magnitude greater than the yearly average) can occur over a short period within the study area but the frequency of these events diminishes with increasing aridity (**Table 4.2**). Similarly, substantial rainfall deficits can occur over a number of years and affect large regions. A decile 1 annual rainfall is roughly equivalent to a deficit of half the average annual rainfall. Such an event occurred in 1995/6 and according to the spatial data extended over approximately 90,000 km$^2$ of the study area in the south while the northern half received slightly above median rainfall (**Fig. 4.2a**). A decile 9 event indicative of big rains occurred in 1981/2 and 1991/2 and in both, the events extended to the southern part of the study area covering an area in excess of 85,000 km$^2$. Above average rainfall continued in 1992/93 but only in the northern part of the study area. During the study, the parameters that described cumulative rainfall in the previous 24 months correlated with latitudinal gradient (r=-0.93) and rainfall deviance from the mean in a 24 month period (r=-0.64) (**Table 4.3**).

Most of the study area consisted of flat or gently undulating plains with low tablelands, although a section of the MacDonnell Ranges, with peaks rising to 1300 m, was included in the southeastern part of the study area (**Fig.4.2b**). The sample plots ranged in elevation

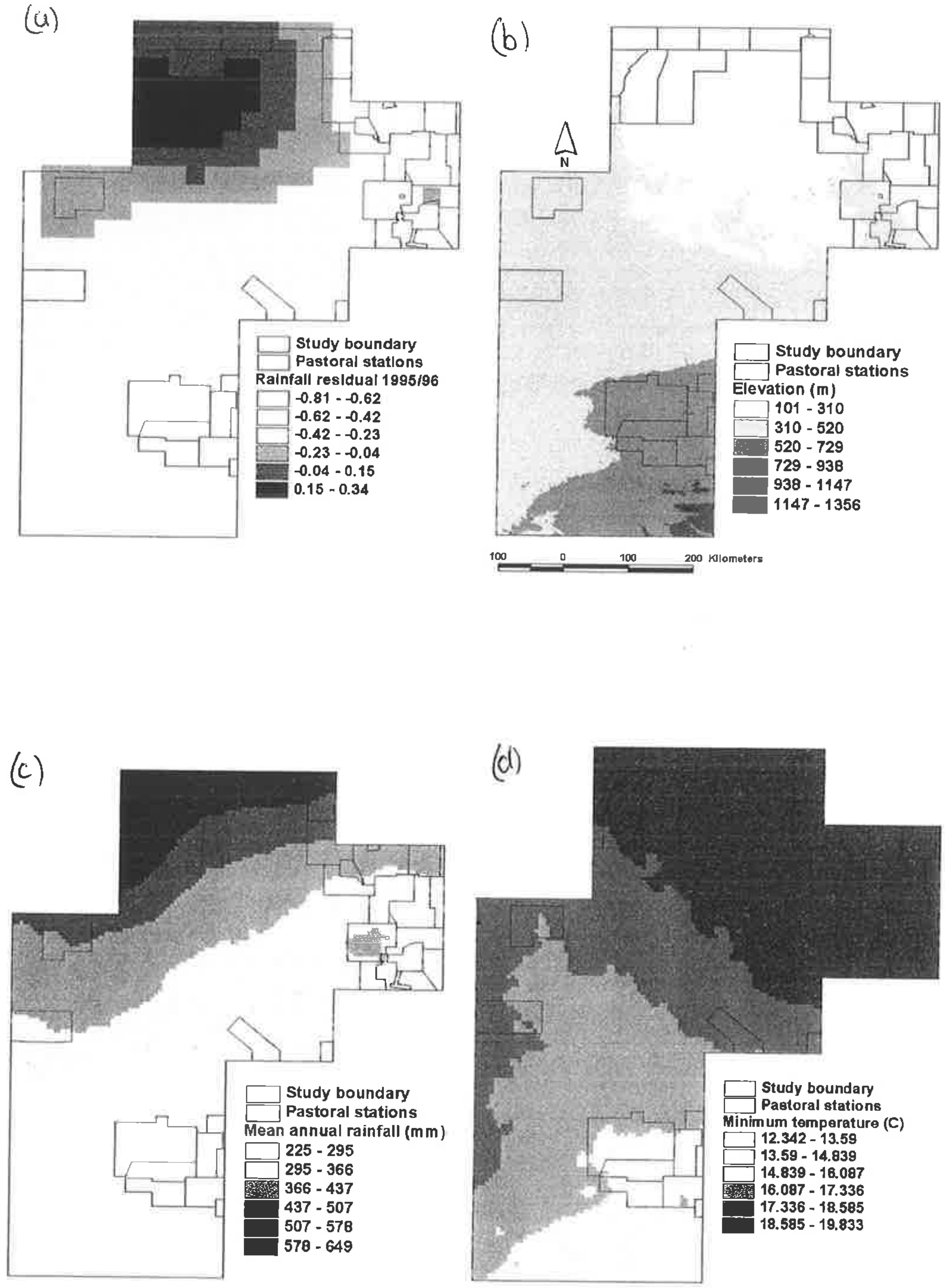


**Fig. 4.2** Elevation and climatic characteristics of the study area: (a) residual deficit of the mean annual rainfall; (b) elevation; (c) mean annual rainfall; and, (d) mean minimum temperature in January

**Table 4.2** Rainfall information from Bureau of Meteorology stations within or surrounding the study area. Temperatures reported are the mean daily temperature for the coolest and warmest month, respectively. HMR refers to the highest monthly rainfall on record and CV refers to coefficent of variation as a percentage.

| Location | n | Decimal degree Latitude | Longitude | Annual rainfall (mm) Decile 1 | Median | Mean (CV) | Decile 9 | HMR | Temperature (°C) Min | Max |
|---|---|---|---|---|---|---|---|---|---|---|
| Wave Hill | 27 | 17.39 | 131.12 | 447 | 654 | 678 (35) | 894 | 454 | 10.7 | 38.7 |
| Elliott | 39 | 17.56 | 133.54 | 316 | 538 | 586 (36) | 872 | 623 | 11.1 | 39.4 |
| Tennant Creek | 27 | 19.64 | 134.18 | 214 | 401 | 451 (37) | 804 | 360 | 12.2 | 37.0 |
| Rabbit Flat | 29 | 20.18 | 129.95 | 187 | 417 - | 429 (39) | 757 | 417 | 6.5 | 38.5 |
| Barrow Creek | 120 | 21.53 | 133.89 | 134 | 281 | 341 (48) | 532 | 454 | 8.2 | 37.0 |
| Yuendumu | 48 | 22.25 | 131.80 | 174 | 346 | 361 (53) | 584 | 561 | | |
| Alice Springs | 59 | 23.81 | 133.88 | 120 | 237 | 285 (51) | 463 | 356 | 4.1 | 36.1 |

**Table 4.3** The correlation among latitude, longitude, elevation, mean annual rainfall, cumulative rainfall in the previous 24 months, rainfall deviation from the mean for 24 months and mean annual maximum and minimum temperature. The correlation analysis used data obtained for each of the 227 plots.

| | Mean annual temperature maximum | minimum | Mean annual rainfall | Elevation | Cumulative rainfall 24mth | Rainfall deviance 24 mth | Distance to recent fire |
|---|---|---|---|---|---|---|---|
| temperature (max) | 1 | | | | | | |
| temperature (min) | 0.75 | 1 | | | | | |
| mean annual rainfall | 0.89 | 0.71 | 1 | | | | |
| digital elevation | -0.83 | -0.87 | -0.73 | 1 | | | |
| latitude | -0.91 | -0.87 | -0.95 | 0.83 | -0.93 | -0.64 | 0.44 |
| longitude | 0.44 | 0.78 | 0.40 | -0.75 | 0.51 | 0.22 | -0.22 |

from 200 m to 545 m (**Table 4.4**) and the southern part of the study area was more elevated than the north. Consequently, there was a strong positive correlation of the plot elevation with latitude (r=0.86) and a weaker negative correlation with longitude (r=-0.75) (**Table 4.3**).

There was also a pronounced north-south rainfall gradient in the study area (**Fig. 4.2c**). Rainfall on the northern edge of the Tanami Desert ranged from 654 mm at Wave Hill and 586 mm at Elliot, to 361 mm at Yuendumu near the southern edge (**Table 4.2**). Spatial data indicated a strong negative correlation with latitude (r=-0.95) and a weak positive correlation with longitude (r=0.40) (**Table 4.3**). The correlation of temperature and rainfall with longitude was largely the result of the plots being skewed diagonally across the study area with those in the north-eastern corner having greater values than those in the south-western corner. The actual rainfall values were more extreme than that derived from the spatial data (**Table 4.4**).

Similarly, there was a pronounced temperature gradient in the study area with both minimum (**Fig. 4.2d**) and maximum temperatures declining from north to south. The mean daily maximum temperature during the hottest month (November in the north and January in the south) was around 39$^{O}$C recorded at Wave Hill and Elliott on the northern edge of the Tanami Desert compared to around 36 $^{O}$C at localities in the south and, similarly, the mean daily minimum temperature during the coldest month (July) in the north was 11.1 $^{O}$C at Elliott and 4.1 $^{O}$C in the south at Alice Springs (Bureau of Metereological records) (**Table 4.2**). Like the rainfall data, these values were more extreme by about 3 $^{O}$C than the mean monthly maximum temperatures derived from the spatially derived data (**Table 4.4**). The minimum and maximum temperature derived from plot localities was negatively correlated with latitude (r=-0.87 and r=-0.91, respectively) (**Table 4.3**). Mean maximum temperatures showed a weaker correlation with longitude than minimum temperature (r=-0.44 and r=-0.78, respectively) and mean maximum and mean minimum annual temperatures (r=0.75) were not strongly correlated because minimum temperatures were more extreme than maximum temperatures in the southern part of the study area. Elevation was also negatively correlated with maximum (r=-0.83) and minimum (r=-0.87) temperature.

### *Substrate pattern*

Pastoral leases occurred mostly in association with rock feature and black soil substrates on the northern and eastern edge of the study area. Within the remainder (core) of the study area, sand plain and dune field substrates were dominant and accounted for 82% of the area (**Table 4.5**). Substrates identified as having slightly better productivity including the laterite and rock feature substrates accounted for 9.6% and the drainage line and calcrete

**Table 4.4** The landscape variables derived from remotely-sensed data for each sample plot (n=227).

| | Unit | Abbreviation | Mean or (Count) | St Error | Median | Minimum | Maximum |
|---|---|---|---|---|---|---|---|
| *Static parameters* | | | | | | | |
| Gradient | | | | | | | |
| Mean annual rainfall | mm | meanrain | 339.9 | 5.1 | 341.0 | 231.2 | 537.6 |
| Maximum temp Jan | degreeC | maxtemp | 33.2 | 0.1 | 33.4 | 31.4 | 34.6 |
| Minimum temp Jan | degreeC | mintemp | 17.6 | 0.1 | 17.2 | 16.2 | 19.6 |
| Altitude | m | DEM | 371.2 | 5.3 | 374.2 | 200.1 | 544.7 |
| Substrate category | calcrete | c | (26) | | | | |
| | drainage | d | (26) | | | | |
| | laterite | l | (27) | | | | |
| | rock features | rf | (11) | | | | |
| | sand plain/dune | s | (137) | | | | |
| Substrate minimum distance (km) from plot to substrate edge | calcrete | c-dist | 19.5 | 2.1 | 7.9 | 0 | 174.6 |
| | drainage | d-dist | 12.6 | 1.3 | 5.2 | 0 | 93.1 |
| | laterite | l-dsit | 12.7 | 0.8 | 8.5 | 0 | 55.1 |
| | rock features | rf-dist | 9.1 | 0.6 | 6.6 | 0 | 47.5 |
| | sand plain/dune | s-dist | 0.3 | 0.1 | 0 | 0 | 3.5 |
| Substrate neighbourhood number of substrates within radius | 1 km | snbr 1 | 1.5 | 0.1 | 1 | 1 | 4 |
| | 2.5 km | snbr2.5 | 2.0 | 0.1 | 2 | 1 | 5 |
| | 5 km | snbr5 | 2.7 | 0.1 | 3 | 1 | 5 |
| | 10 km | snbr10 | 3.5 | 0.1 | 4 | 1 | 6 |
| | 25 km | snbr25 | 4.6 | 0.1 | 5 | 1 | 6 |
| *Dynamic parameters* | | | | | | | |
| Rainfall | | | | | | | |
| Cumulative rainfall (mm) prior to sampling | 3 months | r3mths | 154.5 | 8.6 | 128.3 | 2.8 | 445.3 |
| | 6 months | r6mths | 282.7 | 8.7 | 290.3 | 9.3 | 476.8 |
| | 12 months | r12mths | 343.4 | 9.6 | 345.6 | 29.4 | 762.3 |
| | 24 months | r24mths | 628.7 | 15.6 | 641.8 | 106.4 | 1079.7 |
| Rainfall deviation (mm) | | | | | | | |
| 12 mth rain dev. from avg ann. rainfall | | rdev12m | -71.6 | 8.2 | -89.7 | -298.5 | 297.3 |
| 24 mth rain dev from 2 x avg ann. rainfall | | rdev24m | -201.3 | 8.9 | -215.7 | -555.5 | 54.2 |
| Fire age category | recent (<2ys) | rec-f | (51) | | | | |
| | interm (2-6yrs) | int-f | (65) | | | | |
| | old (>6yrs) | old-f | (65) | | | | |
| Fire min. distance (km) from plot to fire edge | 1 yr | 1yr f-dist | 26.4 | 2.4 | 11.1 | 0 | 300 |
| | 2 yr | 2yr f-dist | 29.6 | 3.3 | 5.3 | 0 | 148.6 |
| | 1+2 yr | rec f-dist | 16.2 | 1.9 | 2.6 | 0 | 148.6 |
| Fire age | years | fage | 8.32 | 0.40 | 5 | 1 | 16 |
| Fire neighbourhood number of fire ages within radius | 1 km | fnbr 1 | 1.26 | 0.03 | 1 | 1 | 3 |
| | 2.5 km | fnbr2.5 | 1.89 | 0.05 | 2 | 1 | 4 |
| | 5 km | fnbr5 | 2.51 | 0.07 | 2 | 1 | 5 |
| | 10 km | fnbr10 | 3.43 | 0.09 | 3 | 1 | 7 |
| | 25 km | fnbr25 | 4.92 | 0.11 | 5 | 1 | 8 |

substrates accounted for 7.7% of the core study area. The drainage line and calcrete substrates were approximately equal in extent in each latitudinal band except the northern latitude where both were largely absent. The drainage lines were linear in nature unlike the laterite and rock feature substrate (**Fig. 4.3a**). Overall, the distribution of substrate types in the Tanami Desert broadly reflected the mosaic pattern of areas with different water and nutrient supplies described by Stafford Smith and Morton (1990) and the relative scarcity of substrates identified as most productive.

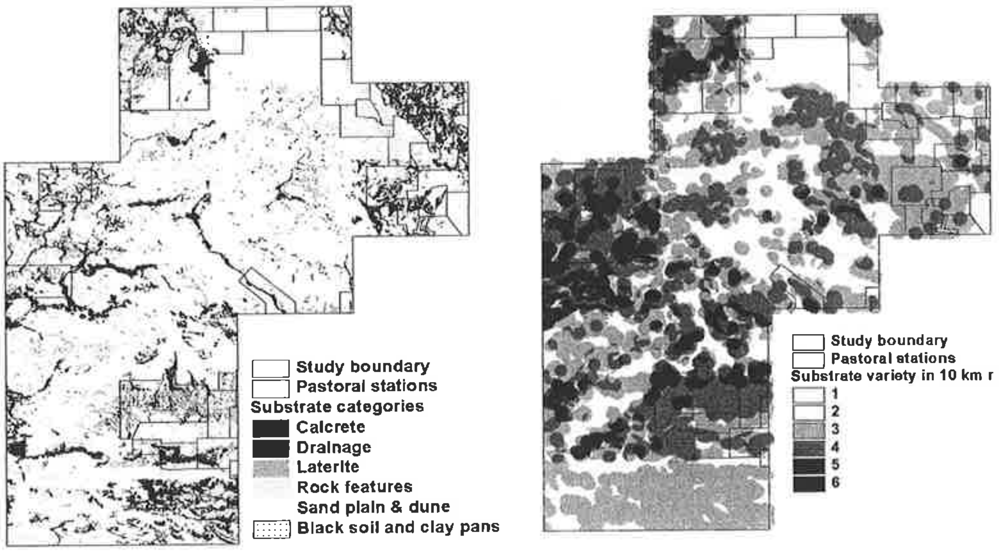
The most heterogeneous region was in the central western part where drainage/calcrete, laterite/rock feature and sand plain/dune field substrates were distributed in a fine-grain mosaic compared to other parts of the landscape. Areas with six substrates in close proximity became conspicuous when the radius of inclusion was extended to around 10 km or more. The lateritic/rock feature and the fluvial substrates were often in close proximity (**Fig. 4.3b**). Calcrete occurred more commonly in the southern part of the study area and sample plot distance to calcrete was negatively correlated with latitude ($r=-0.66$).

### *Vegetation and fire pattern*

Vegetation ground cover was greater in the northern part of the study area and declined in response to greater aridity toward the south. Spinifex was present at 98% of plots ($n=227$) and dominant at 90%. In long-unburnt patches, the cover of spinifex was low on the northern edge and non-spinifex grasses contributed to most cover. In the southern part of the study area, spinifex was the dominant form of ground vegetation but cover declined as plants became smaller and more sparsely distributed. Hence, there was a curvilinear relationship between spinifex cover and latitude (**Fig. 4.4a**). Shrub and tree cover was correlated with latitude, being sparse in the south and central parts of the study area and greatest on the northern edge in association with higher rainfall. Spinifex and shrub and tree cover changed little in association with longitude (**Fig. 4.4b**). The high variance tree and shrub cover was indicative of the greater shrub cover that occurred in relation to paleo-drainage lines in the south and central parts of the study area.

**Table 4.5** The extent of substrate types within the study area.

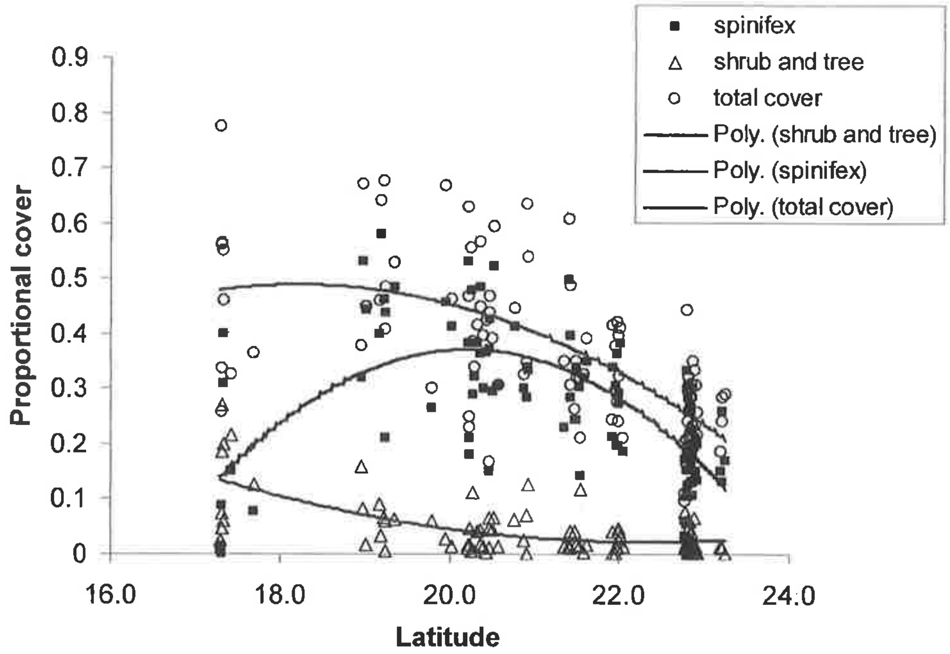
| Substrate type | Entire study area (km$^2$) | % | Core (mainly non-pastoral) study area (km$^2$) | % |
|---|---|---|---|---|
| calcrete | 5 316 | 1.7 | 4 533 | 1.9 |
| drainage | 18 759 | 6.0 | 13 842 | 5.8 |
| laterite | 16 132 | 5.2 | 9 851 | 4.2 |
| rock features | 28 167 | 9.0 | 12 875 | 5.4 |
| sand plain & dune | 234 037 | 74.9 | 194 840 | 82.3 |
| lakes & black soil | 10 122 | 3.2 | 868 | 0.4 |
| total area | 312 533 | 100 | 236 809 | 100 |


(a)

(b)

**Fig. 4.3** (a) Distribution of substrate classes based on geological mapping
(b) Substrate neighbourhood variety within a 10 km radius. '1' denotes a single substrate type and '6' denotes eight different substrate types.

(a)



(b)

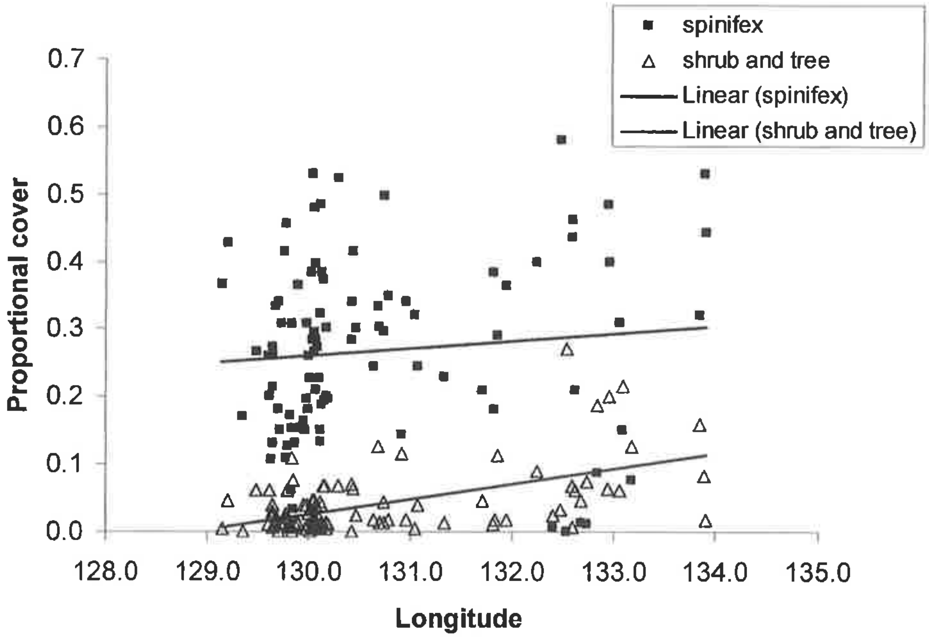


**Fig. 4.4** Spinifex, non-spinifex ground cover and shrub cover in relation to (a) latitude and (b) longitude in the Tanami Desert. The data used were from long unburnt (>13 years) sample plots.

According to fire mapping data, the area burnt each year varied considerably. In 1995/96, less than 0.2% of the study area was burnt, with 1.7% burnt in 1996/97 and 1997/98 (**Table 4.6**). In contrast, a series of fires in 1994/95 burnt 20.6% of the study area and most of the area in the intermediate category shown in **Fig. 4.5a** was the result of these fires. These fires followed exceptional rainfall in 1992/3. The greatest heterogeneity of fire ages occurred on the central western part of the study area where up to eight fire ages were recorded within a 10 km radius (**Fig. 4.5b**).

Fires did not burn uniformly through the landscape. Firstly, fires occur more frequently in the northern Tanami Desert than the south during periods of non-exceptional rainfall. Secondly, proportionally more sand plain substrate was burnt compared to other substrate types using data for the years 1995-1998 (**Table 4.6**). Salt pan/other, drainage and calcrete substrates were under-represented suggesting the lack of vegetation or possibly the vegetation type inhibited the spread of fire. The difference between the observed and expected amount of substrate burnt was less extreme for laterite and rock feature substrates. The salt pan/other category did include black soil plains and hence burnt habitat could be registered on this substrate category.

*Accuracy of spatial data*

The overall ability of the mapping to correctly classify substrate units on the ground (i.e. user's accuracy) was 87% and best for drainage and calcrete (**Table 4.7**). The least accurately mapped unit was sand plain where 84% of the units were correct and several areas classified as drainage should have been classified as sand plain. Poor matching of geological units between adjacent sheets occurred in three of the 18 map sheets and the worst compliance occurred between the Tennant Creek and adjacent map-sheets. The extent of non-complying geological units reduced when geological units were merged to form substrate classes.

A comparison of vegetation mapping and field data indicated that the spinifex (hummock) grasslands were mapped accurately but the vegetation types designated as non-spinifex understorey also contained spinifex (**Table 4.8**). Similarly, the mapping of *Melaleuca* *glomerata* was accurate but this species also occurred at a large proportion of plots mapped as other cover. *Melaleuca glomerata* occurred on 58% of the plots with substrate mapped as drainage and 35% of those mapped as calcrete. No *Melaleuca* spp. occurred on plots with substrate mapped as laterite or rock feature but 12% of plots mapped as sand plain or dune field contained the species.

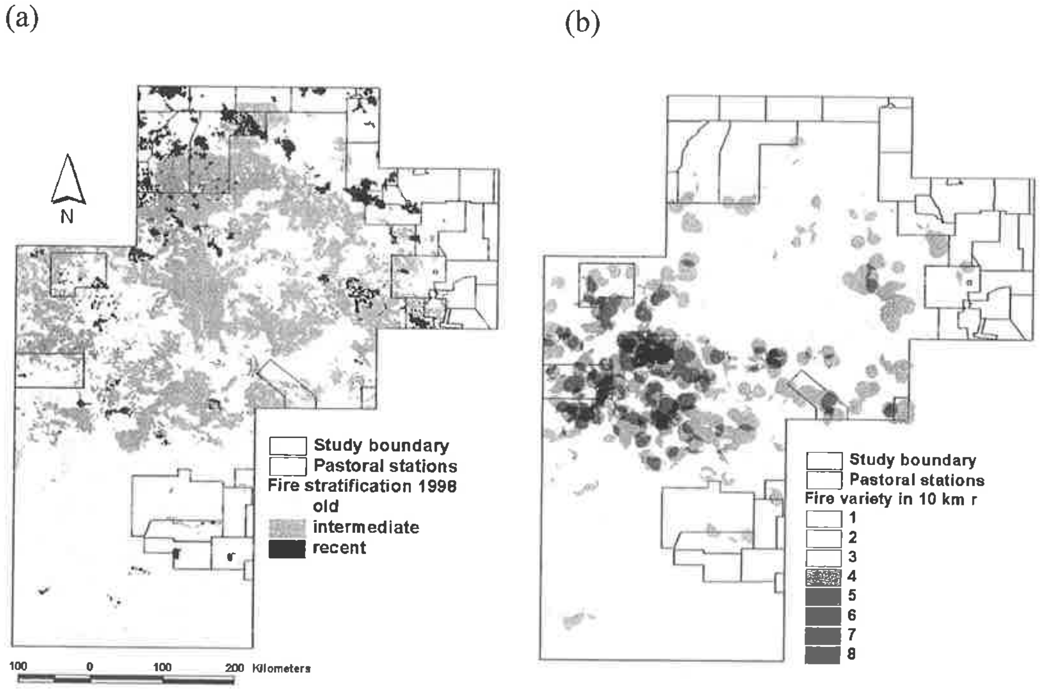


**Fig. 4.5** (a) Fire stratification for 1998. The dark shading represents 'recent' fire 1-2 years old, darker tone represents 'intermediate' fire 3-6 years old and lightest tone represents 'old' fire (> 6 years).
(b) The variety of fire ages within a 10 km radius prior to 1998. '1' denotes a single fire age and '8' denotes eight different fire ages.

**Table 4.6** Amount of burnt habitat in the study area core in relation to substrate type for the years 1995 to 1998. The percentage difference (diff. %) was calculated using the difference between observed substrate burnt and expected substrate burnt divided by the expected. Significance levels for Chi-squared test are *<0.05, **<0.01 and ***<0.001.

| | | 1994/95 | | 1995/96 | | 1996/97 | | 1997/98 | |
|---|---|---|---|---|---|---|---|---|---|
| | Burnt | 20.6% | | 0.2% | | 1.7% | | 1.7% | |
| Substrate | Cells | diff. % | chi sq. | diff. % | chi sq. | diff. % | chi sq. | diff. | chi sq. |
| sand plain | 675089 | 4 | *** | 15 | * | 5 | *** | 5 | *** |
| calcrete | 15821 | -40 | *** | -100 | *** | -83 | *** | -18 | ** |
| drainage | 48209 | -27 | *** | -100 | *** | -25 | *** | -50 | *** |
| laterite | 34165 | -9 | *** | -99 | *** | 14 | *** | -20 | *** |
| rock feature | 44776 | -5 | *** | -4 | ns | -27 | *** | 13 | *** |
| salt pan/other | 3032 | -98 | *** | -100 | ** | 11 | ns | -100 | *** |
| Total | 821092 | | | | | | | | |

**Table 4.7** Error matrix for the reference data (field observation) versus a mapped classification (vector) of substrate categories.

| | Ground referenced substrate class | | | | | | |
|---|---|---|---|---|---|---|---|
| Mapped class | sand plain | sand dune | drainage line | calcrete | laterite/ rock feature | *sum* | field accuracy |
| sand plain | 77 | 4 | 6 | | 5 | 92 | 84% |
| sand dune | 1 | 31 | 1 | 3 | | 36 | 86% |
| drainage line | 1 | 1 | 28 | | | 30 | 93% |
| calcrete | | | 2 | 23 | | 25 | 92% |
| laterite/rock feature | 4 | 1 | | | 38 | 43 | 88% |
| *sum* | 83 | 37 | 37 | 26 | 43 | 226 | (87%) |

**Table 4.8** Error matrix for the ground reference data (ground-truthed field observation) versus mapping classification (vegmap) for spinifex *Triodia* spp. and *Melaleuca* spp.

| | | Ground referenced vegetation class | | | | Field |
|---|---|---|---|---|---|---|
| | | spinifex | non-spinifex | *Melaleuca* | non-*Melaleuca* | acurracy |
| Mapped vegetation class | Spinifex | 203 | 4 | | | 98% |
| | non-spinifex | 20 | 0 | | | 0% |
| | *Melaleuca* | | | 13 | 1 | 93% |
| | non-*Melaleuca* | | | 36 | 177 | 83% |

Based on sample plot data, the overall accuracy of the fire mapping produced by the fire history mapping was 91% (**Table 4.9**). The ability of the mapping to correctly classify units on the ground was similar (89-92%) among fire age categories. The greater extent and frequency of fire in the northern part of the study area resulted in distance-to-recent fire parameter having some correlation with latitude (r=0.44) (**Table 4.3**).

## Discussion

The credibility and adequacy of the largely dimensionless Stafford Smith- Morton model can only be assessed using subjective judgement and within the context of a likely application. The question is whether the ecological model assists in identifying a set of useful environmental variables and gradients for predicting species distribution. A model may be interpreted as less adequate because the key predictors are difficult to represent as accurate spatial data (Austin 2002). Alternatively, key predictors may have to be omitted in an attempt to increase model reality at the expense of generality at a broader spatial scale.

Austin (1980, 2002) suggested that there were three kinds of gradients: direct, resource and indirect. The Stafford Smith - Morton model makes use of variables from indirect gradients (eg. geology, topographic position, slope) and resource gradients (eg. nutrients, water) to propose a pattern for organism distribution based on plausible and causal relations. Direct gradients (e.g. temperature, rainfall) are largely omitted. Guisan and Zimmerman (2000) note that the drawback in using indirect variables is that they can only be applied in a limited geographic context without significant errors, because in a different

**Table 4.9** Error matrix for the reference data (field observation) versus mapping classification (minimum pixel size approximately 1 km) for fire age category.

| | | Ground referenced fire age class | | | | |
|---|---|---|---|---|---|---|
| | | recent<br>< 2 yrs | intermediate<br>3-6 yrs | old<br>>6 yrs | *sum* | field accuracy |
| mapped fire age class | recent | 50 | 2 | 4 | 56 | 89% |
| | intermediate | 1 | 48 | 3 | 52 | 92% |
| | old | 5 | 5 | 105 | 115 | 91% |
| | *sum* | 56 | 55 | 112 | 223 | (91%) |

region the same topographic position can reveal a different combination of direct and resource gradients. This may be the greatest limitation in the Stafford Smith – Morton model which purports to identify the key elements of ecosystem functioning within 70% of the Australian continent.

*Climate*

Stafford Smith and Morton (1990) suggested that the spatial and temporal unpredictability of rainfall was the principal driving force controlling ecological function in Australian deserts. This reflects the pulse-response model proposed by Westoby (1980) and emphasises the importance of the abiotic variables in shaping biotic interactions in arid environments. Rainfall variability is clearly an extremely important feature driving the major biotic changes in the arid zone of Australia (Griffin and Friedel 1985; Paltridge and Southgate 2001; Predavec 1994; Southgate and Masters 1996) and other arid landscapes (Jaksic 2001; Louw and Seeley 1982; Westoby 1980). However, a number of other studies have also described the importance of a gradient in heat and moisture in controlling biological diversity in Australia (Austin *et al.* 1996; Mackey *et al.* 2002; Nix 1982) and this was not discussed by Stafford Smith and Morton (1990).

Within the Tanami Desert there was a strong north-south rainfall gradient with aridity and variability of rainfall increasing with distance from the northern coastline. The temperature gradient followed the same trend, with slightly cooler summer and much cooler winter temperatures influenced by the greater elevation in the southern part of the study area. Rainfall and temperature combined to produce a strong humidity and climatic discomfort gradient in the study area. Relative humidity in the southern part of the study area at 9 am is generally around 30% in the south and over 60% in the north and, in terms of human climatic discomfort, 150-200 days per year occur in the north of the study area compared to 50-100 in the south (Cols and Whitaker 2001). This feature is of significance because the conditions of high humidity and high temperature place great stress on medium to large homeothermic animals in situations where drinking water is scarce (Schmidt-Nielsen 1997). The distribution and prevalence of introduced herbivore and predators, (Southgate *et al.* in press) and a threatened species (Southgate *et al.* submitted) were also associated strongly with climatic variables in the region. Associated with the climatic gradient was a marked change in shrub and tree cover and total ground cover from low woodland communities in the north to sparse shrublands in the south. The northern part includes tree and shrub species that are subtropical such as Bauhinia (*Lysiphyllum caronnii*), lancewood (*A. shirleyi*) and bullwaddy (*Macropteranthes kekwickii*) (Woinarski and Fisher 1995). In the south there are discontinuous communities that can include mulga (*A. aneura*) and areas of scattered desert oak (*Allocasuarina decaisneana*) (Harrington *et al.* 1984).

The high temporal and spatial variability of rainfall described by Stafford Smith and Morton (1990) was certainly a feature within the Tanami Desert. The analysis of the BOM monthly splined rainfall data indicated that irregular large rainfall events could at times affect areas of tens of thousands of square kilometers. Periods of severe rainfall deficits could affect similarly large areas as was observed during the study. However, while such events did affect the abundance of native and introduced predator and herbivore species and cause the death of spinifex in some areas, populations were not eliminated and responded quickly to follow-up rain (Paltridge and Southgate 2001; Southgate, unpublished).

### *Substrate*

The general pattern of substrate distribution outlined in the Stafford Smith – Morton model was largely reflected in the Tanami Desert study area. Larger areas of substrate identified as more fertile (cracking clays, calcareous earths or the foothills in range country) occurred on the northern and eastern edge of the study area and this was being used for pastoralism. Within the remaining (core) area, 82% was sand plain and dune field and the more fertile substrates were of insufficient extent to support a typical pastoral station except in a few parts. Drainage systems and calcrete substrates formed about 8% and laterite and skeletal soils accounted for about 10%.

The more prominent drainage systems include large salt lakes, saline channels and caliche areas and calcrete were identified by Stafford Smith and Morton (1990) as not necessarily the most fertile substrates but areas with reliable production because of the greater availability of water as a result of the scale of recharge. Less saline water may occur in lenses along the margins of these systems. Foulkes *et al.* (1995) found that nutrient gradients do occur across paleodrainage lines in areas of the Tanami Desert but there was no clear trend with soil moisture levels. This possibly resulted because localities examined did not extend sufficiently beyond the edge of the paleodrainage lines into the surrounding sand plain. More extensive areas of calcrete substrate occurred in the southern part of the study area and these areas generally contained vegetation with similar composition (eg. *Melaleuca*) and structural characteristics compared with that found on drainage substrate.

*Fire and substrate heterogeneity*

Fire is recognised as an important driving force in the Stafford Smith – Morton model. The pattern of fire in the Tanami Desert indicates the interplay of rainfall gradient, episodic rainfall events and substrate in plant production and highlights another potentially important predictor omitted by Stafford Smith and Morton (1990). While big fires in the Tanami Desert tended to follow big rains, as elsewhere in central Australia (Griffin and Friedel 1985), the frequency of fires was still greater in the northern parts. Secondly, following exceptional rainfall there are sizable areas that escape being burnt. This is not surprising because a variety of other factors are likely to affect the source and extent of fire spread including substrate type. The low proportion of fluvial surfaces burnt compared to sand plain is consistent with the notion that saline, calcareous and drainage lines tend to act as natural fire breaks. High fire heterogeneity therefore tends to reflect substrate heterogeneity in systems where there is little influence of anthropogenic fire management. This aspect of the physical environment and its likely influence on plant and animal assemblages was also not considered in the Stafford Smith - Morton model. The issue is potentially significant because areas of high substrate and/or topographic heterogeneity provide inherent reliability of resources and protection from some forms of disturbance, acting as significant points of refugia and for species radiation. The heterogeneity of substrate in the Tanami Desert was not uniform, there were large sections of high substrate variety (western Granites latitude) and low variety (eastern the Newcastle Waters latitude) within an equivalent area.

*Accuracy*

Spatial data representing fire and substrate pattern showed approximately 90% accuracy when compared to field data collected at scales that are considered appropriate for the on-ground assessment of flora and fauna. The accuracy of the fire history compiled using NOAA satellite imagery was reasonable despite the large (1 km) pixel. This accuracy was probably improved because the boundary of a mapped fire age was avoided when the location of a plot was selected. Satellite imagery with a smaller pixel size and more frequent compilation would improve the information produced by the fire history mapping. The delineation of vegetation units in 1:1M vegetation mapping (Wilson *et al.* 1990) was found to be less useful in defining areas indicative of higher productivity than the substrate categories derived from geological mapping. This was probably a reflection of the geology mapping being compiled at a finer resolution than the vegetation mapping. The general accuracy of the existing spatial data provide the opportunity to evaluate some of the broad scale hypotheses about the ecology of arid Australia put forward by Stafford Smith and Morton (1990).

## Conclusions

In the Tanami Desert there is clear delineation of some vegetation communities associated with substrate type that indicate the scarcity of productive areas as suggested in the Stafford Smith – Morton model. However, there is also a distinct gradient in vegetation composition and cover that is associated strongly with the rainfall gradient. Clearly, both the climatic gradient and substrate distribution affect the composition and structure of vegetation in the Tanami Desert and both would most likely influence the pattern of higher order consumers. A similar climatic gradient is evident in the Great Sandy Desert in Western Australia (Cols and Whitaker 2001), hence the Tanami Desert is not atypical. Furthermore, the spatial databases used to form these conclusions were found to be relatively accurate and unlikely to have provided spurious patterns.

The omission of direct predictors such as the gradient of temperature and rainfall makes the Stafford Smith – Morton model less adequate to direct the selection of predictor variables than it could otherwise have been. The spatial interpolation of temperature and rainfall is generally considered reasonably accurate (Guisan and Zimmerman 2000).

Models based on resource and direct gradients also tend to be more robust and widely applicable (Austin 2002) and the inclusion of direct gradients may also improve the ability of the ecological model to expose ideas and concepts in relation to a climatically changeable future. This is not to say the Stafford Smith – Morton model does not provide a valuable framework to examine many aspects of the ecology of inland Australia. It is just that its usefulness for applications that require detailed regional understanding or spatial modelling of species' distributions may be limited. Further testing of propositions in the framework with empirical data is needed before the nature and extent of deficiencies can be assessed thoroughly and refinements recommended.

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**Appendix 4.1** The selection process used to define substrate categories from the geological map unit information supplied with the Australian Geological Survey Office 1:250000 geological maps

calcrete: map symbol ='Tt*' or 'Czt' or '–Cmm'
drainage: drain=1 or map symbol = 'Qa*' or 'Qb*' or 'Ql*'and not Tt*
laterite: map symbol ='Qr' or 'Tl*' or 'Qg*'
rock feature: not 'calcrete' and not 'drainage' and not 'laterite' and not 'sand & dune' and not 'salt lakes & black soil'
sand plain & dune: map symbol ='Qs' or 'Qz' or 'Czs' and drain=0
salt lakes & black soil: map symbol = 'Czb*' or 'Qe*'

# Chapter 5

## Modelling introduced predator and herbivore distribution in the Tanami Desert, Australia

*Preamble to Chapter 5*

In this chapter, I examine the pattern of introduced herbivore and predator distribution in the Tanami Desert and test a series of propositions put forward by Stafford Smith and Morton (1990) regarding the functioning of arid Australian environments. These authors proposed that introduced herbivore and predator species would be largely restricted to and reliant on productive refugia.

There was support for the proposition that introduced feral herbivores would be concentrated in the productive habitats but foxes and feral cats did not follow this pattern. Overall, the parameters reflecting the climatic gradient were the most important determinants of introduced species distribution in the Tanami Desert. Substrate-related variables or episodic variables such as fire age were of secondary importance at the scale considered. Furthermore, the variables that reflected episodic rainfall or periods of rainfall deviance did not form a significant component of the minimum adequate models for any of the species.

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## Introduction

Australia has at least 26 species of introduced animal that have established wild populations and become serious pests, causing extensive agricultural and environmental damage (Braysher, 1993). Introduced species such as the European rabbit *Oryctolagus cuniculus*, camel *Camelus dromaderius*, red fox *Vulpes vulpes* and feral cat *Felis catus* are now widely distributed throughout the arid zone and have been implicated in the decline and extinction of a suite of native species (Burbidge and McKenzie, 1989; Morton, 1990; Caughley and Sinclair, 1994; Short and Smith, 1994). Of the 71 species of terrestrial mammal from the arid zone, 11 have become extinct and 20 have declined dramatically and are confined to offshore islands or restricted to the more temperate parts of their range (Burbidge *et al.*, 1997; Morton, 1990). All of the animals that have declined or become extinct are medium-sized and fall into a weight range of 35-5500 g (Burbidge and McKenzie, 1989). To explain the decline of threatened species, we first need to consider the degree of overlap between threatened species and potentially threatening agents such as competitors and predators (Caughley and Gunn, 1996). In the Tanami Desert, we examined the distribution and prevalence of three introduced herbivores and three introduced or naturalised predators thought to pose a threat to native species.

Stafford Smith and Morton (1990) suggested that patchy, subtle patterns in soil and the variability and episodic nature of rainfall primarily control the unique biotic structure in the vastness of the Australian arid zone. They point out that rainfall is very unpredictable with long irregular dry periods and occasional periods of exceptional rainfall and that soils are ancient and well sorted but 'islands' of slightly more fertile soils and reliable moisture occur within this 'sea' of infertility and unreliable conditions. They suggest that medium-sized native mammals and introduced herbivores would be restricted to the limited islands where plant production is more continuous, nutritious and digestible. However, there are also substantial rainfall and temperature gradients present within the Australian arid zone associated with latitude, distance from the coast and altitude (Nix, 1982; Southgate *et al.*, in press) and such gradients also have major influence on the structure and composition of plant and animal communities (Austin *et al.* 1996). Hence, it is plausible that a range of environmental variables with static, graded and episodic characteristics individually or interactively may shape the distribution of biota in the Australian arid regions.

Morton (1990) argued that the decline of medium-sized native mammal species in desert regions results from invading herbivores causing habitat degradation in these refugia. Stafford Smith and Morton (1990) went further and proposed that the paucity of nutrients has had a cascading effect throughout food-webs in the arid Australian landscape and that endothermic predators would also be more abundant and diverse in the richer environments. However, they made no specific predictions regarding the prevalence of higher order organisms in response to fire-age or in relation to other abiotic factors such as temperature and humidity that have been shown to influence the patterns of distribution and abundance of higher-order species (Begon *et al.*, 1996; Hall *et al.*, 1992). For example, apart from the dingoes and cattle, the introduced herbivores and predators discussed in our study are absent or in lower densities in the tropics (King and Smith, 1985; Dickman, 1996; Saunders *et al.*, 1995).

Our study investigated the pattern of distribution of the more common introduced and naturalised species to determine whether it agreed with the propositions of Stafford Smith and Morton (1990). Three hypotheses were derived to reflect the putative influences of the main environmental variables on the distribution of these species:

1. Introduced and naturalised predators and herbivores respond primarily to substrate productivity (static effects). Species prevalence is negative in areas with sand plain substrates and positive in areas with calcrete and drainage substrates.
2. Introduced and naturalised predators and herbivores respond to extreme surplus and deficit rainfall events (episodic effects). Species prevalence is negative in areas that experience a recent severe rainfall deficit and positive in areas that have received a recent rainfall surplus.
3. Introduced and naturalised predators and herbivores respond to climatic gradients (gradient effects). The prevalence of these species' will be negative in areas where ambient temperature and relative humidity are high and where drinking water is scarce, because of the high physiological demands to maintain water balance.

To test these hypotheses, we first derived models using habitat variables that were putatively responsible for the distribution of the introduced and naturalized predators and herbivores. These models were then compared with a global model that drew from all potentially relevant effects (Burnham and Anderson, 2002). Finally, we evaluated how well the most robust regression equations with static variables explained habitat occupancy based on independently collected data (Rykiel, 1996; Vaughan *et al.*, 2003).

## Methods

### *Study area*

The study area was in the Northern Territory and included most of the Tanami Desert bioregion. The characteristics of the study area have been described by Southgate *et al.* (in press). The area was defined by the bounding coordinates of 129 ° - 134 ° E and 17°-23.5 ° S. The pastoral leases on the northern, eastern and south-eastern edges were excluded, leaving a core area of approximately 236 800 km$^2$ (**Fig. 5.1**). This area was divided into four latitudinal zones of at least 170 km width and these were referred to as Newcastle Waters (17 ° -18.5 ° S), Tennant (18.5 ° -20 ° S), the Granites (20 ° -21.5 ° S) and Kintore (21.5 ° -23.5 ° S).

Summers in the Tanami Desert are very hot and winters are cold to mild. The mean daily maximum temperature during the hottest month in the northern part of the study area is 39.3 °C and 36.2 °C in the south. The mean daily minimum temperature during the coldest month (July) in the north is 11.3 °C and 4.1 °C in the south (Bureau of Metereological records). Freezing point temperatures can occasionally occur at night during the winter in the south. The rainfall gradient present in the study area ranged from an annual average of 600 mm on the northern boundary to about 300 mm in the south (**Table 5.1**).

### *Random plots*

Stratified random plots were sampled to provide information on the spatial distribution of species in relation to environmental variables. Track identification was the primary means used to identify the presence of feral cat, fox, dingo, rabbit, camel and cattle on a plot.

Using tracks to detect the occurrence of medium and large animals in desert regions of Australia and elsewhere is being more widely applied (Mahon *et al.*,1998; Edwards *et al.*, 2000; Paltridge and Southgate, 2001; Southgate *et al.*, 2005).

In total, 227 plots were stratified on the basis of fire history and substrate mapping. Geological mapping purchased from the Australian Geological Survey Organisation (AGSO) was used to derive the substrate categories at a resolution of about 0.2 km. Geological units were merged to produce six categories: calcareous (c), drainage features (d), laterite (l), rock (skeletal) features (r), sand plain and dune (s), and black soil and salt lakes (bsl) as described in detail by Southgate *et al.* (in press). The annual extent of fire 1984-1999 in the Tanami region was derived from the Central Australian fire history database (Allan and Southgate, 2002). The Tanami fire history for the period 1986 to 1999 was mapped from Advanced Very High Resolution Radiometer (AVHRR) National Oceanic and Atmospheric Administration (NOAA) satellite imagery with a resolution of approximately 1 km. Fire data were merged to produce three classifications: recently burnt (1-2 years old), intermediate (3-6 years old) and old (greater than 6 years old).

**Table 5.1** Rainfall information from Bureau of Meteorology stations within or surrounding the study area.

| | | Decimal degree | | Annual rainfall | | | | Monthly |
|---|---|---|---|---|---|---|---|---|
| Location | n | Latitude | Longitude | Decile 1 | Median | Mean | Decile 9 | Highest |
| Wave Hill | 27 | 17.38 | 131.11 | 447 | 654 | 678 | 894 | 454 |
| Elliott | 39 | 17.56 | 133.54 | 316 | 538 | 586 | 872 | 623 |
| Tennant Creek | 27 | 19.64 | 134.18 | 214 | 401 | 451 | 804 | 360 |
| Rabbit Flat | 29 | 20.19 | 130.02 | 187 | 417 | 429 | 757 | 417 |
| Barrow Creek | 120 | 21.53 | 133.89 | 134 | 281 | 341 | 532 | 454 |
| Yuendumu | 48 | 22.25 | 131.80 | 174 | 346 | 361 | 584 | 561 |
| Alice Springs | 59 | 23.79 | 133.89 | 120 | 237 | 285 | 463 | 356 |
| Nyirripi | | 22.60 | 130.40 | | | 322 | | |

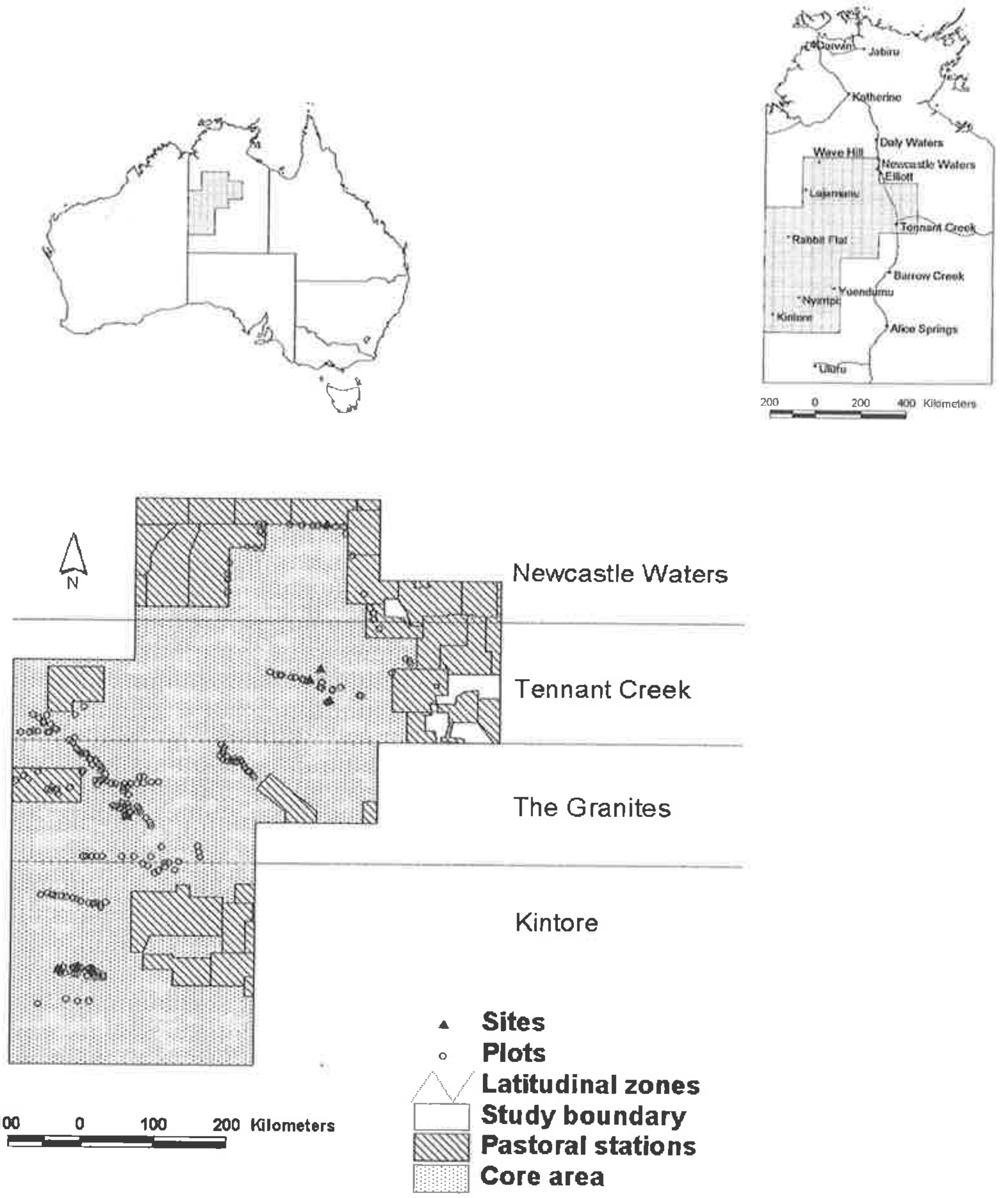

**Fig. 5.1** Location of the study area, pastoral leases, latitudinal zones and the location of random plots, ground truth plots and fixed transects.

At least 10 plots were located in each stratification except the salt pan and black earth substrate class. Each random plot was separated by at least 4 km and did not straddle tracks or roadways because of the propensity of some species to use these as thoroughfares (Mahon *et al.*,1998). The combination of fire history layers used to create this classification was adjusted depending on the year a particular site was sampled. The geographic coordinates of the selected plots were identified in the laboratory and a Geographic Positioning System (GPS) was used to find the locality in the field (**Fig. 5.1**). A random plot was visited once and at each plot, a search for animal tracks was made over a 300x200m quadrat by one person for one hour. Animal species were recorded (with assistance from Aboriginal trackers) as either present or absent based on the identification of prints less than approximately 3 nights old. This age limit was set because sign from larger animals persists for longer periods (Southgate *et al.*, 2005).

At each plot, a 300 point vegetation transect was used to determine vegetation cover as described by Southgate *et al.* (in press). Plots in the Granites and Kintore latitude were sampled mainly in the period May 1996 to June 1997, while sampling in the northern latitudes continued until April 1998.

*Transects*

Transects were monitored at eight sites repeatedly over three years and provided comparative data on the prevalence of species in relation to latitude and two substrate types. Three sites spaced about 25 km apart were located in both the Kintore and Tennant Creek latitudes, and one site was located in the Granites and Newcastle Waters latitude (**Fig. 5.1**). There were two transects located about 5 km apart at each site, one on sand plain/dune and the other on drainage/calcrete. Newcastle Waters lacked drainage substrate, and thus had two sand plain transects. Each transect was 10 km long (4x1 km rectangle) and, in most cases, sampled on three consecutive mornings every four months between March 1996 to December 1998. The transects were examined generally 0.5-3 hours after sunrise while travelling on a 4wd All Terrain Vehicle (ATV) at about 10 km hr$^{-1}$. The surface of each transect was prepared prior to the first day of sampling and on consecutive days by dragging an iron post and chain behind the ATV. A strip width of about 1.4 m was prepared. For the purpose of this study, we present data on the occurrence of given species per sample period. More detail on the relative abundance of predator species on some of these transects is presented by Paltridge and Southgate (2001).

### *Evaluation plots*

Data on the occurrence of introduced herbivores and predators were collected along the flight-path of an aerial survey of bilby sign (Southgate *et al.*, 2005). These occurrence data were used to evaluate the occupancy models derived from random/opportunistic plot data. Each evaluation plot was 300 x 100m with the long edge aligned parallel to the roadway. Parts of the Granites and Tennant Creek latitude were sampled in May 1999 and the parts of Newcastle Waters latitude were sampled in September 1999. No sampling was conducted at the Kintore latitude. In total, 75 evaluation plots were sampled.

### *Climatic data*

The mean annual rainfall, mean minimum temperature and the mean maximum temperature for the study area were derived from the Australian Natural Resource Data library. This splined data surface was a spatial grid of 0.05° (roughly 5 km resolution) derived from data for the period January 1980-December 1999. The digital elevation model, originally calculated at a 0.025° resolution, was also obtained from the Australian Natural Resource Data library.

Monthly gridded rainfall data for the study region were obtained from the Bureau of Meteorology (BOM). These data were provided as a spatial grid at 0.25° resolution (roughly 25 km) and were derived using the Barnes successive correlation technique that links designated weather stations across Australia (Jones and Weymouth, 1997). Rain-years (August-July) were used instead of calendar years to correspond with mapped fire history. The coordinates of each plot or fixed site were intersected with the gridded rainfall data set and this was used to derive antecedent cumulative data and other variables relating to rainfall for a particular locality. During the study, below average rainfall occurred at the fixed sites in each latitude (**Table 5.2**). Close to average rainfall occurred at the Granites, Tennant Creek and Newcastle Waters fixed sites in the three years prior to the study but only 70-80% of the mean was received during the study. At the Kintore sites, below average rainfall (72% of mean) occurred in the three years prior to the study and less (51%) was received during the study. In 1995/6, only 71 mm occurred which was the lowest in the 28 year sample period.

*Analysis*

Generalised linear modelling (GLM) was used in the analysis. For each introduced herbivore and predator species we used presence/absence data as the response variable with a logit link function in the model formulation. The summed presence/absence score for the three introduced predator species recorded at a plot was also used as a response variable and, in this instance, a gaussian link function was used in the model formulation. In each instance, the logistic models were developed using a forward stepwise variable selection procedure (Nicholls, 1991; Pearce and Ferrier, 2000). In the process, only variables that related significantly ($p<0.05$) to the response were considered. After the completion of the stepwise process, the models were examined for interaction among variables and whether the variables expressed as a second degree polynomial significantly increased explanatory power. If there was little difference in power among variables, those that made ecological sense were retained (Mackey and Lindenmayer, 2001; Austin, 2002).

**Table 5.2** Rainfall during specific periods for the fixed sites (or an average of two adjacent fixed sites) from the splined rainfall coverage. Values in parentheses are percentage of the mean (1970-1997). The values for 1992/3, 1983/4 and 1981/2 relate to periods just prior to large fires in parts of the Tanami Desert.

| Latitude (Site) | 3 years prior to study 92/3-95/6 | 3 years during study 95/6-97/8 | 1992/3 | 1983/4 | 1981/2 |
|---|---|---|---|---|---|
| Newcastle Waters (N1) | 565 (95%) | 472 (80% ) | 639 | 762 | 724 |
| Tennant Creek (T1/T3) | 474 (102%) | 371 (80% ) | 650 | 540 | 633 |
| The Granites (S1) | 381 (96%) | 278 (70%) | 511 | 337 | 732 |
| Kintore (K1/K3) | 237 (72%) | 170 (51%) | 314 | 320 | 579 |

With GLMs, deviance reduction can be converted into an estimated $D^2$ (the equivalent of $R^2$ in least squares regression). An adjusted $D^2$ may be used as a measure to compare models with different combinations of variables and interaction terms (Guisan and Zimmerman, 2000) and calculated by the following equation: adjusted $D^2 = 1-((n-1)/(n-p)) * (1- D^2)$ where $D^2$ = (null deviance-residual deviance)/null deviance, p = the number of parameters and n= the number of observations. The relative support for models can also be assessed using the Akaike Information Criterion (AIC) and Akaike weights (Burnham and Anderson 2002). The model with the largest Akaike weight is considered the best out of the set of models considered.

Candidate models were derived using explanatory variables that reflected each hypothesis. The substrate model considered only variables that described substrate type at a plot, distance to a particular substrate type from a plot and richness of substrate variables within the vicinity of a plot. The episodic model considered only the variables that described antecedent and deficit rainfall and the fire pattern at the time of sampling. The climatic gradient model considered variables that reflected the climatic gradient in the study area including average rainfall, temperature and altitude. The strength of each of these models was compared with a minimum adequate model (or full model) which selected from the entire set (substrate, episodic and gradient) of variables. A static model was derived from only substrate and gradient variables if the full model contained episodic variables. This particular model was use to map the probability of occurrence of a species.

Raster (grid) layers of the temperature, annual rainfall, elevation, substrate and fire pattern were derived at 0.002° resolution using ArcView Spatial Analyst software (Environmental Systems Research Institute, 1996). Neighbourhood analysis was performed to determine the variety of substrate and fire age classes in the vicinity of each cell centroid at different sized radii (1, 2.5, 5,10 and 25 km). This was used to indicate the extent to which substrate richness and vegetation age varied with distance from the sampling location in the study area. Plot locations were intersected with each of the raster layers to extract parameter values. The distance of each substrate class and combined substrate classes (eg. d/c, l/rf, s) from a plot location was also calculated to form an explanatory variable and, similarly, the distance to areas burnt in the previous one and two years and less than two year old fires was calculated. The analysis was conducted to match fire age data with the plot sample date.

The predictive performance of each model was compared using the receiver operating characteristic (ROC) technique which is threshold-independent (Guisan and Zimmerman, 2000; Pearce and Ferrier, 2000). A ROC curve is a plot of true positive cases (or sensitivity) on the y-axis against corresponding false positive cases (or 1-specificity) on the x-axis across a range of threshold values (Fielding and Bell, 1997). The area under the curve (AUC) provides a measure of the discrimination ability which can vary from perfect with a value of 1.0 to no better than random with a value of 0.5. The differences between the area under two ROC curves generated by two or more models provides a measure of the comparative discrimination capacity of these models when applied to independent evaluation data (Pearce and Ferrier, 2000). Relationships from regression modelling are purely inferential (Luck, 2002) and, the importance of collecting independent data to evaluate the habitat occupancy models has been stressed by a number of authors (Pearce and Ferrier, 2000; Manel *et al.*, 2001; Rykiel, 1996; Vaughan *et al.*, 2003).

## Results

### *Introduced and naturalised predators*

Random plot sampling indicated that cat tracks occurred on 74% of the random plots and cat prevalence declined with decreasing latitude (**Fig. 5.2**). The fixed transect also indicated that cat activity was extremely widespread but no clear trend in prevalence was evident. Both transect and plot data suggested more cat sign was recorded on sand plain/dune field compared to fluvial surfaces, except at the Tennant latitude (**Table 5.3** and **Table 5.4**). The strength of association between individual variables and cat occurrence using logistic regression suggested substrate and gradient variables were more important than episodic variables (**Appendix 5.1**). A model that selected from only the substrate-related variables captured 6.5% of the deviance and indicated cat occurrence associated positively with high substrate variation within a 25 km radius and proximity to rock feature substrate (**Table 5.5**). Episodic variables accounted for relatively little of the model deviance (2.3%) and the strongest was a single fire-related variable that indicated greater cat prevalence occurred in recently burnt habitat. A model selecting from only the gradient related variables captured 5.4% of the deviance with a single variable of elevation forming the slightly stronger variable than mean annual rainfall. Greater cat prevalence occurred in parts of the study area with higher elevation. The full model which considered substrate, gradient and episodic variables had the greatest Akaike weight and captured 12.1 % of deviance and included a negative association with altitude and a positive association with high substrate variety within a 25 km radius and recently burnt habitat. The probability surface derived for feral cat occurrence that included only static and gradient parameters is shown in **Fig. 5.3a** (see **Appendix 5.2** for regression equation details). This showed the highest probability of cat occurrence occurred south of the study area, particularly where there was greater elevation and mix of substrate types.

Sign of fox was encountered on 22% of plots and fox prevalence declined with decreasing latitude (**Fig. 5.2**). No fox sign was recorded at the Newcastle Waters latitude on either the plots or the fixed transects and most occurred in the Kintore latitude (**Table 5.3 and Table 5.4**). However, fox activity was commonly encountered on the transects at the Tennant Creek latitude. Both sampling techniques indicated that the effect of rainfall and substrate interacted, with fox prevalence increasing on fluvial substrates as aridity increased, although this did not form a significant interaction term in the logistic models.
The substrate model indicated a negative association with laterite and rock features and a positive association with proximity to calcrete but these variables captured relatively little deviance (7%). The episodic model for the fox captured 17% of the deviance and indicated a positive association with recently burnt habitat and an association with antecedent rainfall. During the study, the rainfall within a 24 month period was very low in the southern part of the study area compared to the north and therefore this variable reflected the climatic gradient. Variables within the climatic gradient model had the greatest Akaike weight and captured most deviance (19.8%). It indicated that fox prevalence associated negatively with increasing mean annual rainfall and minimum temperature but positively to increasing maximum temperature (**Table 5.5**). The inclusion of other variables did not

significantly improve the capture of deviance and the gradient model was used to derive the probability surface of fox occurrence. This showed the highest probability of fox occurrence in the south west of the study area (**Fig. 5.3b**).

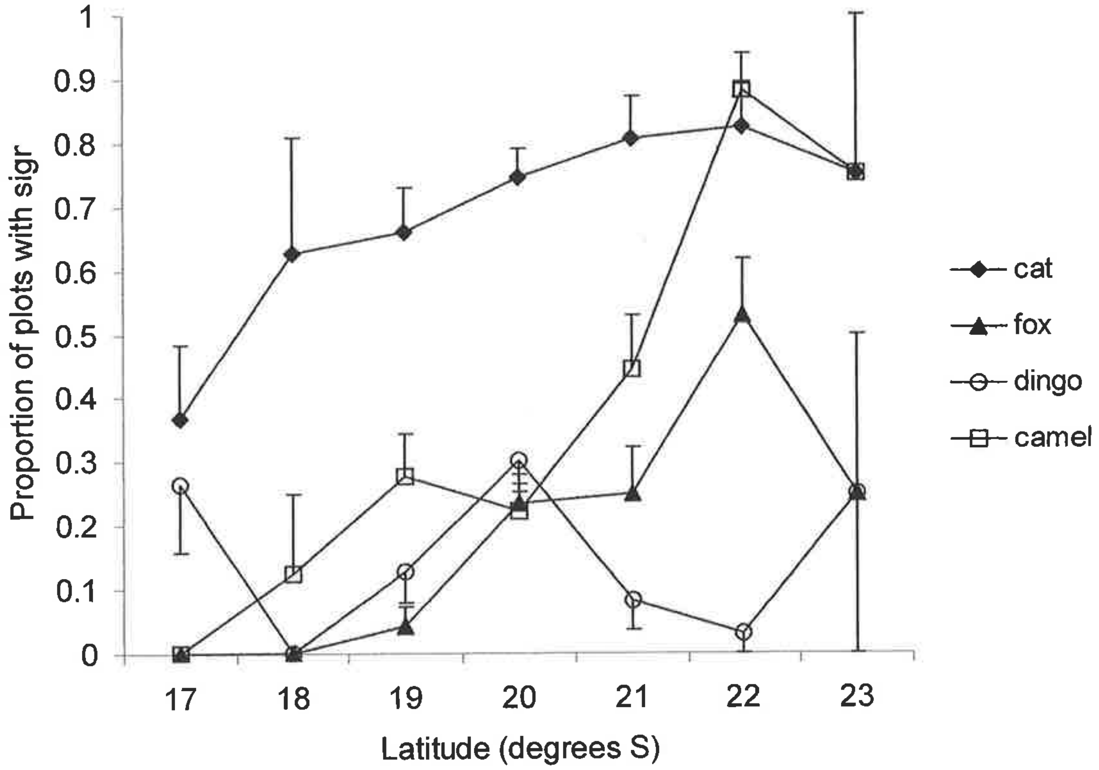

**Fig. 5.2** The relationship between the prevalence of feral cat, fox, dingo and camel sign and latitude

**Table 5.3** The prevalence of predators and herbivores on fixed transects in relation to latitude and habitat. Data indicate the number of transects with the occurrence of a species during a three consecutive day sample period as a proportion the number of samples. Number of samples = no. survey periods x no. sites per latitude. Newcastle Waters (6x1); Tennant (8x3); The Granites (7x1); Kintore (6x3). Asterisk (*) indicates sign of rabbit seen near but not recorded on transect. No sign of cattle was observed on any of the transects.

| | Latitude | dune field+ sand plain | calcareous+ drainage | mean prevalence |
|---|---|---|---|---|
| Cats | Newcastle Waters | 0.67 | - | 0.67 |
| | Tennant | 1 | 1 | 1 |
| | The Granites | 1 | 0.57 | 0.79 |
| | Kintore | 0.72 | 0.67 | 0.69 |
| Foxes | Newcastle Waters | 0 | - | 0 |
| | Tennant | 0.71 | 0.38 | 0.54 |
| | The Granites | 0.29 | 0.29 | 0.29 |
| | Kintore | 0.56 | 0.72 | 0.64 |
| Dingoes | Newcastle Waters | 0.58 | - | 0.58 |
| | Tennant | 0.25 | 0.75 | 0.50 |
| | The Granites | 0 | 0.71 | 0.35 |
| | Kintore | 0.17 | 0.44 | 0.30 |
| Rabbits | Newcastle Waters | 0 | - | 0 |
| | Tennant | 0 | 0* | 0.0 |
| | The Granites | 0 | 0.43 | 0.21 |
| | Kintore | 0* | 0* | 0* |
| Camels | Newcastle Waters | 0 | - | 0 |
| | Tennant | 0 | 0 | 0 |
| | The Granites | 0.14 | 0.43 | 0.28 |
| | Kintore | 0.22 | 0.44 | 0.33 |

Table 4
The occurrence of predators on random plots in relation to latitude and habitat. Data are a proportion of number of plots examined per latitude

| | Latitude | Dune field + sand plain | Rock feature + laterite | Calcareous + drainage | Combined propn | No. plots |
|---|---|---|---|---|---|---|
| Cats | Newcastle waters | 0.17 | — | — | 0.17 | 24 |
| | Tennant | 0.40 | 0.27 | 0.66 | 0.41 | 45 |
| | The Granites | 0.83 | 0.61 | 0.59 | 0.68 | 108 |
| | Kintore | 0.89 | — | 0.67 | 0.84 | 50 |
| Foxes | Newcastle Waters | 0 | — | — | 0.0 | 24 |
| | Tennant | 0.03 | 0.02 | 0.11 | 0.03 | 45 |
| | The Granites | 0.28 | 0.10 | 0.16 | 0.18 | 108 |
| | Kintore | 0.41 | — | 0.75 | 0.49 | 50 |
| Dingoes | Newcastle Waters | 0.07 | — | — | 0.09 | 24 |
| | Tennant | 0.07 | 0.05 | 0.22 | 0.08 | 45 |
| | The Granites | 0.14 | 0.26 | 0.32 | 0.24 | 108 |
| | Kintore | 0.02 | — | 0.08 | 0.04 | 50 |
| Rabbits | Newcastle Waters | 0 | 0 | 0 | 0 | 24 |
| | Tennant | 0 | 0 | 0 | 0 | 45 |
| | The Granites | 0.02 | 0 | 0.06 | 0.03 | 108 |
| | Kintore | 0 | — | 0 | 0 | 50 |
| Cattle | Newcastle Waters | 0.05 | — | — | 0.05 | 24 |
| | Tennant | 0 | 0 | 0 | 0 | 45 |
| | The Granites | 0 | 0.09 | 0.02 | 0.03 | 113 |
| | Kintore | 0 | — | 0 | 0 | 50 |
| Camels | Newcastle Waters | 0.0 | — | — | 0.02 | 24 |
| | Tennant | 0.2 | 0.04 | 0.33 | 0.14 | 45 |
| | The Granites | 0.19 | 0.22 | 0.32 | 0.25 | 113 |
| | Kintore | 0.82 | — | 0.67 | 0.78 | 50 |
| | No. plots | 123 | 43 | 61 | | 227 |

**Table 5.5** Generalised linear models for three predator species, predator richness and the camel. Select models were derived individually from episodic-, gradient- and substrates-related parameters and random plot data. The full model was derived from all available parameters. An additional static model was derived from gradient and substrate parameters if a episodically variable parameter such as fire formed a significant component of the full model. Values for adjusted $D^2$, AIC and Akaike weights ($w_i$) are presented. The static model was used to produce the probability surface to describe a species' distribution (see Appendix 5.2 for details). See Appendix 5.1 for a description of the abbreviations for each variable.

| Variable | Model | variables | adjusted $D^2$ | AIC | $w_i$ |
|---|---|---|---|---|---|
| Feral Cat | H1: Substrate | snbr25 + rf-dist | 0.065 | 250.1 | 0.029 |
| | H2: Episodic | mfire (r:io) | 0.024 | 260.0 | 0.000 |
| | H3: Gradient | dem | 0.055 | 251.8 | 0.012 |
| | Full model | dem + mfire (r:io) + snbr25 | 0.113 | 243.1 | 0.922 |
| | Static model | dem + snbr25 | 0.067 | 249.6 | 0.037 |
| Red fox | H1: Substrate | c-dist + substr (lrf :dcs) | 0.07 | 232.8 | 0.000 |
| | H2: Episodic | r24mths + mfire (ri:o) | 0.17 | 204.4 | 0.103 |
| | H3: Gradient | meanrain + maxtemp + mintemp | 0.19 | 200.1 | 0.897 |
| | Full model | meanrain + maxtemp + mintemp | 0.19 | 200.1 | |
| | Static | meanrain + maxtemp + mintemp | 0.19 | 200.1 | |
| Dingo | H1: Substrate | d-dist | 0.02 | 218.0 | 0.000 |
| | H2: Episodic | 2yrf-dist | 0.03 | 214.1 | 0.000 |
| | H3: Gradient | meanrain + mintemp + $\text{mintemp}^2$ | 0.11 | 200.8 | 0.178 |
| | Full model | meanrain + mintemp + d-dist | 0.13 | 197.9 | 0.822 |
| | Static model | meanrain + mintemp + d-dist | 0.13 | 197.9 | |
| Predator richness | H1: Substrate | rf-dist | 0.07 | 112.8 | 0.009 |
| | H2: Episodic | r24mths + mfire (r:io) | 0.13 | 106.0 | 0.267 |
| | H3: Gradient | dem | 0.06 | 113.9 | 0.005 |
| | Full model | r24mths + rf-dist + mfire (r:io) | 0.15 | 104.1 | 0.694 |
| | Static model | meanrain + rf-dist | 0.09 | 110.8 | 0.024 |
| Camel | H1: Substrate | c-dist | 0.13 | 261.2 | 0.000 |
| | H2: Episodic | fnbr25+mfire (o:ri) | 0.10 | 272.4 | 0.000 |
| | H3: Gradient | maxtemp | 0.19 | 240.1 | 0.005 |
| | Full model | meanrain + c-dist + mfire (o:ri) | 0.24 | 230.0 | 0.780 |
| | Static model | meanrain + c-dist | 0.23 | 232.5 | 0.215 |

Plot and transect samples indicated that dingoes occurred throughout the study area (**Table 5.3** and **Table 5.4**). Sign was recorded on 18% of random plots and distributed unevenly within the study area (**Fig. 5.2**) but the transect data indicated that prevalence declined with increasing aridity. Both plot and transect samples indicated that more dingo sign occurred on fluvial substrates compared to sand plain substrate and the strongest of the mapped variables was proximity to drainage but this was not significant at 0.05 and captured relatively little deviance (1.6%) (**Table 5.5**). Similarly, little deviance (3.4%) was captured by single or combined episodic variables with the strongest being proximity to areas burnt two years prior to sampling. Most deviance (11.3%) was captured with the gradient model and the strongest variables were mean rainfall and minimum temperature with a minimum temperature quadratic term. Slightly more deviance was captured with inclusion of substrate or episodic variables and the full model captured 12.6% of the deviance. The model with the greatest Akaike weight included a positive association with mean annual rainfall and proximity to drainage but a negative association with minimum temperature. The combination of variables indicated dingo prevalence was low in the northeastern and southwestern parts of the study area (**Fig 5.3c**).

Predator tracks were absent on 19% of plots, while 48% had sign of one predator species and 32% had sign of two predator species. Less than 1% had sign of three predator species. Among the substrate variables, greater predator richness associated with proximity to rock features and no other variables combined significantly to increase the deviance beyond 7.2%. Variables in the gradient model similarly captured little deviance (6.4%) and here greater predator richness associated with increasing elevation and none of the other variables combined to increase the amount of deviance captured significantly. The episodic variables captured most deviance (13.2%) and predator richness associated negatively with increasing antecedent rainfall in a 24 month period and positively with recently burnt habitat. The full model had the largest Akaike weight, captured 15.9% of deviance and included a combination of the antecedent rainfall and proximity to recent fire plus distance to rock feature variables (**Table 5.5**). The strongest static model indicated a negative association with increasing annual rainfall and positive association with proximity to rock features and captured 9.7% of deviance.

*Introduced herbivores*

Rabbit sign was recorded on 2% of plots and all were located at the Granites latitude (**Table 5.4**). Sign was also recorded only from a single transect at the Granites latitude, although sparse sign was found close to some transects during the study at the Kintore and Tennant latitude. The majority of the sign from plots and transects (**Table 5.3**) was encountered on drainage substrate. Generalised linear modelling was not conducted because of the small sample size. Similarly, modelling was not conducted with the cattle data. Cattle sign was recorded from 3% of plots and these were located in the close proximity to pastoral leases at the Newcastle Waters and the Granites latitude. Cattle sign was not recorded from any of the transects.

Camel sign was recorded on 36% of plots and with a strong gradient in prevalence (**Fig. 5.2**) with most sign evident in the southern part of the study area (**Table 5.4**). No camel sign was encountered on transects at the Newcastle Waters and Tennant latitudes and more sign was encountered generally on drainage substrates than sand plain (**Table 5.3**). With the substrate model, most deviance (13.4%) was captured by a single variable and this indicated that greater camel prevalence associated with proximity to calcrete substrate. Similarly, a single variable captured all the significant deviance in the gradient model (10%) and indicated that camel prevalence associated positively with increasing elevation. The episodic model included fire age and fire variety variables. Greater camel prevalence was associated with older fire ages and lower fire age variety. The full model included mean annual rainfall, distance to calcrete and the fire age variable, had the largest Akaike weight and captured 24.6% of model deviance (**Table 5.5**). The strongest static model captured slightly less deviance (23.4%) and included only mean annual rainfall and distance to calcrete variables. The probability surface for camel occupancy derived using these variables is shown in **Fig. 5.3d**.

*Model reliability and evaluation*

The 74 evaluation plots were distributed mainly in the northern parts of the study area and included drainage/calcrete, lateritic/rock feature and sand plain substrates. Cat and dingo activity was recorded on 47% and 68% of the plots, respectively. Predator tracks were absent on 21% of plots and two predator species (dingo and cat) were present on 37% of plots. None of the plots had three predator species. Sign of fox was recorded on 1 plot and camels were recorded on 4 plots.

The area under the curve (AUC) of the ROC plots for the original cat model was 0.64 ±0.04, which indicated that the model was able to distinguish correctly between presence and absence around 64% of the time. The discrimination capacity for the cat model was almost identical (0.64±0.06) when applied to the evaluation data. The AUC for the original fox model was 0.67±0.37 but it performed poorly when applied to the evaluation data 0.39 ±0.26 and less fox sign was recorded than expected. A similar discrepancy occurred with the dingo model. The AUC for the original dingo model was 0.74±0.05 but the evaluation data (0.35±0.07) indicated little discrimination power. Far more dingo sign was being recorded than expected in low probability areas. The original camel data provided the best discriminative power of the models (0.79±0.03) and performed well with the evaluation data (0.71±0.06).

## Discussion

### *Patterns of distribution*

The fixed transect and random plot techniques used distinctly different approaches to sample predator activity (Southgate *et al.*, 2005). A consistent pattern of substrate use was produced by each technique for the species considered although differences in the prevalence of some species were evident among latitudes. The overall consistency of substrate use provided weight to our understanding of the relationship of each species to the environment. This is an important consideration in the development of statistical modelling to predict species' distribution (Austin, 2002; Guisan *et al.*, 2002; Guisan and Zimmerman, 2000). The differences in prevalence among latitudes may have resulted because the techniques were not sampled contemporaneously. The contradictory results between plot and transect sampling obtained for cat and dingo occurrence suggest that the interpretation of latitudinal effects from plot data should be treated with caution.

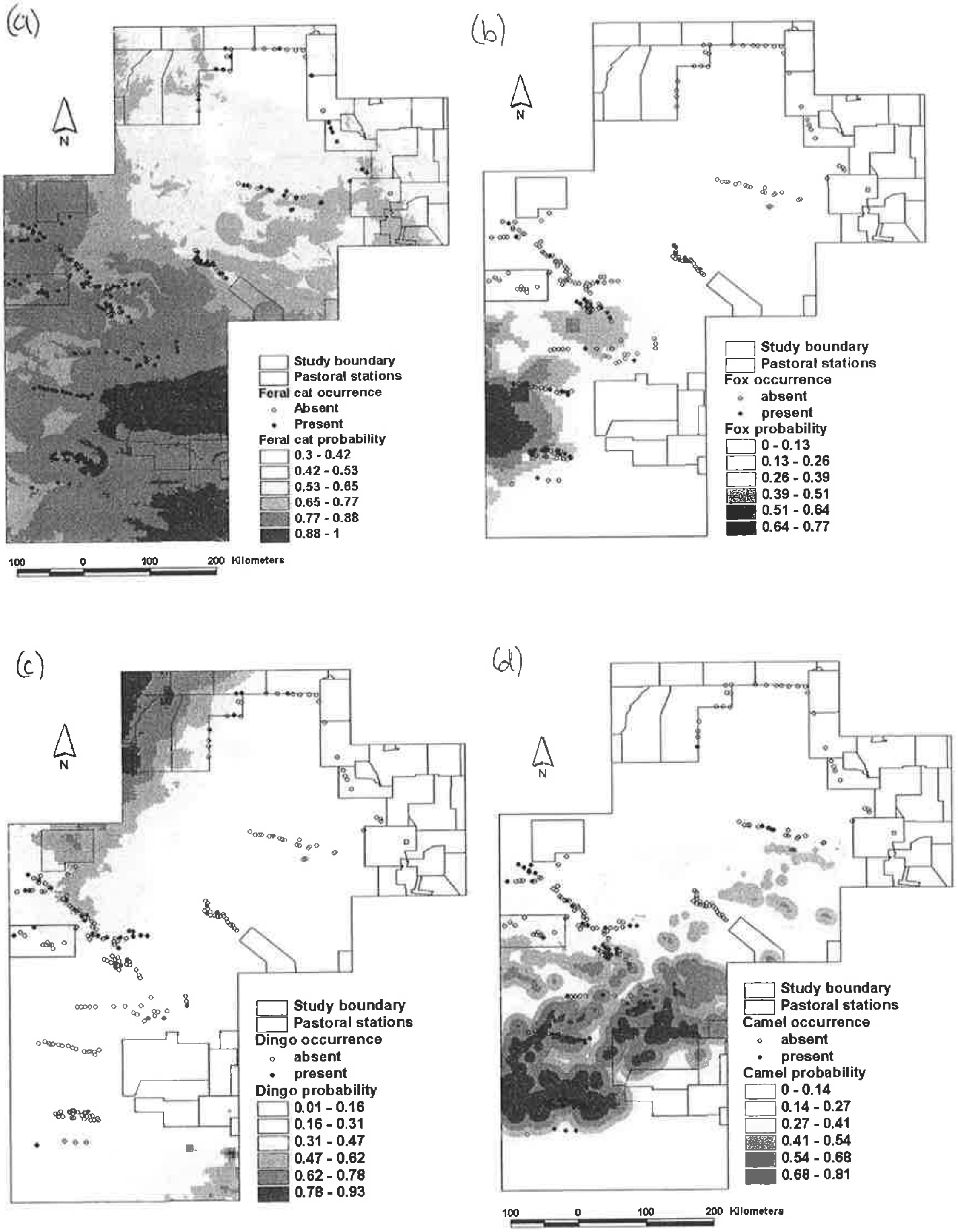

**Fig. 5.3** The occurrence and predicted occupancy of the (a) feral cat, (b) fox, (c) dingo and (d) camel in the Tanami Desert.

Dingoes and feral cats are both widespread in the Australian mainland. The dingo has been a resident for several thousand years and the feral cat, for at least 200 years (Abbott, 2002). Within the study area, transect data indicate that dingo prevalence was greatest in the north and least in the south. However, plot data indicated greatest prevalence at the Granites latitude. The feral cat was the most ubiquitous of the species examined. Plot data indicated cat prevalence was greatest in the south and diminished northwards but the transect data indicated little difference in prevalence among latitudes. Both plot and transect data indicated there was also a strong north-south gradient in fox and camel prevalence with sign absent or rare at the Newcastle Waters latitude and greatest in the south. In comparison with previous survey records, our data suggest that the distribution of these two species may not have reached equilibrium in the Tanami Desert, as both have increased in abundance in the south and extended their distribution north by 150 km in the last 15 years.

Foxes were released in Australia in the mid-1800s but became relatively abundant in central Australia only after the 1930s (Abbott, 2002). Foxes were not recorded during a 1981-1983 fauna survey of the Tanami Desert and Gibson (1986) listed them as rare but noted that a number of fox sightings had been made at localities in the vicinity of the Granites and Rabbit Flat in the period 1960-1980. Our survey found fox sign frequently on random plots and fixed transects in the south and extending to the Tennant Creek latitude. Feral camel herds originated from the escape or release of domestic animals in the 1930s when they were used for exploration and to transport materials in central Australia. Gibson (1986) listed camels as widespread but uncommon and recorded sign no further north than 18.5° S. Our study found camel sign as far north as 17°S. The estimated population of camels in Australia has increased from 30-40,000 in the mid 1960s (Siebert and Newman, 1989) to a conservative current estimate of more than 300,000 (Edwards *et al.*, 2004).

The distribution of rabbits and cattle in the Tanami Desert does not appear to have changed much since the survey of Gibson (1986). The area and intensity of pastoralism has remained largely static within the region since the mid-1970s. Similarly, the rabbit distribution appears to be static with activity widespread and more common in the south but limited to calcareous earths and outcropping and drainage systems further the north (Parer and Libke, 1985). Rabbit haemorrhagic disease (RHD) arrived in the Northern Territory during the study in mid 1996 and caused rabbit populations to decline dramatically (Edwards *et al.*, 2002). However, rabbit prevalence appeared to be very low in the region prior to the arrival of RHD.

*Substrate effects*

The proposal by Stafford Smith and Morton (1990) that the pattern of higher order consumers in arid Australia is limited by the restricted distribution of 'productive' substrates is certainly plausible. Increased productivity means an increased range of resources and this translates generally into an increase in species richness and abundance in most ecosystems in Australia and elsewhere, although there are exceptions (Begon *et al.*, 1996; Reynolds, 2002). The proposed pattern of greater herbivore prevalence in productive habitats was supported in our study. Rabbit sign was found to be restricted largely to the fluvial substrates but camels showed a strong association with proximity to calcrete and not drainage substrates *per se*. However, calcrete distribution correlated with latitude and therefore, partly reflected a gradient effect (Southgate, unpublished). Cattle remained concentrated around water-points on pastoral stations and sign was rarely recorded in the study area core despite the absence of boundary fences.

The suggestion that predator diversity and abundance would be associated with the more productive substrates was not supported. Instead, predator richness was greatest in closer proximity to rock feature substrates. The dingo was the only predator species that showed a positive association with productive substrates. Fox prevalence was positively associated with proximity to calcareous substrates but as noted previously this variable partly reflected a south-north gradient effect (Southgate *et al.*, unpublished). Foxes used drainage lines in areas where dingo prevalence was low but this effect did not remain significant when combined with gradient variables. Feral cat prevalence showed no association with productive substrates and instead associated more with proximity to rock features (indicative of skeletal soils and outcropping) and parts of the landscape with a greater mix of substrate types. Gibson (1986) also noted that feral cats occupied virtually every habitat available but principally rocky outcrops and ranges. The poor association of foxes and cats with productive substrates may be explained by a greater dependence on reptile prey. Most dietary studies of feral cat, fox and dingo in other parts of Australia have shown an overwhelming reliance on mammalian prey, especially where rabbits are common (Coman, 1973; Croft and Hone, 1978; Jones and Coman, 1981; Corbett and Newsome, 1987; Catling, 1988; Marsack and Campbell, 1990; Paltridge *et al.*, 1997). However, dietary analysis of all three predators in the study area conducted by Paltridge (2002) indicated that foxes and feral cats relied heavily on varanids and other lizards for prey whereas dingoes consumed more mammal prey. The reptile fauna is diverse and abundant on a range of substrates dominated by spinifex grasses in central Australia (Morton and James, 1990) and predators able to use this type of prey are evidently able to persist on substrates with low productivity.

### *The effect of episodic rainfall and fire*

The episodic events of exceptional rainfall, drought and fire are clearly important driving forces in the arid zone. Dramatic and conspicuous changes to the abundance of biota in the arid zone of Australia and other arid landscapes can follow exceptional rainfall (Louw and Seeley, 1982; Griffin and Friedel, 1985; Masters, 1993; Predavec, 1994; Southgate and Masters, 1996; Jaksic, 2001) and fire (Friend, 1993; Masters, 1996; Woinarski and Recher, 1997). However, the relationship between rainfall and desert consumers is often not simple, with complex non-linear effects (Brown and Ernest, 2002; Stenseth *et al.*, 2002).

The four species considered in detail here showed differing responses to fire and rainfall and overall, there was little indication that the rainfall-deficit or fire pattern dramatically affected the prevalence of a species. Dingoes, foxes and cats associated positively with more recently burnt habitat whereas camel activity was associated with older fire ages. However, these variables captured little model deviance and a fire-related variable formed a significant component in the full model only for feral cats. Felids typically employ dense cover to stalk or ambush prey, whereas canids do not make use of vegetation when hunting (Murray *et al.*, 1995). Hence, the response of feral cats was contrary to that expected. However, sparse cover has not deterred feral cats from reaching high density in extremely sparsely vegetated habitats in arid Australia such as the Diamantina region of western Queensland when dingoes were in low abundance (Pettigrew, 1993).

Exceptional rainfall did not occur anywhere in the study area during the investigation and had not occurred for 4-5 years prior to sampling and, then only in the northern part of the study area. Therefore, it remains unclear what impact this type of event would have on predator and herbivore prevalence. An increase in the predator population can take 12-24 months to peak following period of exceptional rainfall in central Australia (Southgate, pers. obs.) and the length of time high numbers can be sustained is unclear but may depend on the ability of a predator species to prey switch and on the availability of alternative prey (Corbett and Newsome, 1987). A period of extreme rainfall deficit, which resulted in the unusual and widespread death of spinifex *Triodia basedowii*, did occur in the south during the study. Despite these severe conditions, each predator species persisted at the Kintore latitude albeit at lower levels during 1996 (Paltridge, unpublished) and rainfall deficit was not significant in any of the species'-specific models. The abundance of small mammals remained low (<2% trap success) throughout the duration of the study at both the Tennant Creek and Kintore study areas and showed little response to seasonal conditions (Paltridge and Southgate, 2001).

### *Gradient effects*

The effect of temperature and other climatic factors in constraining the distribution of a species has been described for a range of species and communities from Australia and elsewhere (Nix, 1982; Austin *et al.*, 1996; Begon *et al.*, 1996; van Rensburg *et al.*, 2002). These effects were omitted from the framework of ecology of arid Australia proposed by Stafford Smith and Morton (1990), presumably because they were considered difficult to accommodate and would diminish generality. We found that the conceptual model of these authors was lacking on this account because variables reflecting the north-south climatic gradient, especially mean annual rainfall, were by far the most powerful in describing the prevalence and distribution of the four species considered in the present study. Both mean rainfall and temperature decreased from north to south in the region and this results in a strong gradient in relative humidity (Cols and Whitaker, 2001). It is well documented that humid conditions can place great stress on large homeothermic animals, especially in the absence of freely available water (Schmidt-Nielsen, 1997). Hence, it is possible that the conditions of high temperature and humidity coupled with the absence of free water place individuals of some species under extreme necessity to dissipate metabolic heat and maintain water balance.

The dingo was the only species to show a positive association with the rainfall gradient. In contrast, sign of feral cat, fox and camel became less common with increasing rainfall and minimum temperature. In hot arid areas, the distribution of water is the single most important factor that determines where dingoes can be found (Corbett, 1995). Dingoes do not need to drink water every day but are forced to drink when food is scarce. The size and mobility of dingoes enables them to have large home ranges (32-126 km$^2$) and make daily forays of over 40 km (Corbett, 1995; Palmer, pers. com.). Presumably the greater mobility of the dingo allows it to regularly find drinking water and tolerate localities with high humidity. On the other hand, feral cats and foxes can survive in the absence of free water (Southgate, pers. obs.) but are constrained in their day to day movements below several kilometers (Coman *et al.*, 1991; Edwards *et al.*, 2001; Jones and Coman, 1982). Meeting their water requirements solely from food would be precarious in hot humid environments. The density of feral cats is particularly low in the Top End and Cape York compared to inland environments dominated by open habitat (Dickman, 1996) and foxes have remained absent in hot-humid northern Australia except along the coastline (King and Smith, 1985; Saunders *et al.*, 1995). Camels can persist without drinking for up to four days in summer and several months in winter and can range widely, using a broad mix of habitat types (Dorges and Heucke, 1995). Their body temperature can fluctuate between 37-41° C (Siebert and Newman, 1989) allowing safe storage of excess heat acquired during the day and the loss by heat transfer during the night (Bartholomew and Dawson, 1968; K. Schmidt-Nielsen, 1997). However, problems arise if individuals (eg. juveniles) are not large enough to possess a high thermal inertia or night temperatures remain high and the camels cannot lose heat.

*Limitations of the models*

The mapping of most introduced and native Australian mammals in arid Australia has relied primarily on opportunistic reports combined with data from limited systematic surveys (see Smith and Quin, 1996). This has resulted in a simplistic picture of the distribution of pest and threatened species with insufficient detail to examine how the distribution and abundance of species change through time (James *et al.*, 1995). Our data are significant in that we provide an empirical description of the variables that associate with introduced herbivore and predator occurrence in arid Australia where human intervention is largely absent. The pattern of distribution of these species can be highly distorted by the features associated with the pastoral industry such as the provision of artificial waters, carrion and baiting programs (Caughley, 1987; Corbett, 1995; May and Norton, 1996; James *et al.*, 1999) and where removal and fragmentation of habitats has occurred (Bailey *et al.*, 2002; Burgman and Lindenmayer, 1998).

In relation to the discrimination ability of the models for each species, values between 0.7 and 0.9 indicate a reasonable discrimination ability appropriate for many uses (Pearce and Ferrier, 2000). The model for feral cats provided relatively poor but consistent discrimination ability (0.64) but this is not surprising because the static model used to map feral cat prevalence was much weaker than the full model that included a fire-age variable. The model for camel prevalence was better (0.79), and had reasonable discriminatory power. The validation data produced a similar result and indicated that the model was consistent. The models for dingo and fox were interesting in that they performed particularly poorly with the evaluation data. Both the fox model (0.67) and the dingo model (0.74) based on the training data were not overly strong but performed much better than the evaluation data. The full model for the fox contained only gradient related parameters suggesting this species had the least specific substrate and vegetation-fire age requirements among the predator species. This supports findings from studies conducted in south-eastern Australia (Jarman, 1986; Phillips and Catling, 1991; Catling *et al.*, 2001) and desert areas (Burrows *et al.*, 2003) which report that foxes display a lack of habitat preference.

The evaluation data indicated that dingoes were far more prevalent in areas sampled than expected and that foxes were far less prevalent than expected. These differences may be attributable to differences in collection of the primary and evaluation data. The evaluation data were collected from beside prominent tracks to permit ease of access to conduct ground truthing and the plots were half the width (100 m) of the random plots. The random plots on the other hand were often located off-road and the greater width of each plot meant that habitat further from the road was sampled. The evaluation data are consistent with findings that dingoes use roads and tracks far more readily than foxes and especially more than feral cats (Mahon *et al.*, 1998), and the data suggested foxes avoid interaction with dingoes. This was also evident in drainage lines where dingo prevalence was greater. Cats appear to have a greater ability to persist sympatrically with dingoes than foxes but nevertheless use roads more frequently when dingo prevalence is reduced (Burrows *et al.*, 2003).

Habitat modelling is an iterative procedure whereby the development, evaluation, refinement and re-evaluation should be ongoing until consistent patterns in habitat are identified (Luck, 2002). The models developed in our study while significant are a first step. The approach needs to be applied elsewhere in the sandy arid parts of Australia to test whether the patterns are consistent.

## Conclusions

In the Tanami Desert, our results provide some support for the suggestion by Stafford Smith and Morton (1990) that the prevalence of introduced herbivores is greater in richer habitats but the proposition that endothermic predators show a similar pattern was not supported. The dingo was the only predator species that showed an association with more productive habitats. The adaptability of foxes and feral cats has evidently liberated them from a dependence on mammals for prey and on the use of substrates with high water and nutrient availability as hunting habitat. This allows them to occupy substrates of lower fertility. It is possible that native medium-sized mammals may have once been important prey for these predators and the pattern of prevalence would then have been different (Paltridge, 2002).

The response to episodic events such as fire varied among species. Cats, foxes and dingoes associated positively with recently burnt habitat and camels showed the reverse. We did not have the opportunity to examine the effect of a period of exceptional rainfall. The severe rainfall deficit present in part of the study area affected the relative abundance of species but not result in localised extinction.

Variables reflecting the climatic gradient provided the strongest association with the occurrence of introduced and naturalised predators and herbivores in the Tanami Desert, and we propose that temperature and relative humidity may constrain the abundance of species in areas where drinking water is scarce. Our work suggests that variables such as mean rainfall, temperature and humidity should not be ignored in the development of models to describe the key ecological relationships controlling the biotic structure of higher order consumers in the Australian arid zone.

The continued occupation of the Tanami Desert by significant numbers of feral cats, foxes and camels suggests that the deserts in northern Australia cannot be considered a secure refuge for medium-sized native species such as the bilby. It cannot be assumed that the impact of predator and introduced species is limited to higher nutrient, more productive parts of the landscape, or that only mammal species are at risk.

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**Appendix 5.1** The strength of the relationship between herbivore and predator species and substrate, fire and rainfall explanatory variables derived from random plot data. For each species, the percentage of deviance captured by each variable fitted separately is shown. Values in bold are significant at $p<0.05$.

| Variable | Abbreviation | Predator | Cat | Fox | Dingo | Camel |
|---|---|---|---|---|---|---|
| Substrate actual 3 category (dc,lr,s) | sa3(dc,lr,s) | 0.3 | 1.1 | **2.5** | **4.0** | **2.0** |
| Substrate actual 2 category (dc,lrs) | sa2(dc,lrs) | 0.3 | 0.9 | 0.6 | **1.9** | 0.4 |
| Substrate actual 2 category. (lr,dcs) | sa2(lr,dcs) | 0.1 | 0.0 | 2.4 | 0.8 | **1.9** |
| Substrate map 5 category (d,c,l,r,s) | sm5(d,c,l,r,s) | 0.8 | 2.4 | **2.7** | **6.7** | **2.9** |
| Substrate map 3 category (dc,lr,s) | sm3(dc,lr,s) | 0.0 | 0.6 | 0.5 | 1.8 | 0.8 |
| Substrate map 2 category. (dc, slr) | sm2(dc,slr) | 0.0 | 0.5 | 0.1 | 1.4 | 0.0 |
| Substrate map 2 category. (lr, sdc) | sm2(lr,dcs) | 0.0 | 0.3 | 0.5 | 0.1 | 0.7 |
| Substrate map 2 category. (s, dclr) | sm2(s,dclr) | 0.0 | 0.1 | 0.0 | 1.6 | 0.6 |
| Substrate distance to fluvial (dc) | dist.dc | **6.7** | **4.2** | **2.9** | 0.2 | **3.2** |
| Substrate distance to calcrete (c) | dist.c | **4.5** | **3.1** | **4.7** | 0.9 | **13.4** |
| Substrate distance to drainage (d) | dist.d | **6.1** | **1.5** | 0.4 | 1.6 | 0.7 |
| Substrate distance to laterite (l) | dist.l | 0.2 | 1.2 | 0.0 | 0.1 | **4.2** |
| Substrate distance to rock features (r) | dist.r | **7.2** | **5.6** | **1.6** | 0.4 | **2.2** |
| Substrate distance to sand plain and dune field (s) | dist.s | 0.1 | 0.6 | 0.1 | 0.8 | 0.0 |
| Substrate neighbourhood variety 25 km radius | snbr25r | **5.5** | **4.9** | **3.6** | 0.2 | **9.8** |
| Substrate neighbourhood variety 10 km radius | snbr10r | **2.6** | 1.9 | 0.9 | 0.3 | **4.2** |
| Substrate neighbourhood variety 5 km radius | snbr5r | 0.5 | 0.5 | 0.0 | 0.1 | 0.1 |
| Substrate neighbourhood variety 2.5 km radius | snbr2.5r | 0.0 | 0.0 | 0.1 | 0.9 | 0.0 |
| Substrate neighbourhood variety 1 km radius | snbr1r | 0.3 | 0.0 | 0.6 | 0.1 | 0.0 |
| Rainfall annual mean | rainymean | **6.3** | **4.5** | **14.8** | **3.5** | **17.3** |
| Digital elevation model | dem | **6.4** | **5.5** | **5.9** | 0.2 | **15.4** |
| Temperature (minimum) | tempmin | **6.3** | 2.7 | **8.3** | 0.2 | **14.4** |
| Temperature (maximum) | tempmax | **4.1** | **3.8** | **8.9** | **2.9** | **19.2** |
| Rainfall: cumulative in last 3 mths | r3mth | 1.0 | 0.7 | 0.0 | 0.7 | **8.7** |
| Rainfall: cumulative in last 6 mths | r6mth | 0.5 | 0.3 | **2.1** | 0.0 | **14.3** |
| Rainfall: cumulative in last 12 mths | r12mth | **2.4** | 0.2 | **3.5** | 0.0 | **14.7** |
| Rainfall: cumulative in last 24 mths | r24mth | **7.6** | **2.4** | **13.1** | 0.2 | **24.2** |
| Rainfall deviation from mean over 12 mths | r12mdev | 0.1 | 0.7 | 0.2 | 0.2 | **5.2** |
| Rainfall deviation from mean over 24 mths | r24mdev | **4.1** | 0.1 | **9.3** | 0.1 | **20.6** |
| Fire actual 3 category. (recent, intermediate,old) | fa3(r,i,o) | **2.3** | 1.1 | 0.1 | **3.2** | **3.4** |
| Fire map 3 category (recent, intermediate,old) | fm3(r,i,o) | **4.6** | **3.0** | **3.7** | 1.2 | **6.4** |
| Fire map 2 category (recent:intermediate,old) | fm2(r,io) | **3.4** | **2.3** | 0.7 | 0.6 | **1.8** |
| Fire map 2 category (old:recent,intermediate) | fm2(o,ri) | 0.1 | 0.1 | 0.5 | 1.2 | **6.3** |
| Fire: map years since | myrsfire | 0.3 | 0.2 | 0.1 | 1.3 | **4.4** |
| Fire neighbourhood variety 1 km radius | fnbr1r | 0.0 | 0.1 | 0.0 | 0.2 | 0.8 |
| Fire neighbourhood variety 2.5 km radius | fnbr2.5r | 0.1 | 0.2 | 0.1 | 0.1 | **2.1** |
| Fire neighbourhood variety 5 km radius | fnbr5r | 0.0 | 0.0 | 0.6 | 0.8 | **2.5** |
| Fire neighbourhood variety 10 km radius | fnbr10r | 0.3 | 0.0 | 0.7 | **2.3** | **6.2** |
| Fire neighbourhood variety 25km radius | fnbr25r | 0.0 | 0.0 | **2.3** | **3.0** | **8.0** |
| Fire: distance to <1 yr old fire | dist.f.1yr | 0.7 | 0.8 | 1.2 | 0.9 | **5.8** |
| Fire: distance to 1-2 yr old fire | dist.f.2yr | 0.0 | 0.0 | **2.5** | **3.6** | **6.2** |
| Fire: distance to <2 yr old fire | dist.f.rec | 0.1 | 0.0 | **2.8** | **2.5** | **9.6** |

**Appendix 5.2** Generalised linear models for three introduced predator species, predator richness and the camel using random plot data. Candidate models were derived individually from episodic-, gradient- and substrates-related parameters. The full model was derived from all available parameters. An additional static model was derived from gradient and substrate parameters if a episodicly variable parameter such as fire formed a significant component of the full model. The static model was used to produce the probability surface to describe a species' distribution.

**1) Feral cat**

Substrate variables only
Total Deviance = 262.2, adjusted $D^2 = 0.065$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | 0.1667 | 0.8167 | 226 | | |
| substrate variety 25 km r | 0.2794 | 0.1411 | 225 | 12.8 | 1.98 |
| distance to rf | -0.0419 | 0.0184 | 224 | 5.3 | -2.27 |

Episodic variables only
Total Deviance = 262.2, adjusted $D^2 = 0.024$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | 1.255 | 0.190 | 226 | | |
| map fire cat. (rec:int,old) | 0.449 | 0.190 | 225 | 6.2 | 2.4 |

Gradient variables only
Total Deviance = 262.2, adjusted $D^2 = 0.055$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -1.614 | 0.713 | 226 | | |
| dem | 0.0073 | 0.0020 | 225 | 14.4 | 3.7 |

Full model: all variables considered
Total Deviance = 262.2, adjusted $D^2 = 0.113$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -2.1839 | 0.7996 | 226 | | |
| digital elevation | 0.00578 | 0.00218 | 225 | 14.4 | 2.6 |
| map fire cat. (rec:int,old) | 0.5468 | 0.2006 | 224 | 8.6 | 2.7 |
| substrate variety 25 km r | 0.3064 | 0.1543 | 223 | 4.0 | 2.0 |

Static model: substrate and gradient variables considered
Total Deviance = 262.2, adjusted $D^2 = 0.067$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -2.2046 | 0.7781 | 226 | | |
| digital elevation | 0.0051 | 0.0022 | 225 | 14.4 | 2.3 |
| substrate variety 25 km r | 0.306 | 0.149 | 224 | 4.2 | 2.0 |

**Appendix 5.2** cont.

**2) Red fox**

Substrate variables only

Total Deviance = 239.4, adjusted $D^2 = 0.07$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -1.2926 | 0.3035 | 226 | | |
| distance from calcrete | -0.0294 | 0.0122 | 225 | 11.4 | -2.4 |
| actual substrate (dcs:lr) | 0.5991 | 0.278 | 224 | 5.9 | 2.1 |

Episodic variables only

Total Deviance = 239.4, adjusted $D^2 = 0.17$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | 1.255 | 0.190 | 226 | | |
| rainfall 24 months | -0.00519 | 0.00094 | 225 | 31.3 | -5.494 |
| map fire cat. (rec:int,old) | 0.641 | 0.208 | 224 | 9.7 | 3.1 |

Gradient and full model and static model

Total Deviance = 239.4, adjusted $D^2 = 0.19$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -57.6127 | 20.5299 | 226 | | |
| annual rainfall.5km | -0.0398 | 0.00934 | 225 | 35.5 | -4.2 |
| temperature maximum | 2.5498 | 0.8062 | 224 | 6.7 | 3.2 |
| temperature maximum | -0.8812 | 0.4263 | 224 | 5.2 | -2.1 |

**3) Dingo**

Substrate variables only

Total Deviance =217.4, adjusted $D^2 = 0.02$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -1.260 | 0.206 | 226 | | |
| distance to drainage | -0.021 | 0.013 | 225 | 3.4 | -1.62 |

Episodic variables only

Total Deviance = 217.4, adjusted $D^2 = 0.03$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -1.2204 | 0.1906 | 226 | | |
| distance 2 yr old fire | -0.0125 | 0.0055 | 225 | 7.3 | -2.3 |

Gradient variables only

Total Deviance = 217.4, adjusted $D^2 = 0.11$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -208.46 | 102.19 | 226 | | |
| annual rainfall.5km | -0.0131 | 0.00347 | 225 | 7.7 | -3.8 |
| temperature minimum | 23.535 | 11.412 | 224 | 12.1 | 2.1 |
| temperature minimum$^2$ | -0.6826 | 0.3179 | 223 | 4.9 | -2.1 |

Model: full and static

Total Deviance = 262.2, adjusted $D^2 = 0.12$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -2.2046 | 0.7781 | 226 | | |
| annual rainfall.5km | 0.01599 | 0.00348 | 225 | 7.7 | 4.6 |
| temperature minimum | -0.7772 | 0.2982 | 225 | 12.1 | -2.6 |
| distance to drainage | -0.0317 | 0.0139 | 224 | 7.7 | -2.4 |

**Appendix 5.2** cont.

**4) Predator richness**

Substrate variables only

Total Deviance = 119.5, adjusted $D^2 = 0.072$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | 1.3297 | 0.0648 | 226 | | |
| distance to rf | -0.0208 | 0.0049 | 225 | 8.63 | -4.2 |

Gradient variables only

Total Deviance = 119.5, adjusted $D^2 = 0.064$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -1.614 | 0.713 | 226 | | |
| digital elevation model | 0.00229 | 0.00058 | 225 | 7.5 | 3.9 |

Episodic variables only

Total Deviance = 119.5, adjusted $D^2 = 0.132$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | 1.255 | 0.190 | 226 | | |
| antecedent rain in 24 months | -0.0010 | 0.00019 | 225 | 9.1 | -5.1 |
| map fire cat. (rec:int,old) | 0.1998 | 0.0508 | 224 | 7.1 | 3.9 |

Full model: all variables considered

Total Deviance = 119.5, adjusted $D^2 = 0.151$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -1.8486 | 0.1356 | 226 | | |
| antecedent rain in 24 months | -0.00082 | 0.00002 | 225 | 14.4 | -3.9 |
| distance to rock feature | -0.01264 | 0.0051 | 224 | 4.1 | -2.5 |
| map fire cat. (rec:int,old) | 0.1814 | 0.0508 | 223 | 5.7 | 3.5 |

Static model: substrate and gradient variables considered

Total Deviance = 262.2, adjusted $D^2 = 0.067$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -2.2046 | 0.7781 | 226 | | |
| annual rainfall | -0.0016 | 0.00065 | 225 | 7.5 | -2.5 |
| distance to rock feature | -0.0155 | 0.0053 | 224 | 4.0 | -2.8 |

**5) Camel**

Substrate variables only

Total Deviance = 297.0, adjusted $D^2 = 0.13$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -04624 | 0.231 | 226 | | |
| distance to calcrete | -0.0696 | 0.0159 | 225 | 39.8 | -4.4 |

Episodic variables only

Total Deviance = 297.0, adjusted $D^2 = 0.10$

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -1.1488 | 0.169071 | 226 | | |
| fire variety 25 km r | -0.3169 | 0.0949 | 225 | 23.8 | -3.3 |
| mapped fire (o:ri) | -0.4137 | 0.1598 | 224 | 6.7 | -2.6 |

Gradient variables only

Total Deviance = 297.0, adjusted $D^2$ = 0.155

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -5.953 | 0.965 | 226 | | |
| dem | 0.0140 | 0.00243 | 225 | 45.9 | 5.7 |

Full model: all variables considered

Total Deviance = 297.0, adjusted $D^2$ = 0.24

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | 3.892 | 0.976 | 226 | | |
| Annual rainfall | -0.0139 | 0.0027 | 225 | 51.2 | -5.2 |
| Distance to calcrete | -0.0330 | 0.0128 | 224 | 14.9 | -2.6 |
| Map fire cat. (o:ri) | -0.3671 | 0.1750 | 223 | 4.6 | -2.1 |

Static model: substrate and gradient variables considered

Total Deviance = 297.0, adjusted $D^2$ = 0.23

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | 4.6830 | 0.9036 | 226 | | |
| Annual rainfall | -0.0139 | 0.0027 | 225 | 51.2 | -5.2 |
| Distance to calcrete | -0.0602 | 0.0168 | 224 | 19.2 | -3.6 |

# Chapter 6

## Age classes of the greater bilby *Macrotis lagotis* based on track and faecal pellet size[1]

*Preamble to Chapter 6*

This chapter describes the methods developed to identify different age classes of the bilby in the field based on gait measurements and faecal pellet diameter. These methods were applied to data collected on gait size and faecal diameter from the bilby population in the Tanami Desert.

I aimed to determine whether independent immature bilbies and large male bilbies were evenly distributed throughout the entire study area.

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[1] This chapter has been published in the journal *Wildlife Research*: Southgate, R.I. 2005. Age classes of the greater bilby Macrotis lagotis based on track and faecal pellet size. *Wildlife Research* 32: 625-630.

## Introduction

The interpretation of footprints or tracks is being used more broadly in wildlife science to determine species' occurrence and the characteristics of the individuals present (Kendell *et al.* 1992; Stander *et al.*1997; Engman *et al.* 2000). Tracking techniques have been applied on unprepared sandy substrates (Stander 1998; Mahon *et al.* 1998; Southgate *et al.* 2005) and snow (Drickamer and Stuart 1984; Vivas and Saether 1987, Thompson *et al.* 1989; Zalewski 1999), along prepared or unprepared tracks and trails (Kendall *et al.*1992; Edwards *et al.* 2000; Paltridge and Southgate 2001; Lizcano and Cavelier 2000) and sand pads or plots (Catling *et al.* 1997; Engman *et al.* 2000; Glen and Dickman 2003). Most often the characteristics of the tracks or other sign are used to record species occurrence but the size and shape of tracks or gait may be used to identify age, sex and the identity of individuals (Stander *et al.* 1997; Lizcano and Cavelier 2000). This additional information may be used to remotely and inexpensively access population structure or habitat occupancy (Brooks *et al.* 1998). For example, information on the presence or absence of young individuals may be used to rank source or sink habitat (Pulliam 1988) or indicate breeding season (McCracken 1990).

The greater bilby *Macrotis lagotis* is a species vulnerable to extinction and now restricted to the Tanami, Great Sandy and Gibson Deserts with an outlying population in southwest Queensland (Southgate 1990; Maxwell *et al.* 1996). Individuals are difficult to capture (Southgate *et al.* 1995) but faecal pellets and tracks are relatively easy to find where bilby individuals are present in most parts of their current range (Paltridge and Southgate 2001; Southgate *et al.* 2005). Greater bilbies show sexual dimorphism in size and males can reach a weight of 2500 g and females without pouch young may reach a weight of 1100 g (Johnson 1995). In a study of captive and reintroduced bilbies, both females and males were found to continue to increase in size until the age of about 540 days (Southgate *et al.* 2000). Young become independent around age 90 days and prior to this reside within their mother's pouch or are cached within the natal burrow. At independence, males and females are around 250-300 g weight. Females reach maturity around 180 days and weigh around 500 g but they need to be greater than 650 g to successfully raise young to independence (Southgate *et al.* 2000).

The relationships of skeletal size or body mass derived from known-age animals are often used to age animals in the field (Krebs 1989; Zar 1989) and in this paper, I derive the relationship between a) faecal pellet size and b) track dimensions, and the weight of the greater bilby. I present procedures to measure gait size and faecal pellet diameter, and outline the number of samples and the critical values required to confidently categorise individuals into three age classes: independent-immature; mature female and young male; and large male. The procedures are applied to data collected during a survey of a wild bilby population in the Tanami Desert, Northern Territory, in particular to determine whether immature individuals were evident throughout the study area. The broader application of gait measurements (as opposed to foot imprints) in the identification of species and the size of individuals is discussed.

## Methods

### *Development of the procedures*

Information on weight, pellet and track size was obtained from free-ranging individuals reintroduced to Watarrka National Park (Southgate 1995) located 330 km south-west of Alice Springs in the period 1988-1990 (Southgate and Possingham 1995). Overall, data were obtained from 16 *in situ*-bred or captive-bred individuals that were recaptured regularly using cage traps or yard traps (Southgate *et al.* 1995) and had a reasonably accurate known date of birth (within 7 days).

Faecal pellets were collected from trapped animals and up to five pellets were randomly chosen from the deposit left by each individual per sample time. The lateral section of each scat sample was rotated within the vernier calipers and the maximum diameter recorded to the nearest 0.1 mm (**Fig. 6.1**).

The size of tracks attributable to 16 closely monitored, radio-tagged (Sirtrack Electronics, New Zealand) individuals was recorded and measurements of up to five sets of tracks per individual per sample time were taken. Bilbies have a bounding gait (much like a rabbit) with the hind track placed side by side ahead of the front tracks which are staggered. They maintain this gait while moving between foraging points and sections of 10 or more consecutive gait imprints may be encountered commonly. The length between hind and fore-foot track (gait length) and the width of a gait between the two hind foot tracks (gait width) were measured **(Fig. 6.2)**. A combined measure of paired gait width plus gait length was also calculated. Initially, the hind track length was also measured but it became clear that it was difficult to estimate imprint length accurately unless the prints had a great deal of clarity.

The relationship between animal weight and faecal pellet size, and animal weight and gait size was derived using a regression equation for multiple values of $y$ (i.e. gait or pellet size) (Sokal and Rohlf 1995 p484). The inverse prediction and 95% Confidence Interval (CI) values around $x$ (i.e. weight) were computed using $m$=5 and $m$=10 for the number of values used to derive an average for $y$ (Sokal and Rohlf 1995 p492). Data were examined for evidence of allometric growth and to determine whether logarithmic transformation was required. A number of individuals were sampled more than once and these data were treated as independent samples if the individuals had increased in weight from the previous sample. An individual whose gait or faecal pellet size indicated a weight less than 500 g was considered to be immature and less than 180 days old. After the age of 180 days, males and females grow at a different rate. For example, a female aged 365 days weighs 785 g and a male weighs 1120 g, approximately (Southgate *et al.* 2000). An individual whose gait or faecal pellet size indicated a weight larger than 1200 g was considered to be large male because mature females without pouch young do not exceed this weight in the field.

### *Application of the procedures*

A wild bilby population was surveyed in 1996-1999 to determine distribution and habitat occupancy in the Tanami Desert. The study area and the methods to sample the population are described in Paltridge and Southgate (2001) and Southgate *et al.* (2005). Bilby tracks and faecal pellets encountered during the survey were measured and used to determine the distribution of immature and large male individuals in the study area. The study area was divided into four latitudinal zones of at least 170 km width and these zones were referred to as Newcastle Waters ($17^{O}$-$18.5^{O}$ S), Tennant ($18.5^{O}$-$20^{O}$ S), the Granites ($20^{O}$-$21.5^{O}$ S) and Kintore ($21.5^{O}$ -$23.5^{O}$ S). The plots and transects used to collect information were spaced at least 4 km apart to reduce the possibility of multiple assessments of the same individual and repeat samples from a particular locality were not used if obtained less than three months apart. Generally, five gait measurements were recorded from a sequence of tracks that were clearly produced by a single individual moving along casually and ten faecal pellet produced per individual were usually measured.

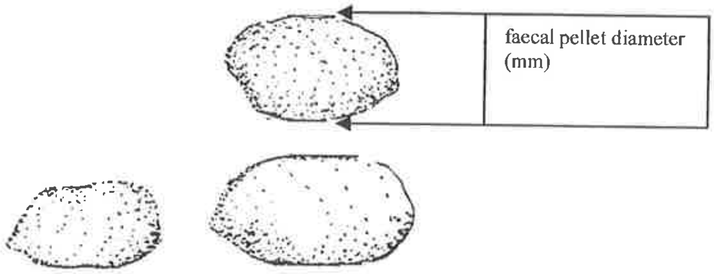

**Fig. 6.1** Bilby fecal pellets showing the measurement of scat diameter.

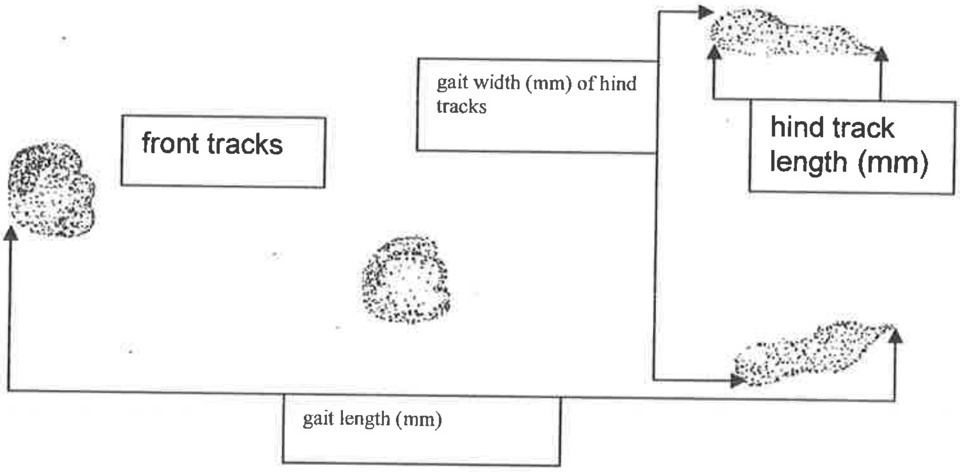

**Fig. 6.2** The track characteristics of the bilby showing the measurement of hind track length, gait width and gait length.

## Results

### *Tracks*

The age of individuals (N=8 males and 8 females) used to gauge gait size ranged from 90 to 1509 days, and weight ranged from 300 to 2054 g. The gait width for the sample ranged from 58 to 117 mm and gait length from 70 to 281 mm. Both gait width and gait length increased with bilby weight (**Fig. 6.3**) and weight explained 76% of the variation in gait width (equation: width= 0.0284weight + 53.81, $F_{1,62}$=642.7, P<0.001, $r^2$=0.761) and 73% of the variation in gait length (equation: length= 0.0669weight + 119.4, $F_{1,62}$= 318.3, P<0.001, $r^2$=0.728). However, there was a stronger relationship between weight and gait width plus gait length that explained 86% of variation (equation: width+length= 0.0953weight + 173.21, $F_{1,62}$=561.3, P<0.001, $r^2$=0.861). Deviation from linearity was not significant ($F_{18,62}$=1.6, P>0.05).

Inverse prediction indicated that a gait width+length size of 202 mm was produced by a 300 g individual and 220 mm was produced by a 500 g individual. A gait width+length size of 288 mm was produced by a female or small male around 1200 g and a gait size greater than 326 mm was produced by an individual greater than 1600 g. The 95% confidence intervals calculated using the mean of five gait width+length measurements indicated a gait size of >335 mm (i.e. individuals weight >1700 g) was required to achieve good separation from females of 1200 g (**Table 6.1**).

If the gait width+length size was derived from an average of 10 values, a gait size of >326 mm (i.e. individuals weight >1600 g) provided good separation from females of 1200 g. To achieve 95% confidence that animals were <500 g using an average of five measurements required a gait size <196 mm. However, a gait size <202 mm derived from an average of 10 measurements indicated with 95% confidence that an individual was <500 g.

*Faecal pellets*

The individuals (N= 10 males and 11 females) used to gauge faecal pellet size ranged in age from 82 to 1301 days and from 160 to 2510 g in weight and the diameter of faecal pellets ranged from 5.0 to 12.0 mm. Pellet diameter increased with bilby weight and 79% of the variation in pellet size was explained with the power relationship (equation: diameter = 1.507weight$^{0.263}$, $F_{1,81}$=1684, P<0.001, $r^2$=0.791). Deviation from linearity was also significant ($F_{27,81}$=15.5, P<0.001) suggesting predictions with the equation should be made with caution. There was broad variation in pellet size once weight of individuals exceeded about 500 g and large males could not be confidently separated from large females using faecal pellet measurements (**Fig. 6.4**). However, individuals greater than 500 g were unlikely to produced pellets <7.0 mm diameter. An average pellet diameter of 6.8 mm derived from 10 samples indicated the pellets were produced by an immature-independent individual of 300 g with upper 95% confidence limits of 510 g (**Table 6.1**). An average of 6.8 mm based on five pellet measurements resulted in an upper 95% confidence interval of 625 g.

**Table 6.1** The 95% confidence intervals calculated around a predicted weight value based on gait width+length (mm) and faecal pellet diameter (mm) derived from an average from five samples (i.e m=5) and from 10 samples (i.e.m=10).

| | Parameters relating to individuals of different size | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Average gait size (mm) | 192.3 | 201.8 | 211.3 | 220.1 | 287.6 | 325.7 | 335.2 | 344.8 |
| Weight average (g) | 200 | 300 | 400 | 500 | 1200 | 1600 | 1700 | 1800 |
| Confidence intervals for average gait size derived from five samples: | | | | | | | | |
| Weight U95%CI (g) | 460.6 | 560.0 | 659.5 | 759.1 | 1458.9 | 1860.9 | 1961.6 | 2062.4 |
| Weight L95%CI (g) | -65.2 | 35.9 | 136.9 | 237.8 | 941.4 | 1341.4 | 1441.1 | 1540.8 |
| Confidence intervals for average gait size derived from 10 samples: | | | | | | | | |
| Weight U95%CI (g) | 391.6 | 490.7 | 589.9 | 689.3 | 1388.4 | 1790.7 | 1891.6 | 1992.6 |
| Weight L95%CI (g) | 3.8 | 105.2 | 206.5 | 307.6 | 1011.9 | 1411.6 | 1511.1 | 1610.6 |
| | | | | | | | | |
| Average pellet diameter (mm) | 6.1 | 6.8 | 7.3 | 7.7 | 9.8 | 10.6 | 10.7 | 10.9 |
| Weight average (g) | 200 | 300 | 400 | 500 | 1200 | 1600 | 1700 | 1800 |
| Confidence intervals for average pellet diameter derived from five samples: | | | | | | | | |
| Weight U95%CI (g) | 418.4 | 624.7 | 834.5 | 1047.8 | 2628.8 | 3588.8 | 3834.2 | 4081.7 |
| Weight L95%CI (g) | 87.1 | 135.6 | 184.7 | 234.0 | 576.1 | 767.7 | 815.1 | 862.4 |
| Confidence intervals for average pellet diameter derived from 10 samples: | | | | | | | | |
| Weight U95%CI (g) | 344.4 | 510.5 | 679.5 | 851.8 | 2144.6 | 2940.5 | 3145.0 | 3351.4 |
| Weight L95%CI (g) | 105.9 | 166.0 | 226.8 | 287.8 | 706.2 | 937.0 | 993.8 | 1050.3 |

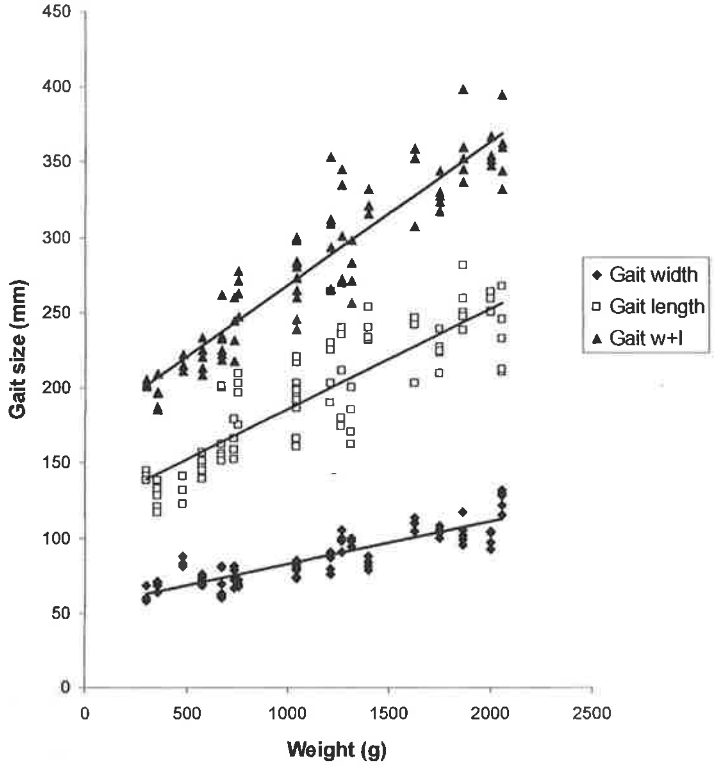

**Fig. 6.3** The relationship between gait width, gait length and gait width+length and bilby weight.

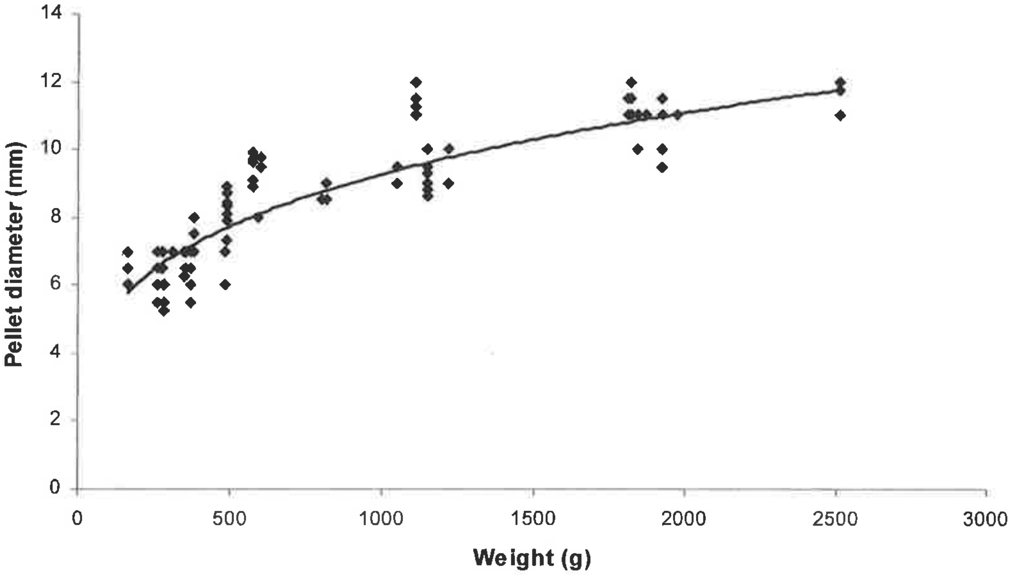

**Fig. 6.4** The relationship between faecal pellet diameter and width and bilby weight

*Application of the procedures*

Estimates of the age class of individuals were made on 80 occasions and from 56 independent locations. A number of individuals were present at a locality on some occasions. Six of the 51 gait measurements and 2 of the 29 faecal measurements indicated immature individuals were present and this sign was restricted to the mid-latitudinal (Tennant Creek and the Granites) zones of the study area (**Table 6.2**). No sign of immature individuals was recorded from the northern zone (Newcastle Waters) or the southern zone (Kintore). Medium-sized individuals (adult females or small mature males) were distributed evenly throughout the study area whereas large males were not evident at the Kintore latitude but relatively common (5 of the 6 gait measurements) at the Newcastle Waters latitude (**Table 6.2**).

**Table 6.2** The occurrence of different age classes of bilby from four latitudinal zones in the Tanami Desert determined from measurements of gait size or faecal diameter. Individuals from more than one age class were recorded at some of the localities sampled. The immature class included individuals with a mean gait (width+breadth) <196 mm or a mean faecal diameter <6.8 mm and the large male class included individuals with a mean gait (width+breadth) >335 mm. The mature Female/small male class had a mean gait (width+breadth) 196-335 mm and the Adult class had a mean faecal diameter >6.8 mm.

| | Gait (width+breadth) measurements | | | | Faecal pellet measurements | | |
|---|---|---|---|---|---|---|---|
| | Immature | Female/small male | Big male | Localities | Immature | Adult | Localities |
| Newcastle Waters | 0 | 3 | 5 | 6 | 0 | 1 | 1 |
| Tennant Creek | 3 | 10 | 1 | 10 | 1 | 14 | 14 |
| The Granites | 3 | 28 | 11 | 32 | 1 | 8 | 8 |
| Kintore | 0 | 3 | 0 | 3 | 0 | 6 | 6 |
| Total | 6 | 44 | 17 | 51 | 2 | 29 | 29 |

## Discussion

*Development of procedures*

Footprint details have been used widely to identify species as well as derive relationships with the body size of some species (Brooks *et al.* 1998; Lizcano and Cavelier 2000). However, gait characteristics are also unique to many species and provide additional opportunity to identify an individual's size and behaviour. A number of field guides are available that provide good descriptions, drawings and size details of footprints (Morrison 1981; Triggs 1996; Walker 1996) but a quantitative description of gait is lacking. This has resulted in an emphasis on the interpretation of the print size and shape to identify a species and the reliance on prepared tracking surfaces to procure clear prints (Engman *et al.* 2000).

There is some advantage in using gait dimensions because the measurement error is relatively less affected by a deterioration of print clarity from the weathering and disturbance of the substrate compared to footprint dimensions. The disadvantage is that gait size and pattern left by a species will depend on how fast the individual was moving and hence, the consistent selection of a particular gait pattern for measurement is necessary to reduce within individual variation if this technique is to be applied successfully.

Both the footprint and gait characteristics allow the bilby to be accurately identified in the field and furthermore, the sexual dimorphism in size among males and females provides an opportunity to identify different size classes among individuals. Although weight is not an accurate indicator of bilby age over the entire life span of an individual, the measure may be used to separate immature young from mature animals and large males from adult females or younger males (Southgate *et al.* 2000). The use of weight as the explanatory variable also allowed a single relationship to be developed for both sexes. The relationship between gait width and gait length, and weight was best when paired values of gait width and gait length were summed. Less variability of a gait width+length measure resulted most probably from a tendency for gait length to increase in size and gait width to reduce as individuals moved forward more quickly. Adding gait length to gait width was compensatory. A gait width+length measurement of 325 mm identified a male of around 1700 g. If the average of five width+length gait measurements was equivalent or greater than 325 mm it could be confidently assumed that the tracks did not belong to a 1200 g female. The upper 95% CI for a 1200 g individual and the lower 95%CI for a 1700 g individual crossed at approximately 1450 g. Individuals with a width+length gait measurement of less than 220 mm were likely to fall within the immature-independent class (<180 days age or 500 g). However, a value of less than 202 mm from an average of 10 measurements was required to achieve 95% confidence that an individual was less than 500 g. In general, the size of confidence intervals surrounding the inverse predicted value were very sensitive to number of measurements used to estimate the *y* value (eg. gait width+length or faecal pellet diameter). Using 10 instead of five measurements to calculate the *y* value significantly narrowed the confidence intervals.

The relationship between faecal pellet diameter and weight was not strong especially for mature males and females. The large spread of pellet sizes for individuals beyond the weight of 500 g made the regression equation impractical to invert and use for the prediction of bilby weight. However, encountering faecal pellets that were less than 6.8 mm diameter based on an average of 10 measurements placed individuals within the immature-independent age class (<180 days age or <500 g approximately).

Collecting an adequate number of samples of gait width+length or faecal pellets to determine the presence or absence of a particular age class is less onerous than trying to capture individuals, especially if many sites are being sampled. It would have been advantageous if both the relationships between pellet size and weight and gait size and weight were strong because faecal pellets can often be recovered from a feeding site long after the tracks of individuals have disappeared and, conversely, bilby tracks are sometimes encountered where there is no obvious feeding activity. Nevertheless, the relationships presented provide an opportunity to identify juveniles where faecal pellets are present and accurately define three age classes where tracks are present thus allowing basic questions regarding the structure of the population to be answered. The collation of gait and pellet measurements from other bilby reintroduction programmes to access the accuracy of the equations presented would be useful.

### *Application of the procedures*

The value of the above approach is exemplified by work in the Tanami where both track and faecal pellet measurements indicated that sign of immature individuals (<500 g) was relatively uncommon and limited to the mid-latitudes of the study area. Monitoring of the spatial pattern and relative abundance of the bilby also indicated that sign was encountered more consistently and commonly in the two mid-latitudinal zones compared to the northern and southern zones (Southgate *et al.* 2005). The results, although based on a small sample size, suggest that the production of bilby young may be restricted to parts of the study area where bilby density is highest. If true, these results imply that much of the bilby distribution in the Tanami Desert, delineated by the extent of occurrence, may function as a dispersal sink. The area of occupancy as delineated by the presence of immature individuals may be a more appropriate and useful means to determine the status of this species than the extent of occurrence. Hence, the procedures to determine the distribution of immature bilby individuals may have important practical implications for the assessment of species status.

The procedures outlined in this paper could be used to develop a quantitative description of gait and track characteristics for a range of species. This would improve the accuracy of sign identification and enable passive monitoring to become broadly applied and less reliant on prepared tracking surfaces. It is worth noting that traditional Aboriginal people rely on both gait and footprints when tracking animals, allowing them to track over a range of surface types as well as interpret information on the characteristics of individual animals or populations.

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# Chapter 7

## Bilby distribution and fire: a test of alternative models of habitat suitability in the Tanami Desert[1]

*Preamble to Chapter 7*

In this chapter, I examine the distribution and prevalence of the bilby in the Tanami Desert and examine the factors that associate with habitat suitability for the species, particularly the influence of fire age or pattern. Four alternative habitat refugia models are derived using environmental variables described in Chapter 4 and the introduced predator and herbivore variables described in Chapter 5. Each reflected hypotheses proposed to explain the decline of medium-sized mammals in central Australia. I compare the deviance captured in each model with the deviance captured by a full model derived from all the potential variables examined. The full model was used to estimate the area of occupancy for the bilby and this is compared with the extent of occurrence, formulated by linking all localities of the bilby recorded during the survey.

The statistical modelling suggested that a single threatening process did not limit bilby distribution. For the entire study area, bilby prevalence associated most strongly with variables of mean annual rainfall, substrate type and the probability of dingo occurrence. Proximity to recently burnt habitat formed a significant predictor of bilby prevalence in a model derived for a reduced party of the study area where most sign was found.

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## Introduction

Virtually every species exhibits patchiness and variability over a range of spatial and temporal scales (Wiens 1995). The key to understanding factors that cause patchiness and limit distribution lies in the elucidation of the mechanisms (or processes) underlying the observed patterns and in the separation of components of variability (Austin 2002b; Caughley and Gunn 1996; Guisan and Zimmermann 2000; Levin 1992). Caughley (1994) pointed out that residual populations of threatened species tend to occur in habitats where threatening processes are least evident and not necessarily in the most favoured habitat. The concept of refugia has emerged to describe this phenomenon (Mackey *et al.* 2002). Refugia are defined as areas containing key habitat elements that allow a species to obtain resources, but where the effects of threatening processes are absent or ameliorated. Management may provide an effective means to improve habitat suitability if a link between species' prevalence and a manageable proximate factor such as fire or predator control can be demonstrated (Caughley and Gunn 1996). In this paper, we examine the refugia characteristics of a threatened species of Australian marsupial and determine whether fire age or pattern is a significant factor associated with habitat suitability.

The bilby *Macrotis lagotis* is a semi-fossorial bandicoot with adult females and males reaching a mass of 1200 g and 2500 g, respectively. The species is part of a suite of medium-sized (35-5500 g) native mammals (including rodents, bettongs, macropods, possums, dasyuirds and other bandicoots) that have declined dramatically or have gone extinct in arid and semiarid parts of Australia (Burbidge and McKenzie 1989; Morton 1990; Smith and Quin 1996). At the time of European settlement, the bilby was distributed over 70% of the Australian mainland, but now occurs in less than 20% of its former range (Southgate 1990a). Wild populations of the bilby are currently restricted to the Great Sandy, Gibson and Tanami Deserts of the Northern Territory and Western Australia, with an outlying population in southwest Queensland. The species is currently listed as vulnerable under national threatened species schedules (EPBC Act 1999). Fire offers potential as a management tool because some of the key food resources used by the bilby are promoted by fire (Southgate 1990b). Furthermore, fire is already a conspicuous feature in the Tanami Desert landscape (Allan and Southgate 2002; Griffin 1984) and Aboriginal people, who are custodians for the majority of the area, are comfortable and proficient in its use (Griffin and Allan 1986).

Statistical modelling provides a means to investigate the importance of ecological processes and spatially predict species distribution and has become a significant component of conservation science and management (Guisan and Zimmermann 2000; Scott *et al.* 2002). Austin (2002a) has argued that a crucial step in this form of modelling is the development of an 'ecological model' that includes the existing ecological knowledge and theory to be used or tested in the study. This consideration leads to the selection of a set of meaningful explanatory variables in relation to the spatial scale of the study (Burnham and Anderson 2002; Guisan *et al.* 2002). In our study, four competing models were tested to identify the characteristics of refugia for the bilby and the processes that may affect habitat suitability and limit the species geographic range, as outlined below.

*Introduced herbivore/ substrate model*

Stafford Smith and Morton (1990) proposed that most of arid and semiarid Australia is innately difficult for herbivorous and omnivorous mammals to inhabit because of the unpredictability of rainfall, poor soil fertility and low availability of moisture. They suggested that medium-sized mammals would be limited largely to paleodrainage lines, calcareous substrates and floodouts where fertility and moisture was greater, especially during drought. Morton (1990) went on to propose that the decline of medium-sized native mammal species in desert regions had resulted from waves of invading herbivores such as rabbits *Oryctolagus cuniculus*, livestock and camels *Camelus dromadarius* causing habitat degradation in the more productive areas. This implies that remnant medium-sized mammals would either not be reliant on these productive substrates for survival or be limited to productive substrates where introduced herbivores were scarce historically. The remnant distribution of the bilby in Australia provides some support for Morton's proposal because the bilby occurrence correlates well with an absence or low abundance of stock and rabbits (Southgate 1990a). If habitat degradation by introduced herbivores was the main process limiting bilby distribution in the Tanami Desert, there should be evidence for an interaction between substrate type and introduced herbivore distribution, with bilby prevalence proportionally greater on more productive substrates in parts of the landscape where introduced herbivores were in low abundance.

### *Introduced predator model*

Some have suggested that increased predation pressure resulting from introduced predators such as the fox *Vulpes vulpes* and feral cat *Felis catus* has been the primary cause of decline of native medium-sized mammals in Australian deserts (Burbidge and McKenzie 1989; Johnson *et al.* 1989; Kinnear *et al.* 1988). Feral cāts are now widespread in Australia (Dickman 1996), and while they do take the bilby as prey (Southgate, pers obs.; Moseby, pers. com.) there is some doubt about their role in the decline of the bilby and some of the other medium-sized mammals (Abbott 2002; Southgate 1990a). Similarly, dingoes *Canis familiaris* are widespread and take the bilby as prey (Paltridge, 2002; Palmer, pers. com.) but they have been in Australia for several thousand years (Corbett 1995) and have not been linked to the decline of the bilby (Southgate 1990a). In contrast, foxes have long been declared a formidable threat to bilbies and other medium-sized native animals (Abbott 2002; Finlayson 1961; Jones 1924). The fox is now widespread and abundant in southern Australia, and historic decline and current distribution of the bilby in Australia corresponds closely with the spread and current distribution of fox (Southgate 1990a). If predation from introduced predators was the main process controlling bilby distribution, it would be expected that bilby prevalence would be greater in parts of the landscape where the overall predator prevalence is low, particularly that of foxes.

### *Altered fire regime model*

An altered fire regime has also been proposed as a cause for the loss of native medium-sized mammals (Bolton and Latz 1978). Australian Aboriginal people have burnt the landscape for millennia (Bowman 1998) and it has been suggested that a mosaic of successional stages is necessary to provide the food and shelter requirements for many medium-sized mammals (Burbidge *et al.* 1988). The size of fires in parts of arid Australia has increased dramatically since Aboriginal people ceased traditional hunting practices and became more sedentary (Burrows and Christensen 1991). Fire is certainly an important process in the ecology of the bilby because seed from fire-promoted plants can form a substantial part of the bilby's diet (Southgate 1990b; Southgate and Carthew 2006) and therefore, fire regime is likely to affect habitat suitability. If the process of fire was important in controlling bilby distribution, it would be expected that bilby prevalence would be greater in parts of the landscape in close proximity to frequently burnt areas and where the heterogeneity of fire ages was high.

*Climatic/vegetation gradient model*

Rainfall and temperature parameters regulate site productivity and microclimate suitability (Begon *et al.* 1996) and these physical environmental components are clearly important for plants (Austin 2002a). However, climatic variables also have considerable importance in predicting faunal occurrence, as demonstrated by bioclimatic models (Burgman and Lindenmayer 1998). For example, the strongest models developed to predict dingo, fox and camel distribution in the Tanami all included mean annual rainfall as a significant variable (Southgate *et al.* 2006b). Short and long term changes in climate may therefore alter the presence of threatening processes and alter the extent of habitat refugia for a species such as the bilby. This model is similar to the *herbivore/substrate model* in that it predicts that greater bilby prevalence will occur in areas with high, persistent productivity, but only in areas where introduced herbivores and predators are scarce. Correspondingly, there would be a stronger association between bilby prevalence and direct variables such as rainfall, temperature or vegetation compared to other more proximate variables such as substrate, fire and herbivore and predator probability of predator occurrence.

Here, we use data from three independent monitoring techniques and opportunistic records to describe bilby distribution and estimate the extent of occurrence. Statistical modelling techniques are applied to detect a functional relationship between the bilby and environmental variables, develop predictive distribution models and assess area of occupancy. The four *a priori* ecological models are used to derive competing statistical models. An analysis is conducted using presence/absence bilby data from 1) the entire study area and 2) part of the study area where 95% of bilby activity was recorded. We rank the strength of each *a priori* model and a global model derived from all the key explanatory variables. The strongest, most parsimonious predictive model was evaluated against independent data by calculating the area under the Receiver Operating

Characteristic (ROC) curve. The approach provides an opportunity to scrutinise the propositions of Stafford Smith and Morton (1990) regarding the functioning of arid Australia and the hypotheses proposed to explain the loss of native species (Burbidge *et al.* 1988; Burbidge and McKenzie 1989; Morton 1990) and thus, the relationship of the bilby population to fire. We also address the question of whether extent of occurrence or area of occupancy should be used to assess the status of the bilby.

## Methods

### *Study area, climate and vegetation*

The study area was conducted over a 236,800 km$^2$ area of the Northern Territory and included most of the Tanami Desert bioregion and part of the Great Sandy Desert Bioregion (Thackway and Cresswell 1995). The area was bounded by coordinates of 129°E to134°E and 17°S to 23.5°S. Pastoral stations surround the study area on the northern, eastern and south-eastern side. The non-pastoral part of the study area, which included the two isolated stations, is referred to as the core area. The region was divided into four latitudinal zones of at least 170 km width and these zones: Newcastle Waters (17°-18.5° S), Tennant (18.5°- 20° S), the Granites (20°- 21.5° S) and Kintore (21.5°- 23.5° S) (**Fig. 7.1**).

Summers in the Tanami Desert are very hot and winters are cold to mild with mean daily maximum temperature during the hottest months of 39.3°C in the north of the study area and 36.2 °C in the south. The mean daily minimum temperature during the coldest month (July) in the north is 11.3 °C and 4.1 °C in the south (Bureau of Metereological records). Freezing point temperatures can occasionally occur at night during the winter in the south. A rainfall gradient occurs in the study area ranging from an annual average of 600 mm on the northern boundary to about 300 mm in the south. Rainfall unpredictability increases with greater aridity (Southgate *et al.* 2006a) and about 92% of mean annual rainfall occurs during summer in the north compared to 77% in the south.

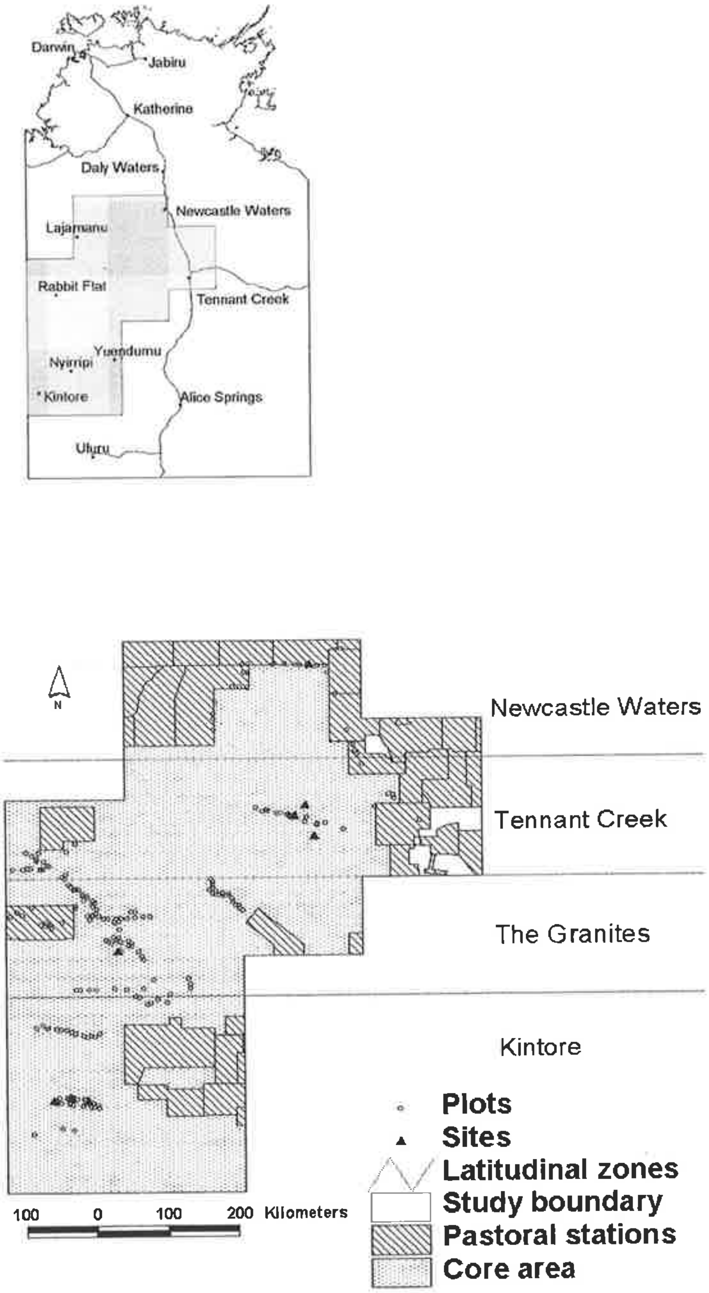


**Fig. 7.1** The study area situated in (a) the Northern Territory and the (b) location of random plots and sites and latitudinal zones.

The southern parts of the region are dominated by three spinifex or hummock grass species: *Triodia pungens, T. schinzii* and *T. basedowii,* with an overstorey of scattered shrubs and trees including species of *Grevillea, Acacia* and *Eucalyptus*. Areas of tea-tree *Melaleuca* spp. are associated with paleodrainage depressions and calcareous soils throughout study area (Foulkes *et al.* 1995; Gibson 1986). In the south there are discontinuous communities of mulga (*A. aneura*) and extensive areas of desert oak (*Allocasuarina decaisneana*) (Harrington *et al.* 1984). Spinifex grasses become less dominant on the northern edge of the study area and are replaced by other grass species. Trees and shrubs including subtropical species such as Bauhinia (*Lysiphyllum caronnii*), lancewood (*A. shirleyi*) and bullwaddy (*Macropteranthes kekwickii*) also increase in height and cover. Fire is a common feature in the Tanami Desert, especially in the central and northern parts (Allan and Southgate 2002).

### *Animal identification and monitoring techniques*

Animal tracks were the primary method used to identify the occurrence of animal species on plots or transects during the study (Paltridge and Southgate 2001; Southgate *et al.* 2005). The European people involved in the fieldwork were skilled in the identification of animal sign and were assisted by traditional Aboriginal people who accompanied us on all trips. The range of species identified included the bilby *Macrotis lagotis*, European rabbit *Oryctolagus cuniculus*, camel *Camelus dromedarius*, red fox *Vulpes vulpes*, feral cat *Felis catus* and dingo *Canis familiaris*. Tracks were scored as either *fresh* (<3 nights) or *old* because animal size and environmental conditions affect track persistence and clarity (Southgate *et al.* 2005). Only plots with fresh sign were considered in the generalised linear modelling to determine habitat occupancy. Random plots and transects were located away from vehicle tracks and roads because of the propensity of some species to use these thoroughfares (Mahon *et al.* 1998).

### Random and opportunistic plots

In total, 207 random plots were selected using restrictive random sampling stratified on substrate and fire age categories (see Southgate *et al.* 2005 for a description of stratification). The combination of fire history layers used to create this classification was adjusted depending on the year a particular site was sampled. Each random plot was separated by at least 4 km and the selected random plots were given coordinates in the laboratory. A geographic positioning system (GPS) was used to locate the plots in the field (**Fig. 7.1**). Opportunistic plots were localities where bilby sign was encountered opportunistically, mostly on the edge of the species' known range. The random and opportunistic plots were visited once and a search for animal tracks was conducted within a 200 x 300 m quadrat over the period of one hour. In addition, a 300 point vegetation transect was sampled using a point intersect method with a wheel point apparatus (Griffin 1989). Bare ground, litter or foliage was recorded at each point plus the species and height of foliage. Ground cover was categorised as spinifex, soft grass (non-spinifex), forb, or litter. The cover of shrubs or trees in the overstorey (>0.5 m) was also calculated. The substrate type and fire age were assessed during the vegetation sampling (see Southgate *et al.* 2006a). Plots in the Granites and the Kintore zone were sampled mainly in the period May 1996 to June 1997. Sampling of plots in the northern zones concluded in April 1998.

Fixed transects

Track activity of animals was monitored 6-8 times on 16 fixed transects located at eight sites to determine whether a locality were occupied by bilbies persistently during the study. Three sites, spaced about 25 km apart, were located in both the Kintore and Tennant Creek zones and one site was located in each of the Granites and Newcastle Waters zone (**Fig. 7.1**). The sites consisted of two 10 km tracking transects: one located in sand plain/dune substrate and the other in drainage substrate. The exception was Newcastle Waters zone where both transects were located in sand plain because of the absence of drainage substrate. Each transect was separated by about 5 km from the other and located more than 500 m from permanent vehicular tracks. Transects were divided into 500 m cells and the presence or absence of tracks of each species in each cell was recorded (Paltridge and Southgate 2001). In most cases, transects were sampled while travelling on a 4wd All Terrain Vehicle (ATV) at about 10 km $hr^{-1}$ on three consecutive mornings every four months between March 1996 to December 1998. The surface of each transect was prepared prior to the first day of sampling and on consecutive days by dragging an iron post and chain behind the ATV. A strip width of about 1.4 m was prepared.

### Aerial transect and validation plots

A Robinson two-seater helicopter was used to search for sign of bilby diggings. This aerial survey method provided an opportunity to measure the distance between putative bilby sign along a largely linear transects and to estimate the dispersion of bilby activity in the study area. The helicopter was flown at a ground speed of 30-40 knots $hr^{-1}$ (55-74 km $hr^{-1}$) at a height of 15-20 m above the ground and a search strip of about 20 m width was surveyed by the observer. The observational data and the route of the helicopter were logged with a Magellan Pro Mark X GPS and down-loaded to a laptop computer in the field using the Mstar capture program. The technique was used to survey an area north-west of the Granites to the Western Australian border in May 1999 and another area between Newcastle Waters and Wave Hill Station at the end of August 1999.

Validation plots (300 x 100 m) were visited under the flight-path and used to determine the rate of false-positive and false-negative error of data collected by the aerial survey technique. A comparison of ground-truth data with that collected from the air indicated that less than 4% of true bilby activity was missed from the air and putative bilby sign recorded during the aerial survey was extremely conservative in its reflection of actual bilby activity (Southgate *et al.* 2005). The bilby occurrence data collected from the validation plots were used to evaluate the occupancy models derived using random plot data. The plots were screened to remove those less than 4 km apart and in total, data from 74 were used.

### *Explanatory variables*

Arcview 3.1 (Environmental Systems Research Institute, 1996) with the spatial analyst extension was used as the geographic information system (GIS) platform. Plot locations were intersected with spatial data to extract explanatory data for each point. The GIS was also used to determine the number of attribute classes within a specified radial distance of a plot, otherwise referred to as a neighbourhood analysis. Polygon data were converted to a raster data at 0.002 ° resolution. Not all environmental variables used in the modelling were stored or transferable to spatial layers.

### Climate variables

Raster coverages of mean annual rainfall and mean minimum and maximum temperature in the study area were derived from the Australian Natural Resource Data library. These splined data surfaces are at 0.05° resolution (roughly 5 km) and were derived from data for the period January 1980–December 1999. To overcome the scarcity of rainfall stations in the vicinity of the study plots, raster layers of estimated monthly rainfall data for the study region were purchased from the Bureau if Meteorology (BOM). These data were provided at 0.25° resolution and were derived using the Barnes successive correlation technique that links designated weather stations across Australia (Jones and Weymouth 1997). These data were used to derive antecedent cumulative rainfall for 3, 6, 12 and 24 month periods, rain since fire and residual rainfall for 12 and 24 month periods for plot locations.

### Substrate variables

Stafford Smith and Morton (1990) and James (1995) ranked the productivity of substrate type in arid Australia. Sand plains and dunes were classed as least productive because of low fertility and poor water holding ability of sediments. Deep red earths, red sandy loams with lateritic content and the skeletal soils associated with outcrops were considered slightly more productive than sandy substrates. Both the lateritic and skeletal soils mostly occur in slightly elevated situations and consequently inundation is infrequent, but the small-scale redistribution of water can support more nutritious grasses as well as large woody perennials including mulga *Acacia aneura*. Calcareous earths and cracking clays were considered more fertile again and support chenopod shrublands and tussock grasslands. The areas regarded as the most productive run-on and deposition zones are represented by flood-outs and paleodrainage lines and these areas can be subject to inundation following exceptional rainfall.

Geological mapping produced by Australian Geological Survey Organisation (AGSO) was purchased and geological units were merged to produce six substrate categories: calcareous (c), drainage features (d), laterite (l), rock (skeletal) features (r), sand plain and dune (s), and black soil and salt lakes (bsl). The selection process is outlined in Southgate *et al.* (2006c). The grain-size of substrate types was approximately 0.2 km, based on the diameter of the smallest mapped vector. This mapping was found to be 87% accurate when assessed against ground truth data (Southgate *et al.* 2006a).

A number of substrate classifications were produced with different merged combinations of the six categories. Salt lakes and areas of black clay soils and productive calcareous and drainage substrates accounted for less than 8% of the core study area. Lateritic and skeletal soils associated with outcropping occurred on ~10% of the core study area, and sand plains and dunes accounted for the remainder (Southgate *et al.* 2006a). A neighbourhood analysis was performed to determine the variety of the six substrate classes in the vicinity of each cell centroid at different sized radii (1, 2.5, 5,10 and 25 km). This provided an indication of the extent to which substrate richness varied with *grain-size* in the study area. The distance from a plot to each substrate class and some merged substrate classes (eg. calcrete+drainage) was calculated.

### Fire and vegetation variables

The annual extent of fire 1984-1999 in the Tanami region was derived from the Central Australian fire history database (Allan and Southgate 2002). The fire history for the period 1986 onwards was mapped from Advanced Very High Resolution Radiometer (AVHRR) National Oceanic and Atmospheric Administration (NOAA) satellite imagery at a resolution of approximately 1 km. The fire data were stored in vector format with a separate coverage for each year from 1995 onwards. Fire data were merged to produce three categories: *recently burnt* (1-2 years old), *intermediate* (3-6 years old) and *old* (greater than 6 years old) based on previous studies that examined the recovery of spinifex following fire (Griffin 1992). This mapping was found to be 91% accurate when assessed against ground truth data (Southgate *et al.* 2006a). Time since fire was also used as a variable.

Distance from a plot to areas burnt in the previous one, two and one+two years was calculated. A neighbourhood analysis of fire ages at different radii (1, 2.5, 5, 10 and 25 km) was conducted to indicate changes in fire-age heterogeneity across the study area.

Because the plots were sampled over a number of years, the set of fire history information used in the analysis was adjusted according to the sample date of a particular plot.

Finally, the percentage cover of spinifex, total ground cover and shrub cover recorded at each plot were used as separate explanatory variables because the available vegetation mapping was found to be too coarse grained and relatively inaccurate (Southgate *et al.* 2006a).

Predator and herbivore variables

The predicted probability of feral cat, fox, dingo and camel occurrence across the study area was derived using similar generalised linear modelling procedures (Southgate *et al.* 2006b) as described here. These data layers provided explanatory data to examine the substrate/herbivore and the predator ecological models. The occurrences of rabbit and feral stock were too few to warrant analysis. Cats were by far the most widespread species and sign was encountered on 74% of plots. A statistical model consisting of only significant static variables had little discrimination function (64±4%). Fox sign was encountered on 22% of plots and the model of fox probability of occurrence also had relatively little and imprecise discriminative power (67±37%). Dingo sign was encountered on 18% of plots and the model had reasonably good discriminative power (74±5 %). Camel sign was encountered on 36% of plots and the model also provided reasonable discriminative power (79±3%). Discriminative power greater than 70% is considered good (Pearce and Ferrier 2000) and therefore, caution is needed with the interpretation of results based on the probability of occurrence for foxes and feral cats because of the low discriminative power and poor precision.

*Variable selection and model fitting*

Generalised linear modelling (GLM) has been widely applied to examine the relationship between a response variable and the variety of explanatory covariates (Guisan *et al.* 2002; McCullagh and Nelder 1989) and to predict the habitat occupancy and species distribution (Gibson *et al.* 2004; Lindenmayer *et al.* 1995; Manel *et al.* 1999; Osborne *et al.* 2001). GLMs are a useful form of statistical model because binary variables and non-normally distributed response variables can be accommodated and was used here. A two step process was used in variable selection and model fitting. The variables examined included a mixture of actual (eg. dingo occurrence) and mapped (eg. dingo probability of occurrence) variables. This approach was used to explore whether inaccuracies between the mapped and actual data affected modelling outcomes and investigate the impact of variables that lacked adequate spatial mapping (eg. vegetation cover). All 51 variables were initially fitted and the strongest significant ($p<0.05$) variables were considered further to develop multi-variable models (see **Appendix 7.1**). Statistical models were derived for each *a priori* ecological model using a backwards step variable selection routine (Venables and Ripley 2003) in R from the subset of the relevant variables. Key variables identified in the candidate models were used to derive a global model, again with a backward step variable selection routine. Analysis was conducted on data collected from 1) the entire study area and, 2) a reduced part of the study area containing the two central zones (Tennant Creek and the Granites) as this area contained greatest bilby presence and evidence of recruitment (Southgate 2005).

A number of considerations were taken into account when developing each candidate statistical model. The variables contained within a model were scrutinised for ecological realism using partial plots of univariate fitted functions. The colinearity of variables used in the models was assessed and highly correlated (>0.7) distil variables were removed in favour of more proximate variables. Harrell *et al.* (1996) recommended that the number of predictors offered for inclusion in a model should be limited to less than $m/10$ where $m$ equals to the least prevalent class of a response variable. In our situation, $m$ was 29 for the full study area and thus no more than three predictors were included in a model.

Akaike's information criterion (AIC) and the amount of deviance reduction were used to select among models within a study area, and that with the largest Akaike weight ($w$) considered the best. An adjusted $D^2$ provides a measure of deviance reduction to compare models with different combinations of variables and interaction terms between the reduced and entire study area, where $D^2 = 1-((n-1)/(n-p)) * (1- D^2)$ where $D^2 =$ (null deviance-residual deviance)/null deviance, p = the number of parameters and n= the number of observations (Guisan and Zimmermann 2000).

*Model evaluation*

The predictive performance of the strongest model was examined using independent evaluation data with the receiver operating characteristic (ROC) technique (Guisan and Zimmermann 2000; Pearce and Ferrier 2000). A ROC curve is a plot of true positive cases (or sensitivity) on the y-axis against corresponding false positive cases (or 1-specificity) on the x-axis across a range of threshold values (Fielding and Bell 1997). The area under the curve (AUC) provides a measure of the discrimination ability, and can vary from perfect with a value of 1.0 to no better than random with a value of 0.5. The differences between the area under two ROC curves generated by two or more models provides a measure of the comparative discrimination capacity of these models when they are applied to independent evaluation data (Pearce and Ferrier 2000).

## Results

### *Spatial and temporal trends in bilby prevalence*

Bilby sign was found on the fixed transects in the Newcastle Waters, Tennant Creek and the Granites latitudinal zones, but not in the Kintore latitudinal zone. Although greatest bilby prevalence was found in the north compared to the mid-latitudes overall (**Table 7.1**), a large proportion of this activity was recorded when sampling began in 1995 (**Fig. 7.2**). Repeated sampling of fixed transects indicated bilby prevalence appeared to decline in all the latitudinal zones during the study period, especially in the Newcastle Water zone. However, chi-squared analysis using data combined from these zones indicated that the proportion of transects with bilby sign was not significantly different among years using the measure of activity/ sample period ($\chi^2_{,3df}$ =4.05, p>0.05) or activity/ sample days ($\chi^2_{,3df}$ =5.35, p>0.05). Few localities were occupied persistently. Although bilby sign was recorded on eight of the 16 fixed transects, sign was recorded more than twice on only three and regularly on only one. At this latter locality, sign was recorded on seven consecutive samples from the eight visits between September 1995 and July 1997. Similar persistent activity was observed at a non-transect locality near the transect in the Granites zone where sign was noted on five consecutive occasions between May 1996 and May 1998.

Bilby sign was found on 38 of the 207 random plots sampled in the entire study area. Fresh bilby sign was recorded on 29 of these plots. Most bilby sign was recorded in the Tennant Creek and the Granites latitudinal zones, where fresh bilby sign was encountered on 25 of the140 plots sampled (**Table 7.1**). The random plot technique indicated that bilby sign was distributed evenly across the study area but was curvilinear in response to latitude (**Fig. 7.3**). Bilby prevalence was less in the northern latitudinal zone (Newcastle Waters)

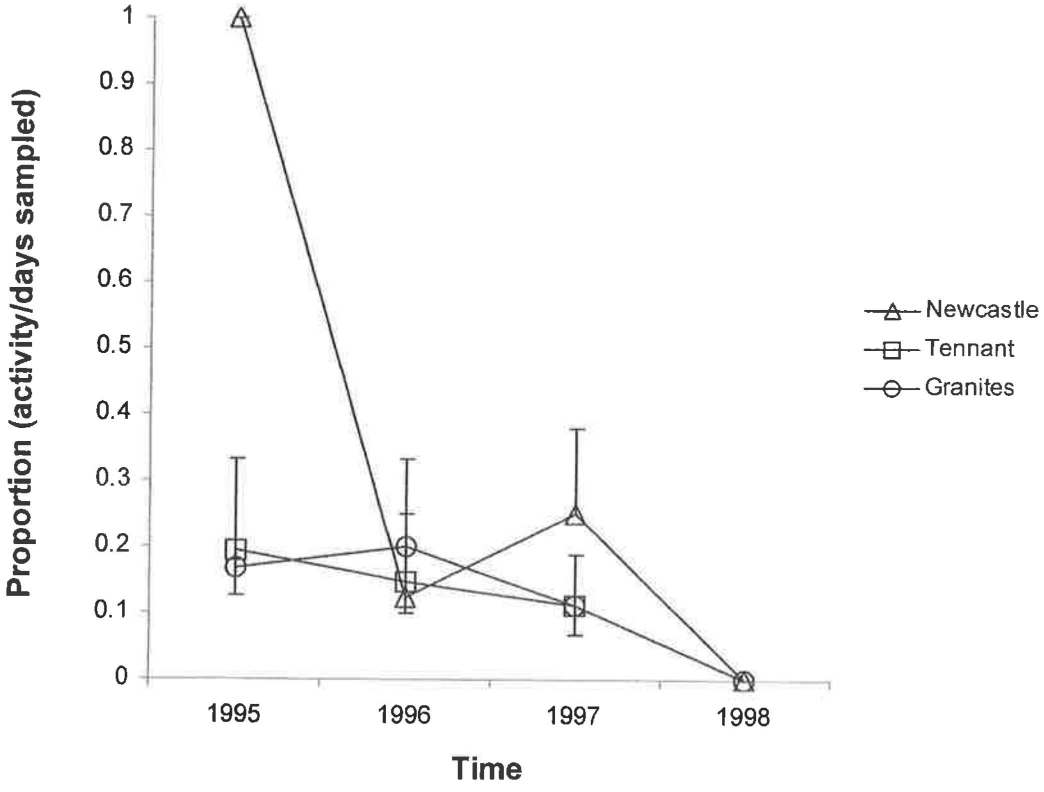


**Fig. 7.2** Changes in the amount of bilby activity recorded on fixed transects. The data represent the proportion of transects within a latitudinal zone with bilby sign + se.

compared to the two mid-latitudinal zones (Tennant and the Granites), and no activity was recorded on the plots in the southern zone (Kintore), where it was encountered only opportunistically.

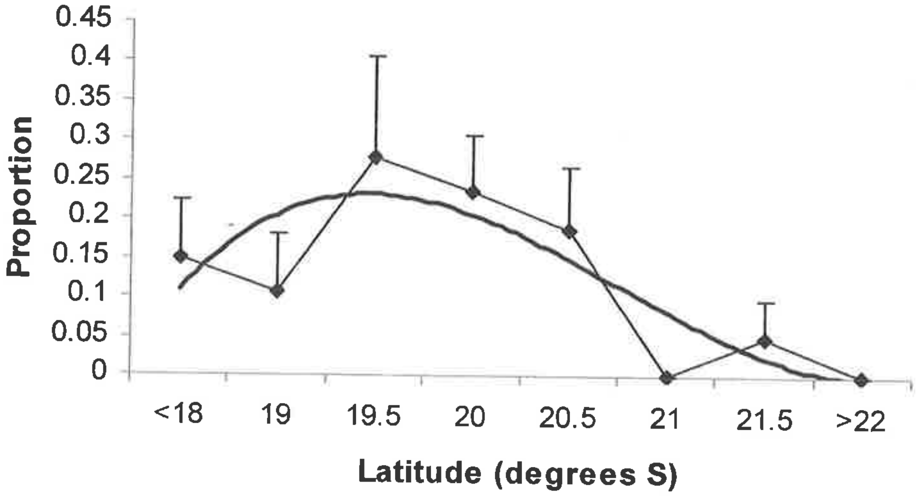
All of the 1084 km of aerial transect surveyed was in the Newcastle Waters, Tennant Creek and the Granites latitude. Putative bilby sign was encountered more frequently in the two mid latitudes and least in the northern latitude (Newcastle Waters) (**Table 7.1**). This equated to putative bilby sign being located every 143 km in the Newcastle Waters zone and every 18 km and 22 km in the Tennant and the Granites zone, respectively.

The total area of occurrence for the bilby in the Northern Territory derived from all records obtained during this study was estimated at over 235,000 km$^2$ but bilby prevalence clearly varied considerably within this area (**Fig. 7.4**).

**Table 7.1** Bilby prevalence recorded on fixed transects and random plots in relation to habitat type and latitudinal zone. The sample size (n) equates respectively to the sample period x number of transects for the fixed transects, the number of random plots sampled and the number of 4 km long cells sampled during the aerial survey. The number in parentheses indicates the mean distance in km between putative bilby sign.

| Substrate | Sand plain | Laterite/rock feat. | Drainage/calcrete | Combined | n |
|---|---|---|---|---|---|
| *Fixed transects* | | | | | |
| Newcastle Waters | 0.42±0.14 | - | - | 0.42±0.14 | 12 |
| Tennant Creek | 0.13±0.07 | - | 0.37±0.10 | 0.25±0.06 | 48 |
| The Granites | 0 | - | 0.57±0.20 | 0.28±0.12 | 14 |
| Kintore | 0 | - | 0 | 0 | 44 |
| *Random plots* | | | | | |
| Newcastle Waters | 0.19±0.09 | 0 | 0 | 0.17±0.08 | 24 |
| Tennant Creek | 0.13±0.05 | 0.41±0.12 | 0.14±0.14 | 0.26±0.07 | 42 |
| The Granites | 0.17±0.09 | 0.43±0.11 | 0.25±0.07 | 0.23±0.04 | 98 |
| Kintore | 0 | 0 | 0 | 0 | 43 |
| Mean | 0.14±0.04 | 0.41±0.08 | 0.23±0.06 | | |
| *Aerial survey* | | | | | |
| Newcastle Waters | 0.03±0.02 | - | - | 0.03±0.02 (143.8) | 108 |
| Tennant Creek | 0.23±0.04 | 0.19±0.1 | 0.16±0.11 | 0.22±0.04 (18.3) | 119 |
| The Granites | 0.04±0.04 | 0.46±0.27 | 0.41±0.15 | 0.18±0.06 (22.2) | 44 |
| Kintore | - | - | - | - | - |
| Mean | 0.12±0.02 (34.5) | 0.17±0.07 (23.4) | 0.26±0.09 (15.2) | | |

(a)



(b)

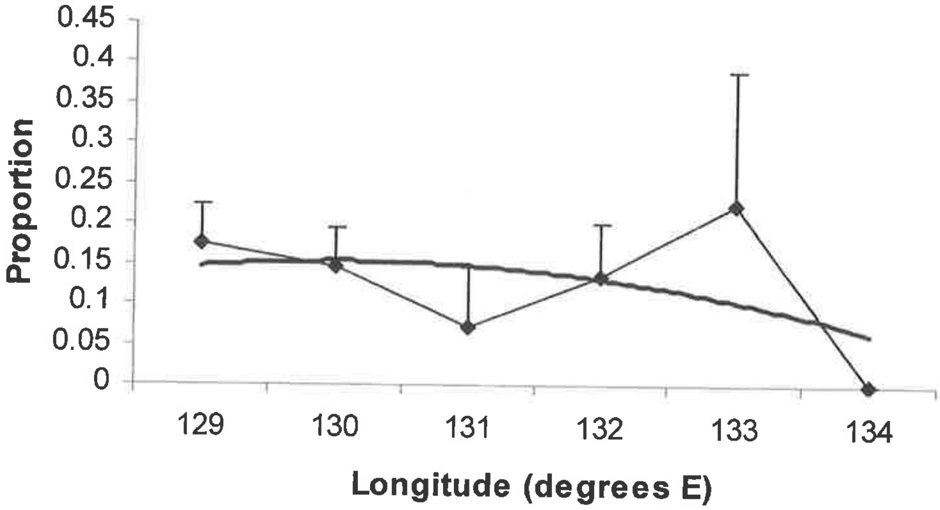


**Fig. 7.3** Bilby occurrence based on random plot sampling in relation to (a) latitude and (b) longitude. The data represent proportion of plots with bilby sign + se for each category of latitude or longitude. A fitted line through the data is also shown.

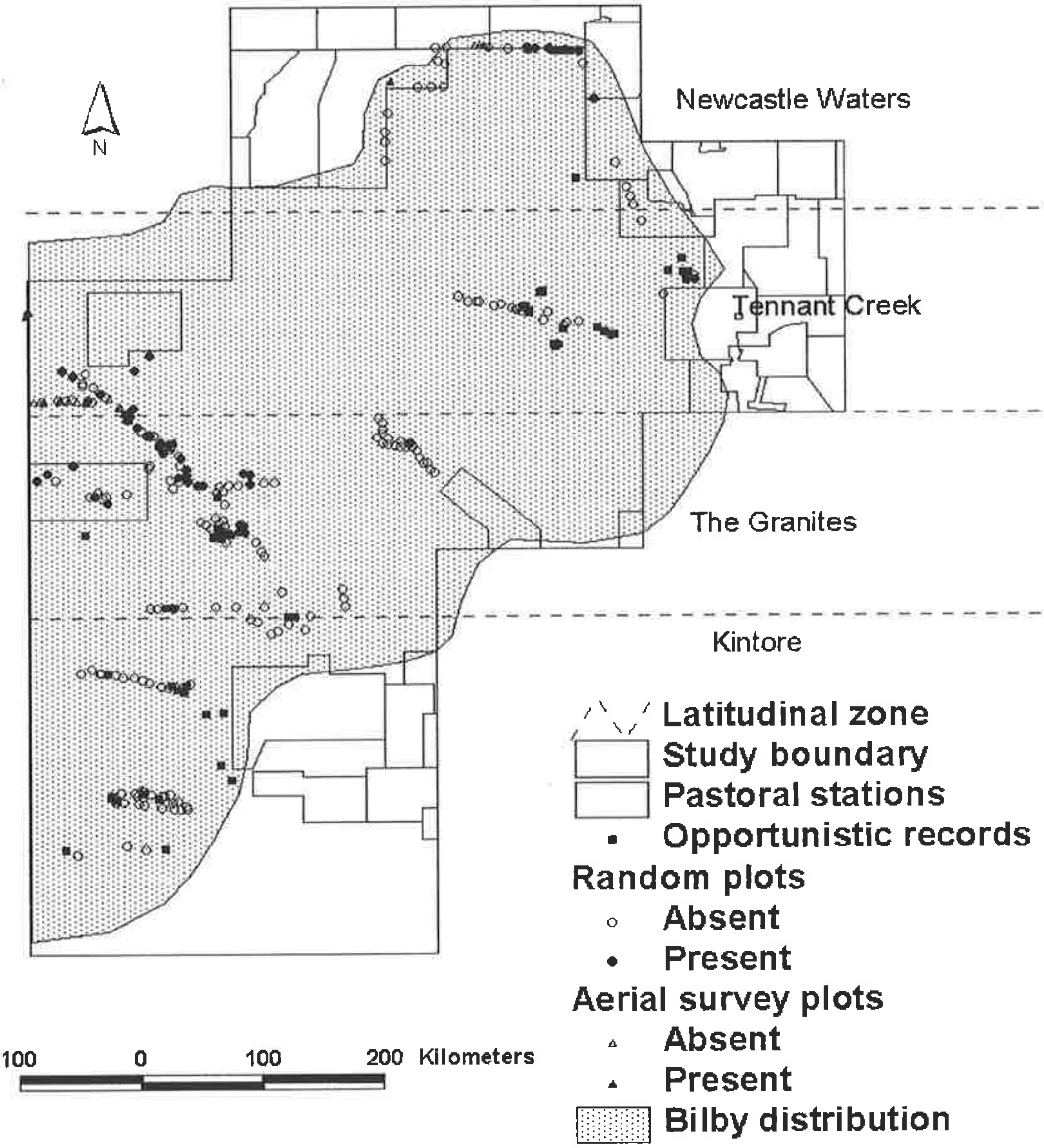


**Fig. 7.4** The estimated extent of occurrence of the bilby during the study period

### *Bilby–environment relationship*

#### Substrate & herbivores

The distribution of bilby sign varied substantially among substrate types (**Table 7.1**). All three survey techniques indicated that least sign was encountered on the sand plain and dune substrate that dominated the study area. Bilby prevalence increased on sand plain substrate in northern part of the study area and reduced in the south where sign became more restricted to laterite/rock feature or drainage/calcrete substrates. The random plot technique indicated that more bilby sign occurred on laterite/rock feature substrate compared to drainage/calcrete substrate, and the aerial survey data indicated the reverse with more bilby sign on drainage/calcrete substrate.

Substrate became a significant explanatory variable in the *introduced herbivore/ substrate* candidate models derived for the entire and the reduced study area. The model for the entire study area predicted greater prevalence of bilby activity on laterite and rock feature substrates, with increasing distance from drainage and calcrete substrates and where there was a higher substrate variety within a 2.5 km radius (**Table 7.2**). There was a negative association between bilby prevalence and camel probability of occurrence (see **Appendix 7.1**). However, this variable did not make a significant contribution to the multivariate model, nor was there a significant substrate: camel interaction in the relationship.

The model for the reduced study area included the same categorical substrate variable and the substrate variety variable found in the model for the entire study area. This model indicated that greater prevalence of bilby activity associated negatively with fluvial substrates (drainage and calcrete) and sand plain substrates and positively to areas where substrate variety was high within a 2.5 km radius. There was no significant substrate: camel interaction and the model for the entire study area captured more deviance than that for the reduced study area.

#### Predators

For the entire study area, the strongest *introduced predator* candidate model predicted that bilby prevalence would decline with the increasing probability of fox occurrence (**Table**

7.2). There was also a significant interaction between the probability of fox and the probability of dingo occurrence indicating there was little shared habitat use among the two predator species. A model that included only dingo probability as the sole variable was the next strongest model, with dingo probability associating positively with bilby prevalence.

For the reduced study area, the strongest model included the probability of dingo occurrence as the sole variable, and similarly predicted that bilby prevalence would increase with greater dingo probability of occurrence. Far greater deviance was captured by the predator model for the reduced study area compared to the model for the entire study area. Inclusion of the variables for cat, fox and dingo occurrence and the richness of predator species failed to improve model strength for the entire and the reduced study area.

**Table 7.2** Generalised linear models for the bilby from plots in the entire area and a reduced study area. Candidate models were derived from predator-, herbivore/substrate- and fire/vegetation-related variables (see Appendix 7.1 for detail on abbreviations). The full model was derived from all variables and the static model from only the gradient and substrate variables (see Appendix 7.2 for details).

| Data set | Model | Variables | adjusted $D^2$ | AIC | $w_i$ | Rank |
|---|---|---|---|---|---|---|
| Entire study area<br>n=207 | Substrate/ herbivore | substrate category + distance from substrate + substrate variety | 0.159 | 147.6 | 0.0017 | 5 |
| | Predator | fox probability + fox:dingo interaction | 0.118 | 147.2 | 0.0020 | 4 |
| | Fire | distance from area burnt | 0.066 | 157.7 | <0.0001 | 6 |
| | Climatic/vegetation | annual rainfall + annual rainfall$^2$ + minimum temperature | 0.186 | 143.8 | 0.011 | 3 |
| | Global model | substrate category + distance from substrate + dingo probability | 0.258 | 135.2 | 0.874 | 1 |
| | Static global model | substrate category + annual rainfall + minimum temperature | 0.211 | 139.1 | 0.120 | 2 |
| Reduced area<br>(Tennant Cr. & the Granites)<br>n=140 | Substrate/ herbivore | substrate category + substrate variety | 0.137 | 118.6 | 0.0043 | 4 |
| | Predator | dingo probability | 0.164 | 118.4 | 0.0049 | 3 |
| | Fire | fire category + distance from area burnt + fire variety | 0.102 | 124.3 | 0.0002 | 6 |
| | Climatic/vegetation | mean annual rainfall | 0.117 | 120.0 | 0.0022 | 5 |
| | Global model | substrate category + dingo probability +distance from area burnt | 0.24 | 107.9 | 0.922 | 1 |
| | Static global model | substrate category + annual rainfall | 0.178 | 113.2 | 0.066 | 2 |

### Fire

The strongest *altered fire regime* candidate model for the entire study area included a single significant variable of distance from area burnt in the previous 1 year and predicted that bilby prevalence would decline with increasing distance from recently burnt habitat. Other variables including the neighbourhood variety of fire ages within a 25 km radius and distance to areas burnt in the previous 1+2 years were significant but individually captured less deviance.

The strongest model for the reduced study area indicated bilby prevalence had a positive association with the category of recently burnt (<2 yr) habitat and negative association with increasing distance from areas burnt <1 yr. The fire model for the reduced study area captured more model deviance than for the entire area.

### Climate and vegetation

The *climate/vegetation gradient* candidate model for the entire study area included a positive association with mean annual rainfall and a negative association with rainfall as a quadratic term and lower mean minimum temperature. The quadratic function reflected the curvilinear response of bilby prevalence to the rainfall gradient in the study area (which corresponds closely with latitude).

The strong association between bilby prevalence and annual rainfall was also evident in the model derived for the reduced study area. No other variables contributed significantly to this model and it captured less deviance than the one derived for the entire study area. The inclusion of vegetation variables such as percentage ground, spinifex and shrub cover failed to improve the strength of the final models.

### Global model

Considering all potential variables, the strongest *global model* for the entire study area included substrate and dingo probability variables and captured 25.8% of the model deviance. The model predicted that greater bilby prevalence would occur on laterite and rock feature substrates located further from fluvial surfaces and with increasing dingo probability of occurrence (**Table 7.2**). A static model selecting from only climatic and substrate variables captured 22.1% of deviance.

The *global model* for the reduced study area indicated bilby prevalence associated negatively with sand plain and fluvial substrates and greater distance from areas burnt in <1 year and positively with greater dingo probability of occurrence. This model captured slightly less deviance (24%) than the one for the for the entire study area. A static model for the reduced study area that drew on only the variables of substrate and rainfall captured 19.8% of deviance.

*Model ranking, prediction and evaluation*

The AIC weights ($w_i$) indicated that the global (and static) models for both the entire and the reduced study area were stronger than each candidate model. For the full study area, the climatic/vegetation model was the next strongest followed by the predator and substrate/herbivore models, with the fire model ranked weakest. For the reduced study area, the predator model was slightly stronger than the substrate/herbivore model, followed by the climate/vegetation and fire models.

A probability surface derived from the equation for the global model for the entire study area indicated that bilby occupancy was greatest in a band that extended from the mid-west to the northeast part of the study area (**Fig. 7.5a**). With the type and intensity of sampling conducted during the study there was little probability ($p<0.15$) of encountering bilby activity in greater than 75% the core study area. The high predicted probability of occurrence identified in the northwest and southeast corner of the core study area coincides with parts of the region that were poorly sampled. The area under the curve of the ROC plot for the global model of bilby occupancy in the entire study area was 0.81±0.04 and indicated that the model was 81% accurate in distinguishing between presence and absence. The model had poor discriminatory power (0.44±0.09) when evaluated with the data from the 74 validation plots sampled in 1999. These plots were distributed mainly in the northern and western parts of the study area and bilby sign was recorded on 10 of these plots (**Fig 5b**).

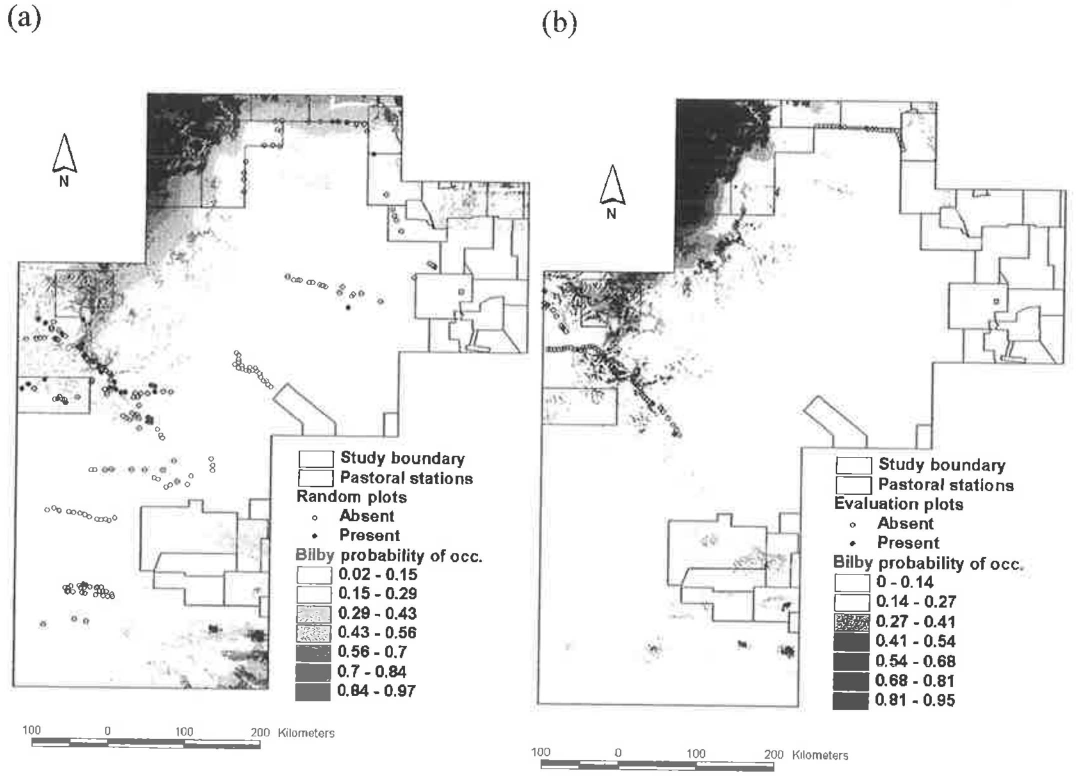


**Fig. 7.5** The predicted area of occurrence for the bilby based on the global model derived for (a) the entire study area and (b) the reduced study area. Random plots are shown in (a) and evaluation plots are shown in (b).

The global model for the reduced study area (n=140) produced a similar area under the ROC plot (0.79±0.04) and also had relatively poor discriminatory power (0.52±0.10) when evaluated with the plots sampled in 1999 (n=49). It also indicated that bilby prevalence would largely restricted to the northwest edge of the study area. Less of the southern part of the study area was identified as high quality habitat when compared to the model for the entire area.

## Discussion

### *Extent of occurrence*

Less than a century ago the bilby had a distribution that extended across approximately 50% of the Northern Territory and 70% of mainland Australia (Southgate 1990a; Watts 1969). By the mid-1980s, the geographic range had been halved with the remnants restricted largely to the least productive and arid/subtropical parts of the former range. This pattern of range contraction shown by the bilby is unusual because most other medium-sized mammals have disappeared from the desert and become restricted to the more temperate parts of their former range (Burbidge and McKenzie 1989).

Compared to the assessment of geographic range made in the mid-1980s, our study indicated that the extent of bilby occurrence in the Tanami Desert has not changed substantially. The records collected along the northern boundary in the present study actually provided an extension northward from the distribution presented by Southgate (1990a) and closer to the estimated distribution limit produced by BIOCLM (see Southgate 1990a) and reported by Finlayson (1961). However, a biological survey of lancewood habitat to the north of the study area failed to record the bilby (Woinarski and Fisher 1995) and it appears that bilby distribution is truncated abruptly on pastoral land to the north and similarly on pastoral land to the east of the study area. The southern and southeastern boundary of distribution is less clearly defined, with sign becoming highly scattered but with continued occasional reports from around Kintore and Nyirripi and occasionally as far south as Uluru/Docker River (J. Gillen, pers com.). There is no evidence of an abrupt truncation in distribution on the western edge of the study area and bilby activity still extends beyond the study region through parts of the Great Sandy Desert and the Gibson Desert into Western Australia (Burbidge and Pearson 1989; Southgate 1990a).

### *Area of occupancy*

Within the estimated extent of occurrence, bilby prevalence was greater in the northern and mid-latitudinal zones and extremely sparse in the south. Furthermore, sign of juvenile activity was restricted to the two mid-zones (Southgate 2005), suggesting that the northern and southern zones may be operating largely as a demographic sink where mortality is greater than natality (Pulliam 1988). A low probability of occurrence (i.e. $p<0.15$) corresponded with parts of the study area where sign was often greater than 25 km apart and stratified random plot or transect sampling generally failed to record any bilby activity. Indeed, less that 25% of the study area was predicted to have bilby probability of occurrence $p>0.15$, and clearly, the extent of occurrence provides an over-estimate of the area of occupancy for the bilby in the Tanami Desert.

Low site fidelity and high mobility of individuals appears to be a feature of the bilby populations occupying the sandy deserts of central Australia. In a previous study, only eight of the 16 localities with bilby sign revisited after 12 months remained active (Southgate 1987). Data from wild, radio-tracked animals in the Granites zone indicated that individuals have a large foraging range. For example, a mature female sometimes moved 1.5 km between burrows on consecutive days and a large male (>1800 g) used burrows 2.6 km apart (Southgate, unpublished data). Movements of a similar magnitude have been recorded for reintroduced bilbies within a 60 $km^2$ predator proof area at Roxby Downs (Moseby and O'Donnell 2003) and for free-ranging reintroduced bilbies at Watarrka National Park in the Northern Territory. At Watarrka, individuals were recorded moving 15 km in a few weeks and males regularly moved 2-3 km and up to 5 km between burrows used on consecutive days (Southgate and Possingham 1995). Movements of this size are much greater than those recorded for other bandicoots and medium-sized mammals in other parts of Australia (Cockburn 1990; Lobert 1990) and suggest the bilby is well adapted to respond to spatial variability of resources in arid regions.

Although bilby prevalence appeared to decline during the study, the change was not significant among years when data were pooled across zones. Paltridge and Southgate (2001) reported a similar finding using relative abundance data collected from the fixed transects at the Tennant Creek zone. However, the repeated sampling of the fixed transects indicated that bilby prevalence may be more labile on the northern edge of the bilby distribution than in the mid-zones.

### *Habitat suitability and refugia characteristics*

None of the individual competing candidate models for either the reduced or the entire study area captured as much deviance as the global models, suggesting that a number of processes act in concert to limit bilby distribution. Variables relating to substrate, climate and predator distribution were most important. Bilby prevalence diminished as the probability of dingo occurrence, mean rainfall and temperature and site productivity declined. Proximity to recent fire was also an important component, but not throughout.

Statistical modelling has multiple uncertainties and should not be viewed as a completely accurate representation of species habitat (Wintle *et al.* 2005). Altering the variable selection routine, the number of variables offered for selection and the representations of environmental variables would have almost certainly altered the composition of the final models. However, the process of defining a small set of candidate models based on practical and prior knowledge and then the critical assessment of the variables and performance of the statistical models reduces the chance of reaching implausible outcomes (Burnham and Anderson 2002). It is also important to note that inferential statistics do not permit us to identify the causal mechanisms that may be involved in limiting bilby distribution but the analyses can assist in the identification of parameters that are likely to have a negative effect and those that are mitigating (Austin 2002b; Guisan and Zimmermann 2000).

Overall, the relatively weak statistical model derived from fire variables indicated that fire in isolation was unlikely to exert a strong controlling effect on bilby prevalence especially throughout the entire study area. Nevertheless, the initial predictions of the *altered fire regime model* were supported by the analysis and bilby prevalence was associated with close proximity to recently burnt habitat and areas with high fire age heterogeneity. Among the fire variables, the distance from areas burnt in the previous year (<1 yr) was the strongest and this variable formed part of the global model but only for the reduced study area. From this it can be concluded that fire may play an important role in improving the habitat favourability for the bilby but in limited parts of its geographic range.

The statistical models derived from substrate/ herbivore variables in isolation were stronger than fire models but there was little support for the *introduced herbivore/ substrate model* proposed by Morton (1990). There was no interaction between substrate and herbivore variables and model strength was derived principally from the effect of substrate. Rabbit and camel activity was greater in the southern part of the study area, concentrated on the drainage/calcrete substrates (Edwards *et al.* 2004; Southgate *et al.* 2006) and negatively associated with bilby prevalence. However, bilby prevalence was greater on drainage/ calcrete substrate in the southern part of its range compared to further north. This feature would not be expected if introduced herbivores had caused degradation of this key habitat as proposed by Morton (1990). Furthermore, the strong correlation between camel and fox distribution (r=0.88) meant that the negative association between bilby prevalence and camel occurrence could simply reflect a fox effect.

The statistical models derived from predator variables were reasonably weak, particularly for the entire study area. This outcome is at odds with a number of reintroduction studies in arid Australia that have demonstrated the impact of foxes and cats on medium-sized native mammal populations unambiguously (Christensen and Burrows 1995; Gibson *et al.* 1994; Moseby and O'Donnell 2003; Risbey *et al.* 2000). In support of the predictions from the *introduced predator model*, fox probability of occurrence and overall predator richness did associate negatively with bilby prevalence. However, it became evident that each predator species was responding to different environmental characteristics (Southgate *et al.* 2006b) and this resulted in compensatory and interactive effects at a regional scale. Although the random plot data indicated that feral cat prevalence declined in the north, it was common throughout the entire study area and consequently the probability of cat occurrence performed weakly as an explanatory variable. In contrast, fox prevalence was limited largely to the southern two thirds of the study area and associated negatively with increasing mean rainfall. The dingo showed a reverse geographic pattern to the fox, being positively associated with mean rainfall, but it was more widespread and also positively associated with proximity to drainage lines.

It was not expected that dingo probability of occurrence would associate positively with bilby prevalence and form part of the global model for the entire and reduced study area. It suggested that the bilby and dingo favoured similar environmental conditions but also that dingo presence may provide a rescue effect and improve habitat favourability for the bilby. The rescue effect provided by dingoes is a realistic proposition as dingoes were an important predator of feral cats in the study area (Paltridge 2002) and possibly displaced fox activity (Southgate *et al.* 2006b) as has been suggested elsewhere (May and Norton 1996).

A climatic variable was a component of the global model for the entire study area and formed the strongest model among the competing single process models for the entire study area but not for the reduced study area. This is consistent with the tendency for direct variables to provide better predictions of an organism's geographic range on a broad spatial scale (Guisan and Zimmermann 2000). It also reflects the power of temperature and rainfall in shaping the geographic range of species, as is becoming more fully appreciated with increasing research on the impact of climate change (Hughes 2003). The initial predictions of the *climate/vegetation model* were supported by the analysis and the strongest variables indicated greater bilby prevalence associated positively with higher rainfall and temperature and hence, areas with more continuous production. While greater and more reliable rainfall and warmer temperatures may result in greater food availability for the bilby, it is also possible that these climatic factors make habitat occupancy intolerable for species like the fox (Southgate *et al.* 2006b) and thus provide refugia where the effect of predators is reduced.

*Predictive performance of the global models and limitations*

*Post hoc* evaluation of a statistical model is crucial to determine its ability to discriminate and identify valuable habitat (Pearce and Ferrier 2000; Wintle *et al.* 2005). The global models for the entire and reduced study areas performed well with training data according to ROC area analyses but these resubstitution methods tend to give optimistically-biased estimates of model performance (Fielding and Bell 1997). The poor performance of the models using independent evaluation data indicated that their ability to identify areas of habitat value for the species was not good. It signaled that problems might exist with the evaluation data or in the model formulation. In regard to the evaluation data, the sample size was small, a different plot size and stratification technique was used to collect data and a large proportion of plots was sampled outside the training area. Hence, the data collection and stratification methods were not ideal for model evaluation (Wintle *et al.* 2005). In regard to the model formulation, the exclusion of important explanatory variables or the inclusion of overly-weighted variables may place too much emphasis on those that are weakly related to the occurrence of a species in the evaluation data (Pearce and Ferrier 2000). These problems again relate to the adequacy of the sampling approach, sample size and geographic spread of data used to derive the models. A restriction in the number of predictor variables used to derive the models may have resulted in the exclusion of important explanatory variables. It was found that a model with four variables derived for the entire study area achieved a ROC area of 0.67±0.09 with evaluation data (Southgate, unpublished). While the discriminative power was still not good, it was better than could be achieved for a similar model limited to three variables. The elevated importance of laterite and rock features and subsumation of drainage substrates in the random plot data and the reverse trend identified from the heli-sampling data also suggested that not all ecologically relevant processes were being specified in the models. A sizeable proportion of evaluation plots with bilby sign occurred on drainage lines and hence, in habitat that was identified as having a low probability of occurrence.

Collectively, it is likely that the factors identified above have resulted in a high rate of prediction error. Great caution is required when applying the model to identify habitat suitability for the bilby in parts of the study areas where there were few training data collected and at a finer-grain spatial scale. It also highlights the need to further test, improve and make the models more robust through iteration.

*Implications for conceptual models for arid Australia*

Both Burbidge and McKenzie (1989) and Morton (1990) drew attention to the likely role of productivity in the widespread extinction and decline of mammals in Australia over a short period. They argued that metabolically expensive terrestrial organisms (especially herbivorous and omnivorous mammals) would have difficulty in occupying arid Australia because of the endemic low productivity resulting from the unreliable, low rainfall coupled with poor soil fertility. Although there are some characteristics in the pattern of bilby prevalence that fit the model explaining the distribution of native medium-sized mammals proposed by Morton (1990) and Stafford Smith and Morton (1990), there are important and notable differences. These need to be taken into account in producing a more robust conceptual framework to better explain the biotic structure of the Australian arid zone. Firstly, the effect of a climatic gradient (temperature and rainfall) is not specifically identified as a major factor acting upon the distribution of medium-sized mammals in the model developed by Morton (1990) and Stafford Smith and Morton (1990), although the unpredictability of rainfall and infrequent occurrence of large rainfall events are recognised as important driving forces in creating patterns of biota in the physical and biotic environments, in general terms. In the Tanami Desert study, the climatic gradient was found to be a primary determinant of not only bilby prevalence, but also other higher order consumers including the camel, red fox, feral cat and dingo (Southgate *et al.* 2006b). Mean annual rainfall and other climate-related attributes were found to be the main variables associating with the distribution pattern of these species. Franklin (2005) has shown that the decline in granivorous birds in northern Australia was more severe in areas of lower annual rainfall with greater year-to-year variation in rainfall, along with factors including grazing intensity, fire regime and topographic and vegetation diversity.

Secondly, laterite and rock feature substrates were as important to the bilby as those characterised with high continuous production such as riverine strips and paleodrainage channels. This phenomenon is not restricted to the bilby as other species including the mulgara *Dasycercus cristicauda* and spectacled hare- wallaby *Lagorchestes conspicillatus* also occur commonly on laterite (Gibson 1986; Masters *et al.* 1997). There are a number of possible reasons why laterite and rock feature substrates are important to the bilby and other medium-sized mammals. These substrates in the Tanami Desert typically have slight relief and elevation and therefore, are areas with a mix of run-off and run-on. The availability and continuity of moisture may be less than in paleodrainage systems but the water quality and hence the availability of nutrients to plants may be greater. Lateritic rises also support an assemblage of shrub species (eg. *Acacia hilliana, A. kempeana, A. rhodophylla*) that contain root dwelling larvae (Latz 1995) which would provide an important persistent food resource for the bilby. The architecture of spinifex hummocks associated with laterite and rock feature substrates is typically more uniform and discrete, with clear runways between hummocks. This may permit greater ease of movement and foraging (Southgate, unpublished). There was also some indication that the prevalence of foxes and cats was lower on the combined substrate category of laterite and rock feature, although cat activity was greater in closer proximity to rock feature substrates (Southgate *et al.* 2006b).

*Implications of management and assessment of status*

The criteria to assess the conservation of a species such as those used by the IUCN include the extent of occurrence, area of occupancy or population abundance. These criteria are used either singularly or in combination to determine whether a species should be listed as vulnerable or endangered etc. (Burgman and Lindenmayer 1998). Our study found the extent of occurrence based on outlier records from opportunistic reports provided a misleading indication of true status of the bilby. The area of occupancy derived from systematic random sampling produced a less biased and more accurate indicator and should be used to assess the status of the bilby in the future.

Custodial management needs to ensure the northern parts of the Tanami Desert are protected from the expansion and development of pastoralism, particularly areas of drainage and laterite/ rock feature substrates. Far greater appreciation of the importance of lateritic and stony substrates for conservation of bilbies and other threatened species in arid Australian environments is required. Lateritic areas are often targeted to site mine infrastructure and accommodation, airstrips, and tailings and over-burden dumps because of the low susceptibility to inundation of these substrates (R. Teale, pers. com., Southgate, pers. obs.). Areas where dingoes and cats occur in low abundance in the northern part of the Tanami and Great Sandy Deserts offer greatest refugia potential for the bilby.

The association of predators with bilby occurrence suggests that manipulative management would be best focussed on reducing fox distribution. Although predator control through baiting and trapping has achieved success in protection of medium-size mammals in parts of temperate Australia (Friend and Thomas 1995; Kinnear *et al.* 1988), it is extremely costly and yet to be applied effectively in arid parts of Australia (Christensen and Burrows 1995; Gibson *et al.* 1994). Broad-scale baiting conducted in the Gibson Desert using a light aircraft to distribute meat baits laced with 1080 resulted in selective removal of dingoes and foxes but this allowed cat abundance to increase and the reintroduced bettongs and bandicoots still declined (Burrows *et al.* 2003; Christensen and Burrows 1995). There is evidently a complex relationship among predator species in the Tanami Desert and more work is needed to fully determine the interaction among predator species, the effects of baiting on the dynamics of the predator and prey community and the development of more discriminate measures to remove particular predator species. Control techniques that target foxes and cats and not dingoes need to be developed. Selective hunting by Aboriginal people may achieve the desired levels of predator density in some areas if adequate incentives were offered (Paltridge, pers. com.).

There is also some scope for the use of fire to improve habitat suitability for the bilby in the Tanami Desert because of the greater acceptability of this form of management to the Aboriginal community and the ease of implementation compared to a baiting operation on a broad scale. However, the importance of fire-promoted plants in the diet of the bilby and the role of fire in the production of important food producing plants need to be demonstrated before a fire management program is developed (see Southgate and Carthew 2006).

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## **Appendix 7.1** The strength of the relationship between herbivore and predator species and substrate, fire and rainfall explanatory variables. For each species the percentage of deviance captured by each variable fitted separately is shown. Entire study area: null model df=206, residual deviance= 167.7. Reduced study area, Tennant and the Granites zone: null model df=139, residual deviance=131.4.

| | | | Entire study area | | Reduced study area Tennant and the Granites zone | |
|---|---|---|---|---|---|---|
| Variable | Abbreviation | df | deviance | Prob (Chi) | deviance | Prob (Chi) |
| Introduced herbivores | | | | | | |
| herbivore richness | herbvar | 1 | 0.1 | 0.8 | 0.7 | 0.4 |
| camel occurrence | cameloc | 1 | 1.6 | 0.2 | 0.004 | 0.9 |
| camel probability | camelpr | 1 | 7.9 | 0.005 | 0.8 | 0.4 |
| substrate map 5 category (d,c,l,r,s) | sm5(d,c,l,r,s) | 4 | 22.8 | 0.0001 | 19.3 | 0.0007 |
| substrate map 3 category (dc,lr,s) | sm3(dc,lr,s) | 2 | 19.7 | 0.00005 | 17.2 | 0.0002 |
| substrate map 2 category (dclr,s) | sm2(dclr,s) | 1 | 5.6 | 0.02 | 6.4 | 0.01 |
| substrate map 2 category (lr,dcs) | sm2(lr,dcs) | 1 | 17.9 | 0.00002 | 15.5 | 0.00008 |
| substrate distance to drainage+calcrete | sdist.dc | 1 | 2.7 | 0.1 | 0.09 | 0.7 |
| substrate distance to calcrete | sdist.c | 1 | 0.8 | 0.3 | 1.1 | 0.3 |
| substrate distance to drainage | sdist.d | 1 | 0.04 | 0.8 | 1.2 | 0.2 |
| substrate distance to laterite | sdist.l | 1 | 0.04 | 0.8 | 2.1 | 0.1 |
| substrate distance to rock feature | sdist.r | 1 | 0.5 | 0.5 | 9.0 | 0.003 |
| substrate distance to sand plain+dune | sdist.s | 1 | 0.8 | 0.4 | 0.7 | 0.4 |
| substrate neighbourhood variety 1 km r | snbr1r | 1 | 3.0 | 0.08 | 2.2 | 0.1 |
| substrate neighbourhood variety 2.5 km r | snbr2.5r | 1 | 7.8 | 0.005 | 9.6 | 0.002 |
| substrate neighbourhood variety 5 km r | snbr5r | 1 | 2.1 | 0.1 | 4.5 | 0.03 |
| substrate neighbourhood variety 10 km r | snbr10r | 1 | 1.2 | 0.2 | 6.2 | 0.01 |
| substrate neighbourhood variety 25 km r | snbr25r | 1 | 0.6 | 0.4 | 4.4 | 0.04 |
| Introduced predators | | | | | | |
| cat occurrence | catoc | 1 | 0.1 | 0.7 | 0.004 | 0.9 |
| fox occurrence | foxoc | 1 | 1.8 | 0.2 | 0.1 | 0.7 |
| dingo occurrence | dingooc | 1 | 2.6 | 0.1 | 2.5 | 0.1 |
| cat probability | catpr | 1 | 0.6 | 0.4 | 3.3 | 0.06 |
| fox probability | foxpr | 1 | 14.1 | 0.0002 | 4.6 | 0.03 |
| dingo probability | dingopr | 1 | 22.1 | 0.000001 | 17.0 | 0.00004 |
| predator richness | predvar | 1 | 2.0 | 0.1 | 3.8 | 0.05 |
| predator+herbivore richness | predherbvar | 1 | 0.8 | 0.4 | 3.5 | 0.06 |
| *Fire* | | | | | | |
| fire map 3 category (rec,int,old) | fm3(r,i,o) | 2 | 3.9 | 0.1 | 3.7 | 0.1 |
| fire map 2 category (rec,int+old) | fm2(r,io) | 1 | 3.6 | 0.06 | 3.4 | 0.06 |
| fire: map years since | fmyrs | 1 | 1.1 | 0.3 | 1.0 | 0.3 |
| fire neighbourhood variety 1km r | fnbr1r | 1 | 0.3 | 0.6 | 0.7 | 0.4 |
| fire neighbourhood variety 2.5 km r | fnbr2.5r | 1 | | | 0.3 | 0.5 |
| fire neighbourhood variety 5 km r | fnbr5r | 1 | 2.5 | 0.1 | 1.5 | 0.2 |
| fire neighbourhood variety 10 km r | fnbr10r | 1 | 1.5 | 0.2 | 0.1 | 0.7 |
| fire neighbourhood variety 25 km r | fnbr25r | 1 | 7.0 | 0.008 | 3.9 | 0.05 |
| fire: distance to < 1yr old fire | fdist1yr | 1 | 11.1 | 0.0008 | 7.9 | 0.005 |
| fire: distance to 1-2 yr old fire | fdist2yr | 1 | 0.9 | 0.3 | 0.4 | 0.5 |
| fire: distance to < 2yr old fire | fdistrec | 1 | 14.0 | 0.0002 | 7.9 | 0.005 |
| *Climate and vegetation* | | | | | | |
| rainfall: cumulative in last 3 mths | r3mth | 1 | 0.6 | 0.4 | 6.5 | 0.01 |
| rainfall: cumulative in last 6 mths | r6mth | 1 | 0.2 | 0.7 | 0.7 | 0.4 |
| rainfall: cumulative in last 12 mths | r12mth | 1 | 4.4 | 0.03 | 0.01 | 0.9 |
| rainfall: cumulative in last 24 mths | r24mth | 1 | 4.2 | 0.04 | 0.2 | 0.7 |
| rainfall :residual from 12 mth mean | r12mdev | 1 | 1.5 | 0.2 | 0.07 | 0.8 |
| rainfall: residual from 24 mth mean | r24mdev | 1 | 1.7 | 0.2 | 0.9 | 0.3 |
| rainfall: cumulative since fire | rsincef | 1 | 0.2 | 0.6 | 1.3 | 0.2 |
| rainfall: annual mean | ryrmean | 1 | 13.8 | 0.0002 | 15.5 | 0.00008 |
| temperature (minimum) | tempmax | 1 | 0.1 | 0.8 | 2.0 | 0.2 |
| temperature (maximium) | tempmin | 1 | 11.6 | 0.0007 | 4.2 | 0.04 |
| vegetation: total cover | vegcov | 1 | 0.8 | 0.3 | 4.7 | 0.03 |
| spinifex: total cover | spincov | 1 | 2.7 | 0.1 | 3.3 | 0.07 |
| shrub: total cover | shrbcov | 1 | 0.3 | 0.6 | 6.0 | 0.01 |
| plant species richness | plntspp | 1 | 0.4 | 0.5 | 0.1 | 0.7 |

**Appendix 7.2** Generalised linear models indicating the strength of association between bilby sign and proposed introduced herbivore- and substrate-related parameters for the a) entire study area and b) the reduced (source) study area. See Appendix 7.1 for an explanation of variable abbreviations. Estimate values for categorical variables are identified in italics

1. Introduced herbivore and substrate

a) entire study area

Total Deviance = 167.7, adjusted $D^2 = 0.159$, AIC= 147.6

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | -3.989 | 0.732 | 206 | <0.001 |
| sm2(lr,dcs) *lr* | 1.652 | 0.486 | 205 | <0.001 |
| sdist.dc | 0.033 | 0.011 | 204 | 0.002 |
| snbr2.5r | 0.611 | 0.275 | 203 | 0.026 |

b) reduced study area

Total Deviance = 131.4, adjusted $D^2 = 0.137$, AIC=118.6

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | -1.735 | 0.880 | 139 | 0.048 |
| sm2(lr,dcs) *dcs* | -1.522 | 0.505 | 138 | 0.003 |
| snbr2.5r | 0.504 | 0.282 | 137 | 0.054 |

2. Predators

a) entire study area

Total Deviance = 167.7, $D^2 =0.118$, AIC=147.2

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | -1.438 | 0.343 | 206 | <0.001 |
| fox.pr | -11.026 | 3.392 | 205 | <0.001 |
| fox.pr:dingo.pr | 47.591 | 14.370 | 204 | <0.001 |

b) reduced study area

Total Deviance = 131.4, adjusted $D^2 = 0.164$, AIC=118.4

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | -3.350 | 0.584 | 139 | <0.001 |
| dingo.pr | 6.561 | 1.698 | 138 | <0.001 |

3. Fire

a) entire study area

Total Deviance = 167.7, $D^2 = 0.066$, AIC=157.7

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | -1.254 | 0.253 | 206 | <0.001 |
| fdist.1yr | -0.0344 | 0.0139 | 205 | 0.013 |

b) reduced study area

Total Deviance = 131.4, adjusted $D^2 = 0.102$, AIC=124.3

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | -4.208 | 1.622 | 139 | 0.009 |
| fa2(r,io) *r* | 0.982 | 0.481 | 138 | 0.041 |
| fdist.1yr | -0.056 | 0.0253 | 137 | 0.027 |
| fnbr25r | 0.493 | 0.258 | 136 | 0.056 |

### 4. Climatic, vegetation

a) Entire study area
Total Deviance = 167.7, adjusted $D^2$ = 0.182, AIC=143.8

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | 10.2513 | 6.108 | 206 | 0.093 |
| ryrmean | 0.0187 | 0.0044 | 205 | <0.001 |
| ryrmean$^2$ | -11.940 | 5.214 | 204 | 0.022 |
| tempmin | -0.731 | 0.347 | 203 | 0.035 |

b) reduced study area
Total Deviance = 131.4, $D^2$ = 0.117, AIC=112.0

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | 11.315 | 2.976 | 139 | <0.001 |
| ryrmean | 0.027 | 0.00798 | 138 | <0.001 |

### 5. Global model derived with consideration of all variables

a) entire study area
Total Deviance = 167.7, adjusted $D^2$ = 0.258, AIC=135.2

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | -4.222 | 0.594 | 206 | <0.001 |
| sm2(lr,dcs) *lr* | 1.680 | 0.502 | 205 | <0.001 |
| sdist.dc | 0.032 | 0.010 | 204 | 0.001 |
| dingo.pr | 6.507 | 1.666 | 203 | <0.001 |

b) entire study area (static model)
Total Deviance = 167.7, adjusted $D^2$ =0.221, AIC=139.1

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | 5.426 | 5.359 | 206 | <0.311 |
| sm2(lr,dcs) *lr* | 1.717 | 0.481 | 205 | <0.001 |
| ryrmean | 0.016 | 0.004 | 204 | <0.001 |
| tempmin | -0.778 | 0.358 | 203 | 0.03 |

c) reduced study area
Total Deviance = 131.4, adjusted $D^2$ = 0.24, AIC=107.9

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | -1.236 | 0.748 | 139 | 0.098 |
| sm(lrf,dcs) *dcs* | -1.75 | 0.522 | 138 | <0.001 |
| dingo.pr | 4.884 | 1.777 | 137 | 0.006 |
| fdist1yr | -0.0393 | 0.0232 | 135 | 0.09 |

d) reduced study area (static model)
Total Deviance = 131.4, adjusted $D^2$ = 0.198, AIC=110.7

| Variable | Estimate | Std. Error | df | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | -8.343 | 3.078 | 139 | 0.006 |
| sm2(lr,dcs) *dcs* | -1.493 | 0.502 | 138 | 0.002 |
| ryrmean | 0.0215 | 0.0081 | 137 | 0.008 |

# Chapter 8

# The diet of the bilby *Macrotis lagotis* in relation to substrate, fire and rainfall characteristics in the Tanami Desert

*Preamble to Chapter 8*

In the previous chapter, I presented information on the environmental variables that associated with bilby prevalence. The proximity to recently burnt habitat formed a significant variable in part of the study area. In this chapter, I examine whether that functional relationship maybe related to the use of fire-promoted plant foods.

I aimed to determine whether there was a link between bilby prevalence, dietary composition and the environmental variable of fire. The diet was described from the analysis of faecal pellets collected at random plots and fixed transects. The change in dietary composition over time was also examined at two localities.

Seed from a fire-promoted plant (*Yakirra australiense*) and the bulb from *Cyperus bulbosus* were found to be the most important plant components of the diet and termites and beetles were the most important invertebrates. Substrate, time since fire, and antecedent rainfall were found to be important environmental variables associated with amount of *Yakirra* contained in the diet.

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## Introduction

Dietary analysis provides an opportunity to identify specific resources used by a species and to examine the processes that shape a species' spatial pattern (Krebs 1989). Although there is still much debate regarding the relative importance of different factors regulating population numbers (Andrewartha and Birch 1954; Caughley and Sinclair 1994; Krebs 2002), there is little dispute that the availability of food resources is a key limiting process (Begon *et al.* 1996; Predavec 1994) and management of a food resource can be used to alter the demographic characteristics of a population (Caughley and Gunn 1996). Changes in demographic parameters such as reproduction, immigration and survivorship have been demonstrated for a range of terrestrial species through the experimental manipulation of food availability (Boutin 1990; Broughton and Dickman 1991; Dickman 1989; Predavec 1994). Unfortunately, the task of deriving a relationship between food abundance and a species' pattern is not often straightforward. The availability of food may be difficult to measure simply because accessibility to consumers may be constrained by many factors and not relate closely to the actual abundance of the food resource (Wiens 1984). Furthermore, a relationship is made all the more difficult to derive if a species can draw from a wide range of foods, each with a different set of factors affecting abundance and availability. A starting point is to determine the primary foods consumed and develop an understanding of the environmental conditions that associate most closely with the occurrence or relative abundance of these food types in the diet.

Studies of the diet of the bilby *Macrotis lagotis* have shown that they consume a wide range of foods, including root-dwelling larvae, nasute termites, hypogeal fungi, bulb, fruit and seed (Gibson 2001). Moreover, the diet may vary from being predominantly herbivorous to insectivorous spatially and temporally (Southgate 1990b). Despite the use of many plant species, the bulk of the plant material consumed is restricted to several prolific seed-producing species and one bulb-producing sedge, *Cyperus bulbosus*. The environmental conditions that affect overall food availability and dietary composition of the bilby are poorly understood. Similarly, the extent to which the dispersion of bilby populations is influenced by diet is unclear. Nevertheless, a number of characteristics that affect the production of key plant foods can be identified. *Cyperus bulbosus* is restricted mostly to sandy soils in watercourses and responds following substantial rainfall. Latz (1995) described the species as previously one of the most important plant foods for traditional Aboriginal people in central Australia, especially in times of drought. The main seed producing plants used by the bilby are annuals that emerge after rainfall following a disturbance event like fire or drought. The elimination of the pre-existing perennial vegetation provides an opportunity for these plants to emerge. In this paper, these annual plants are referred to as 'fireweeds' because fire is the most common and widespread form of disturbance within the study area. *Yakirra (Panicum) australiense* and *Dactyloctenium radulans* are by far the most important of these species in the bilby's current range (Southgate 1990a). Seed from these grasses also provided important food sources for traditional Aboriginal people (Latz 1995).

Fire is recognized as an important process in the spinifex (*Triodia* spp.) grasslands of Australia and plays a crucial role in maintaining plant diversity and recycling of nutrients (Stafford Smith and Morton 1990). The understorey of the Tanami Desert is dominated by spinifex and in some years, more than a quarter of the region can be burnt (Allan and Southgate 2002). The interval between fires can range from less than three to more than 30 years depending on rainfall and fuel development. The greatest heterogeneity of and size occurs in the mid latitudes of the Tanami Desert where substrate heterogeneity is also high. It is also where greatest bilby prevalence is encountered and, in this region, the proximity to recently burnt habitat was found to associate significantly with bilby occurrence (Southgate, unpublished data).

Thus, fire and the promotion of key food plants are likely to be important processes affecting bilby distribution, and fire management may present an opportunity to improve habitat suitability and the status of the bilby. However, the strength of the relationship between fire, food production and bilby prevalence remains unclear because fire may affect the diversity of a range of plant and animal species (Friend 1993; Woinarski and Recher 1997) and hence affect the availability of many plant and non-plant foods for the bilby. In addition, reduced ground cover following fire may affect the foraging ability of not just the bilby, but also felid and canid predator species that prey on the bilby (Murray *et al.* 1995).

Justification for management to supplement food to improve the status of a species requires a 'vein of logic' to run between species' prevalence and diet and through to a manageable proximate factor (Caughley and Gunn 1996). In other words, before fire management can be clearly advocated, it needs to be demonstrated that bilby prevalence is associated with dietary composition and that dietary composition is affected by proximity to recently burnt habitat and the consumption of fire-promoted foods.

This study describes the diet of the bilby in the Tanami Desert in relation to substrate, rainfall and fire but specifically aimed to test three predictions: 1) fire-promoted foods would dominate the bilby diet at recently burnt localities, 2) fire-promoted plants would form a significant proportion of the plant foods used by the bilby, and 3) bilby prevalence and persistence would be greater in parts of the study area where more plant material was consumed. The relationship between the size of faecal pellet (reflecting the size of an individual) and dietary composition is also examined to determine whether diet composition changes with animal size.

## Methods

### *Study area*

The study area included most of the Tanami Desert bioregion plus a small part of the Great Sandy Desert Bioregion (Thackway and Cresswell 1995) and was bounded by the Northern Territory/Western Australian border and pastoral leases on the northern, eastern and south-eastern edges (**Fig. 8.1**). The study area is mostly Aboriginal Freehold land and is sparsely populated and largely undeveloped.

Summers in the Tanami Desert are very hot while winters are cold to mild. The mean daily maximum temperature during the hottest month in the northern part of the study area is 39.3°C compared to 36.2 °C in the south. The mean daily minimum temperature during the coldest month (July) is 11.3 °C in the north and 4.1 °C in the south (Bureau of

Metereological records). Frosts can occasionally occur at night during the winter in the south.

The rainfall gradient present in the study area ranged from an annual average of 600 mm on the northern boundary to around 300 mm on the southern boundary. In the north, 90 % of mean annual rainfall occurs during summer compared with 77% in the south. Cyclonic incursions occasionally cause exceptional rainfall events, when more rainfall can occur within one month than the annual average. The variability of rainfall among years becomes greater with increasing aridity, but the magnitude of extreme above-average rainfall events remains similar throughout (Southgate, unpublished data).

The soils are variable with earthy sands predominating on the plains, red siliceous sands on the dunes and red and calcareous earths more sparsely distributed. The large salt lakes, saline channels, caliche areas and ephemeral freshwater river systems still evident in the Tanami and other parts of Australia are fossilised remnants of a pluvial period in the Miocene and earlier. The infilled and mostly saline areas are referred to as paleodrainage systems (van de Graaf *et al.* 1977). The elevation of the weathered sediments ranges from 200-600 m above sea level. Spinifex species from the genus *Triodia* form the dominant ground cover with an overstorey of scattered shrubs and trees including *Eucalyptus, Corymbia, Acacia* and *Grevillea. Melaleuca* spp. are typically found in paleodrainage systems.

### *Faecal collection and bilby prevalence*

Tracks and diggings can be used successfully to identify the presence of bilby activity in the field and faecal pellets can often be found deposited beside bilby diggings. Faecal samples were collected while sampling random plots and fixed transects between March 1995 and May 1998 during a study to examine factors affecting bilby distribution (Southgate *et al.* 2005). The 207 random plots were sampled once and selected using restrictive stratified random sampling from five substrate categories and three times since fire categories. The plots were spaced at least 4 km apart (see Southgate *et al.* 2005).

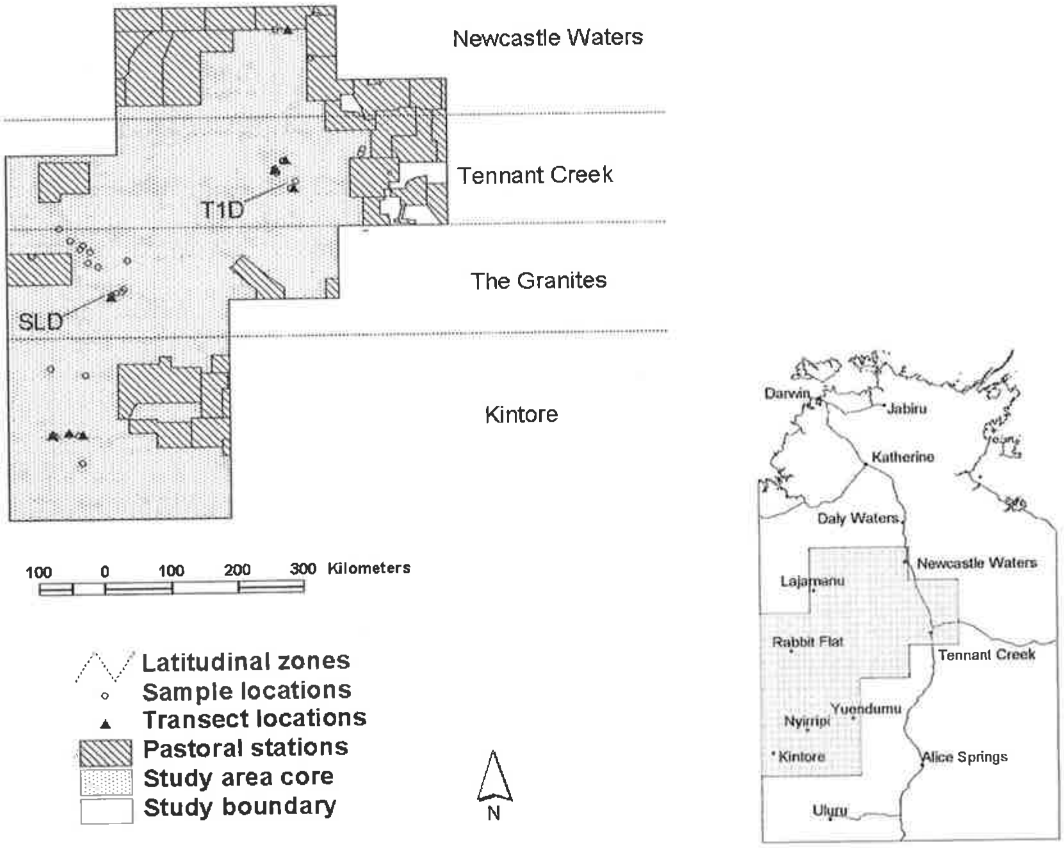

**Fig. 8.1** The distribution of the study area and location of plots where faecal samples were collected. Fixed transects are shown along with the location of the two persistent populations (T1D and SLD). The inset shows the study area in relation to the Northern Territory.

Fixed transects were visited repeatedly over the same period. Eight sites were located within four latitudinal bands: Newcastle Waters (17-18.5° S), Tennant Creek (18.5-20° S), the Granites (20-21.5° S) and Kintore (21.5-23.5° S), with three sites spaced about 25 km apart in both the Kintore (K1-K3) and Tennant Creek (T1-T3) latitudes and one site was located at each of the Granites (G1) and Newcastle Waters (N1) latitude (**Fig. 8.1**). At each site, one 10 km transect (a 4x1 km rectangle) was located in sand plain/dune habitat (S) and the other in drainage line habitat (D). The exception was Newcastle Waters latitude where both transects were located in sand plain habitat because of the absence of drainage habitat. Transects were separated by about 5 km and located more than 500 m from permanent vehicular tracks (see Paltridge and Southgate (2001) for more detail). Each transect was monitored using an all terrain vehicle on three consecutive mornings every four months during the sample period. Bilby activity was also encountered while travelling between plots and sites.

Repeated sampling of the fixed transects was used to assess whether a locality was being occupied persistently and allowed faecal samples to be collected over time. Persistent bilby activity was encountered at only one of the 16 transects (site T1D at the Tennant Creek latitude). Faecal samples were collected along a 1.5 km section of this fixed transect. Bilby activity was also regularly encountered along an access track used to reach the fixed transect (G1D) at the Granites latitude. This site is referred to as the Sangsters long dune site (SLD) and faecal samples were collected within 200-300m either side of the 1 km long dune. Both sites with persistent activity were situated on drainage lines.

The sampling of random plots, fixed transects and an aerial survey of bilby diggings was used to assess bilby prevalence (see Southgate *et al.* 2005 for details). The random plots and the aerial survey indicated that bilby prevalence was greatest in the two mid latitude zones (Tennant Creek and the Granites) (**Table 8.1**). Data from the fixed transects showed a similar trend except that more activity was encountered in the Newcastle Waters zone. Bilby sign was encountered only opportunistically at the Kintore latitude.

**Table 8.1** Prevalence of the bilby within each latitudinal zone as measured by the proportion of random plots, transects and aerial transect sections with bilby activity recorded (see Southgate *et al.* 2005 for details).

| | Newcastle Waters | Tennant Creek | The Granites | Kintore |
|---|---|---|---|---|
| Random plots sampled | 24 | 42 | 98 | 43 |
| Proportion ±sd | 0.17±0.08 | 0.26±0.07 | 0.23±0.04 | 0 |
| Fixed transects, period x transect sampled | 12 | 48 | 14 | 44 |
| Proportion ±sd | 0.42±0.14 | 0.25±0.06 | 0.28±0.12 | 0 |
| Aerial transects, 4 km sections sampled | 108 | 109 | 44 | - |
| Proportion ±sd | 0.03±0.02 | 0.22±0.04 | 0.18±0.06 | |

*Faecal analysis*

At most localities, 10 separate deposits of faecal pellets were collected. The faecal pellets were stored in dry conditions until analysis and a single faecal pellet (referred to as a sample) was selected randomly from each group for analysis. The diameter of the widest part of the pellet was measured using vernier calipers. Samples were prepared for examination under light microscope by crushing the pellet into a petri dish and adding water until the material was evenly suspended. Large pellets weighing more than 0.6 g were sub-sampled. The water was then allowed to evaporate, leaving a film of faecal material. These remains were examined under 6-25 magnification.

Each sample was initially searched for different dietary items. Plant remains in faeces were identified to species, and fungi and invertebrates were identified to order where possible, using a reference collection. Food items were placed into 12 categories: fire- promoted seed, other seed, bulb, fruit, other plant (stem, leaf), fungal spore, termite, ant, beetle/bugs, larvae, grasshopper/cricket, other/unidentified invertebrate. Plants promoted by fire and considered fireweeds included *Yakirra australiense, Dactyloctenium radulans*, *Paspalidium* spp., *Paranactenium nova, Portulaca olerace* and *Amaranthus* spp. based on Latz (1995). The only bulb identified was *Cyperus bulbosus*. Sand and unidentified material provided two additional categories. An item was recorded as unidentified if it could not be readily designated as plant, fungal spore or invertebrate.

The proportion of samples containing a particular item was used to estimate the frequency of occurrence for each sample period at each locality. In addition, the relative abundance of food types within a sample was estimated using an optical grid. The first 25 identifiable food items were assigned to one of the 12 categories listed above and the number of times sand and unidentified particles were encountered was also recorded. This procedure was used to ensure a reasonable number of identifiable food fragments were registered. Any bilby hair in the faecal samples was ignored. The scores in each category from each faecal sample were combined for a site or plot. A coefficient of variation (CV) was used to indicate the dietary components that were least variable. Simpson's reciprocal diversity index (Krebs 1989) was used to measure the heterogeneity of the relative abundance of items from each plot and site.

Both the relative abundance and frequency of occurrence of food items was reported to facilitate comparison of the diet of the bilby with the findings for other bandicoots and medium-sized mammals. Relative abundance data typically underestimate the importance of large and soft-bodied items such as larvae and fruit but provide an accurate account of small, common prey items with parts that persist through digestion such as ants, termites and seeds (Lou *et al.* 1994). The husks of *Cyperus bulbosus* also persist through digestion. Statistical analysis was conducted mostly on abundance data because of the study's focus on fireweed seed and bulb.

*Environmental variables*

Geological mapping provided by the Australian Geological Survey Organisation (AGSO) at a scale of 1: 250 000 was used to identify substrate types in the study area. Substrates in the study area were categorised as drainage (d), calcrete (c), laterite (l), rock feature (r) and sand plain and dune (s) based on geological mapping. Analysis was also conducted on grouped categories. For example, a three category amalgamation of substrates could be specified as dc, lr and s.

The annual extent of fire from1984-1998 in the Tanami region was derived from the Central Australian fire history database (Allan and Southgate 2002). Prior to 1986, the fire history was mapped by visual interpretation of multi-temporal Landsat images and aerial photographs (Allan 1993). The fire history for the period 1986 to 1996 for the Tanami was mapped from Advanced Very High Resolution Radiometer (AVHRR) National Oceanic and Atmospheric Administration (NOAA) satellite imagery at a resolution of approximately 1 km$^2$. The closest distance of a plot to the edge of a substrate type or a patch burnt in the year prior to sampling and two years prior to sampling was calculated using GIS. The burn age classification identified areas that were recently burnt (<2 years old), intermediate (3-6 years old) and old (>6 years old).

Historic, splined monthly rainfall data at a resolution of approximately 25 km (0.25 degree raster surface) covering the study area were purchased from the Bureau of Metereology (Jones and Weymouth 1997). These data were used to derive cumulative rainfall occurring three months, six months and 12 months prior to sample date and the deviation of rainfall from the mean expected rainfall for a 12 and 24 month period prior to the sample date for each sample. Average annual rainfall for each site was also calculated from a raster surface of mean annual rainfall derived from the Australian Natural Resource Data library.

At each random plot, a 300 point vegetation transect was sampled using a wheel-point apparatus (Griffin 1989). Vegetation composition and cover were measured at points spaced 1 m apart and the proportional cover of spinifex, non-spinifex grasses, forbs, standing litter and shrubs were estimated. In addition, the occurrence of fire-promoted or encouraged plant species was recorded. At each fixed transect, a 2000 point vegetation transect with points spaced 1 m apart was sampled annually in spring to track changes in the vegetation over time. One hundred points of wheel-point data were collected at 20 locations spaced 500 m apart perpendicular to the10 km transect. These locations were also used to estimate the abundance of fireweed and fire-promoted food plants over a 50 m transect in late summer or autumn. Food plants were identified as fire-promoted or encouraged and their abundance was rated as 0=absent, 1=present or <1% cover, 2=abundant >1% cover.

Generalised linear modeling (Splus6, Insightful) was used to examine the strength of relationship between key dietary items and habitat variables. The relative abundance of a dietary item from each site, weighted for the number of samples, was used as the response variable. The parameters used as explanatory variables included latitude and longitude data, substrate categories, distance to a substrate category, burn age category, time since fire, distance to a fire category, antecedent cumulative rainfall for 3, 6,12 and 24 months, antecedent cumulative rainfall since fire, vegetation cover and vegetation composition. A Poisson link function was used in the logistic regression and a forward stepwise selection procedure was used to fit a model. A minimum adequate model was derived that captured maximum deviance but included only variables that contributed significantly after considering all the available variables (Crawley 1993).

## Results

### *Faecal analyses and overall dietary composition*

Faecal samples were collected at 33 sites (**Fig. 8.1**) and a total of 218 faecal samples were examined. Vegetation data and other habitat variables were collected at 29 of these locations. To investigate changes in diet composition over time, a further 86 faecal samples were collected at two localities (T1D and SLD) over six sampling periods.

Fireweed seed was the most commonly consumed plant item, being found in 64% of samples and making up 36% of the identifiable parts in samples collected at the 33 plots (**Table 8.2**). Seed from a number of fireweeds (including *Yakirra, Paspalidium* spp., *Paranactenium nova, Portulaca olerace* and *Amaranthus* spp.) was found occasionally together in a sample but *Yakirra* was by far the most frequently and widely encountered seed. It occurred in 92% of the samples collected where a fireweed was present, and at each of the four latitudes (**Table 8.2** and **Table 8.3**). Non-fireweed seed occurred in 25 % of samples but in low abundance. *Triodia* spp. and *Eragrostis eriopoda* were the most common species detected. The bulb of *Cyperus bulbosus* was present in 27% of samples and contributed to 18.5% of the overall relative abundance of identifiable foods. It was most common in the middle latitudes, and was absent from the northern latitude and in trace amounts from the southern latitude (**Table 8.2**). Sign of fruit from *Solanum* spp. was similarly absent from samples collected in the northern and southern most latitudes (**Table 8.3**). Fungal spore was present in 16.5% of samples and contributed to 1.2% of relative abundance but was absent from the northern latitude. The fungal spore was of hypogean origin and probably from at least two species. The spores were black or brown, spherical, often clustered together and easily identifiable under 6-25 magnification. Only one faecal sample was found to contain vertebrate material. This was the foot of a small agamid. Among the invertebrate categories, Coleoptera and Hemiptera (beetles and bugs) were the most commonly encountered (85.8% of samples) and accounted for 13.5% of the relative abundance. Isoptera (termites) were also commonly encountered (73.1%) and this category contributed 19.1% to the relative abundance overall. Termites accounted for 33% and 39% of the relative abundance of identifiable foods in the southern and northern latitudes, respectively. Hymenoptera, represented exclusively by ants, were also commonly encountered (45.4%) but had low relative abundance (4.1%). Larvae, grasshoppers/crickets and other invertebrates were encountered infrequently and contributed comparatively little to relative abundance.

Faecal samples generally contained 3-4 food types with a maximum of six and minimum of one (**Table 8.2b**). Some samples were dominated completely by plant material such as *Cyperus bulbosus*, while others consisted of a single category of invertebrate such as termite. Among the 218 samples, bulb was negatively correlated with fireweed seed ($r=-0.53$, $p<0.001$). Sand was present in all samples but positively correlated with the abundance of invertebrate material ($r=0.55$, $p<0.001$), especially termite ($r=0.48$, $p<0.001$). Diet diversity was negatively correlated with the proportion of plant material consumed ($r=-0.47$, $p<0.001$) and positively correlated with proportion of beetle/bug consumed ($r=0.38$, $p<0.001$). The diameter of faecal pellets ranged in size from 6.2 to 15.0 mm. The relationship between the abundance of dietary items and the size of the faecal pellet (as a surrogate for bilby size/age) was not significant except for fireweed seed ($r=0.15$, $p<0.05$) and termite ($r=-0.16$, $p<0.05$) with larger faecal pellets containing more fireweed seed and less termite.

**Table 8.2** The percentage frequency of occurrence and relative abundance of dietary items in faecal samples from 33 plots categorised in relation to latitude (Spatial plots) and at two sites where multiple samples were collected over time (Temporal sites). The diet diversity and mean item count were calculated using the 12 categories of food.

a) Percentage frequency of occurrence

| | Spatial plots | | | | | Temporal sites | |
|---|---|---|---|---|---|---|---|
| | Newcastle Waters | Tennant Creek | The Granites | Kintore | Total | Tennant T1D | The Granites SLD |
| Plots/Sites | 5 | 8 | 14 | 6 | 33 | 1 | 1 |
| Samples | 27 | 78 | 59 | 54 | 218 | 59 | 47 |
| Fireweed seed | 92.6 | 76.9 | 45.8 | 51.9 | 64.2 | 97.9 | 30.5 |
| Other seed | 37.0 | 6.4 | 22.0 | 46.3 | 24.3 | 72.3 | 22.0 |
| Bulb | 0.0 | 12.8 | 81.4 | 1.9 | 27.1 | 0.0 | 76.3 |
| Fruit | 0.0 | 7.7 | 25.4 | 0.0 | 9.6 | 6.4 | 6.8 |
| Other plant | 44.4 | 10.3 | 1.7 | 7.4 | 11.5 | 4.3 | 5.1 |
| Fungal spore | 0.0 | 16.7 | 30.5 | 9.3 | 16.5 | 46.8 | 47.5 |
| Termite | 88.9 | 61.5 | 69.5 | 88.9 | 73.9 | 78.7 | 72.9 |
| Ant | 44.4 | 60.3 | 27.1 | 44.4 | 45.4 | 70.2 | 52.8 |
| Beetle | 81.5 | 91.0 | 79.7 | 87.0 | 85.8 | 87.2 | 78.0 |
| Larvae | 11.1 | 3.8 | 11.9 | 22.2 | 11.5 | 2.1 | 13.6 |
| Grashopper/ cricket | 0.0 | 2.6 | 6.8 | 5.6 | 4.1 | 0.0 | 6.8 |
| Other invertebrate | 25.9 | 0.1 | 3.4 | 9.3 | 6.4 | 10.6 | 5.1 |
| Total plant | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| Total invertebrate | 100.0 | 93.6 | 100.0 | 88.9 | 95.0 | 100.0 | 98.3 |

b) Percentage relative abundance

| | Spatial plots | | | | | Temporal sites | |
|---|---|---|---|---|---|---|---|
| | Newcastle Waters | Tennant Creek | The Granites | Kintore | Total | Tennant T1D | The Granites SLD |
| Plots/Sites | 5 | 8 | 14 | 6 | 33 | 1 | 1 |
| Samples | 27 | 78 | 59 | 54 | 218 | 59 | 47 |
| Fireweed seed | 33.9 | 57.4 | 18.9 | 24.8 | 36.0 | 48.9 | 2.2 |
| Other seed | 5.2 | 0.0 | 0.9 | 8.5 | 3.0 | 16.6 | 0.5 |
| Bulb | 0.0 | 9.2 | 56.1 | 0.1 | 18.5 | 0.0 | 55.7 |
| Fruit | 0.0 | 0.2 | 2.4 | 0.0 | 0.7 | 0.3 | 1.1 |
| Other plant | 7.3 | 0.8 | 0.1 | 0.5 | 1.3 | 0.8 | 0.0 |
| Fungal spore | 0.0 | 0.9 | 2.2 | 1.1 | 1.2 | 3.5 | 8.3 |
| Termite | 33.2 | 9.4 | 7.6 | 38.7 | 19.1 | 10.0 | 10.9 |
| Ant | 6.2 | 5.2 | 1.2 | 4.6 | 4.1 | 6.6 | 5.6 |
| Beetle/bugs | 11.3 | 16.3 | 9.3 | 15.1 | 13.5 | 11.5 | 6.9 |
| Larvae | 0.7 | 0.3 | 0.5 | 5.3 | 1.7 | 0.0 | 0.8 |
| Grasshopper/cricket | 0.0 | 0.3 | 0.2 | 0.1 | 0.2 | 0.4 | 0.0 |
| Other invertebrate | 2.2 | 0.1 | 0.5 | 1.1 | 0.7 | 0.6 | 1.4 |
| *Total plant* | 46.4 | 67.6 | 78.5 | 33.9 | 59.6 | 65.8 | 63.6 |
| *Total invertebrate* | 53.8 | 31.6 | 19.3 | 64.8 | 39.2 | 29.7 | 31.8 |
| Diet diversity | 2.5 | 1.7 | 1.8 | 2.2 | 1.9 | 2.3 | 2.0 |
| Item count | 4.1 | 3.5 | 3.9 | 3.7 | 3.7 | 4.5 | 4.1 |
| Identified | 62.5 | 68.1 | 84.4 | 50.4 | 67.4 | 70.4 | 76.6 |
| Unidentified | 8.4 | 2.0 | 2.4 | 1.4 | 2.7 | 3.1 | 2.9 |
| Sand | 29.0 | 30.0 | 13.2 | 48.2 | 29.8 | 26.5 | 20.5 |

**Table 8.3** Species of plant identified from the analysis of bilby faecal pellets collected from 33 spatial plots and two temporal sites. The plots were categorised in relation to latitudinal zone and the occurrence of plant species on substrate types as follows: drainage and calcrete (dc), laterite and rock features (lrf), sand plain and dune field (s).

| | Spatial plots | | | | Temporal sites | |
|---|---|---|---|---|---|---|
| | Newcastle Waters | Tennant Creek | The Granites | Kintore | Tennant T1D | The Granites SLD |
| Plots/Sites | 5 | 8 | 14 | 6 | 1 | 1 |
| Samples | 27 | 78 | 59 | 54 | 59 | 47 |
| Fireweed seed | | | | | | |
| *Amaramthus* spp. | | dc | | | | |
| *Paranactenium nova* | s | s | | | | |
| *Paspalidium* spp. | | s | s | | | |
| *Portulaca* spp. | | dcs | | | | |
| *Yakirra australiense* | s | dclrfs | dclrfs | s | dc | dc |
| Other seed: | | | | | | |
| *Eragrostis eriopoda* | | dc | | | dc | |
| *Fimbristylus* spp. | | | dc | | | dc |
| *Triodia* spp. | | s | | sdc | | |
| unknown spp. | s | dcs | dc | | | |
| Bulb: *Cyperus bulbosus* | | dc | dc | dc | | dc |
| Fruit: *Solanum* spp. | | dcs | dlrf | | dc | dc |

The faecal samples collected in the northern and southern latitudes contained less total plant material ($\chi^2$=10.1, df=1, p<0.01), less bulb ($\chi^2$=23.7, df=1, p<0.001), less non-fireweed seed ($\chi^2$=8.2, df=1, p<0.01) but more termite material ($\chi^2$=21.3, df=1, p<0.001) compared to the two mid-latitudes where bilby prevalence was greater. There was no significant difference in the relative abundance of fireweed seed ($\chi^2$=2.4, df=1 p>0.05).

### *The relationship of dietary composition with environmental variables*

The landscape variables that associated most significantly with key dietary components included annual rainfall, substrate, time since fire, cumulative rainfall and vegetation cover (**Table 8.4**). The components of beetle/bug and spore were not related significantly to any of the variables and 'other seed' was associated most significantly with proximity to 1-2 year old burnt areas.

The minimum adequate model for fireweed seed included three parameters and described a positive association with substrate, time since fire and cumulative rain in the previous 6 months and a negative interaction between the fire and substrate variables (**Table 8.5a**). This model captured 60% of deviance. It indicated that a greater amount of fireweed seed was consumed on sand or lateritic/rock feature substrates that had been recently burnt and received more antecedent rainfall in six month period than elsewhere. Antecedent rainfall in a shorter (eg. 3 month) or longer (eg. 12 month) period captured less model deviance than rainfall in a six month period (**Table 8.4**).

The minimum adequate model for bulb included two parameters and described a negative association with distance to drainage and a positive association with distance from recently burnt (<2 yrs) habitat and captured 73% of deviance (**Table 8.5b**). The model indicated that faecal samples collected closest to drainage substrates but furthest from recently burnt habitat contained a greater amount of bulb. Unlike fireweed seed, there was little association with parameters describing rainfall. More bulb was also associated with low shrub cover and spinifex cover (**Table 8.4**) but these did not form significant components of the minimum adequate model.

The minimum adequate model for total plant included distance to drainage and antecedent rainfall in a six month period (**Table 8.5c**). The model captured 56% of deviance and indicated that plant material was greater in samples collected in closer proximity to drainage substrate where greater rainfall had occurred in the preceding six months.

The minimum adequate model for the abundance of termites in the faecal pellets captured 53% of the deviance and indicated that more termite was contained in samples collected further from drainage or calcrete substrates and when rainfall deficit in the previous 12 months was greater (**Table 8.5d**).

**Table 8.4** The strength of the relationship between the abundance of dietary items and explanatory environmental variables. For components of the diet, the percentage of deviance captured by each variable fitted separately is shown. Values in bold are significant at $p<0.05$. Abbreviations used in the table: cat=category, dist=distance, ante=antecedent, mdev=deviation from the mean; K=Kintore, G=Granites, T=Tennant Creek, N= Newcastle Waters; rec=recent <2 years, int=intermediate 3-6 years, old=>6yrs

| parameter | df | fireweed | other seed | bulb | total plant | termite | beetle |
|---|---|---|---|---|---|---|---|
| null deviance | | 112.2 | 19.8 | 128.8 | 68.0 | 60.7 | 14.1 |
| Latitude: decimal degrees | 1 | **10.94** | **34.5** | 0.14 | **10.05** | **11.44** | 0.02 |
| Longitude: decimal degrees | 1 | **18.72** | **24.4** | **8.26** | 3.07 | 4.24 | 0.73 |
| Latitude: 4 cat (K,G,T,N) | 3 | **23.89** | **48.8** | **60.47** | **41.98** | **44.38** | 12.20 |
| Latitude: 2 cat (K/N,T/G) | 1 | **3.93** | **40.2** | **30.36** | **37.48** | **44.18** | 0.27 |
| Substrate: 5 cat (d,c,l,rf,s) | 4 | **21.04** | 4.2 | **61.86** | **29.40** | **33.06** | 22.67 |
| Substrate: 3 cat (dc,lrf,s) | 2 | **20.23** | 2.3 | **61.86** | **28.53** | **25.14** | 14.53 |
| Substrate: 2 cat (lrf, rest) | 1 | **10.54** | 0.8 | **61.86** | **14.67** | **9.78** | 10.04 |
| Substrate: 2 cat (dc, rest) | 1 | **15.70** | 2.0 | **8.42** | **5.81** | **9.11** | 1.25 |
| Burn 3 cat: (rec,int,old) | 2 | **31.41** | 17.4 | **23.94** | **15.36** | **29.10** | 1.72 |
| Burn 2 cat: (rec, rest) | 1 | **31.13** | 8.5 | **18.62** | **7.73** | **20.04** | 1.71 |
| Fire: years since fire | 1 | **23.33** | **22.5** | 1.17 | **15.12** | **26.63** | 1.77 |
| Substrate: dist to calcrete | 1 | 2.95 | 0.2 | **24.32** | 1.35 | 5.38 | 0.13 |
| Substrate: dist to drainage | 1 | 0.10 | 0.1 | **65.53** | **11.42** | **12.09** | 0.60 |
| Substrate: dist to dc | 1 | 0.02 | 0.0 | **58.94** | 5.38 | **8.25** | 0.15 |
| Substrate: dist.to laterite | 1 | **4.42** | 3.6 | 2.14 | **9.35** | **15.07** | 0.12 |
| Substrate: dist to rockfeat. | 1 | 0.12 | 0.1 | 1.12 | 1.14 | 1.06 | 0.74 |
| Substrate: dist to lrf | 1 | 0.74 | 1.1 | 0.79 | 2.54 | 2.94 | 1.21 |
| Substrate: dist to sand pl. | 1 | 0.23 | 4.1 | 2.87 | 2.79 | 4.05 | 3.94 |
| Fire: dist to <1yr old | 1 | **7.53** | **40.9** | **4.04** | **13.75** | **20.52** | 3.16 |
| Fire: dist to 1-2 yr old | 1 | 3.26 | **46.3** | **25.95** | **27.86** | **48.61** | 2.04 |
| Fire: dist to <2yr old | 1 | 4.24 | **39.1** | **10.52** | **14.48** | **17.77** | 1.31 |
| Rainfall: annual mean | 1 | **7.45** | **26.3** | 0.83 | **5.03** | 4.62 | 0.01 |
| Rainfall: ante since fire | 1 | **5.89** | 1.5 | 0.13 | 2.93 | **8.32** | 3.84 |
| Rainfall: ante in 3mths | 1 | 2.10 | 0.5 | 1.28 | **8.54** | **9.76** | 4.38 |
| Rainfall: ante in 6mths | 1 | **21.42** | **18.7** | 0.00 | **21.21** | **32.13** | 0.03 |
| Rainfall: ante in 12mths | 1 | **14.08** | **31.8** | 0.16 | **17.56** | **25.08** | 0.30 |
| Rainfall: ante in 24mths | 1 | **13.54** | **21.7** | 0.06 | **13.70** | **20.88** | 0.58 |
| Rainfall: mdev in 12mths | 1 | **11.48** | **36.4** | 1.48 | **19.89** | **36.84** | 1.01 |
| Rainfall: mdev in 24mths | 1 | **16.03** | 13.5 | 0.10 | **19.21** | **39.09** | 2.87 |
| Vegetation: % total cover | 1 | 1.17 | 5.6 | 5.53 | 1.36 | 3.05 | 2.61 |
| Vegetation: %spinifex cov | 1 | **14.20** | 0.6 | **11.78** | 0.50 | 0.43 | 3.54 |
| Vegetation: %shrub cover | 1 | 1.40 | 0.9 | **32.45** | **6.54** | 5.74 | 0.69 |
| *Yakirra* presence/absence | 1 | **15.20** | 8.6 | **8.31** | 2.60 | **6.35** | 0.05 |
| *Yakirra* % cover | 1 | **4.46** | 0.1 | **14.70** | 0.15 | 0.04 | 0.01 |

**Table 8.5** The minimum adequate model for the relative abundance of key dietary items. Abbreviations used in the table: rec= <2yr old, rest= intermediate 2-6 yr old and old >6yr old; lrfs=laterite, rock features and sand plain, dc=drainage and calcrete; 6 mth antecedent rainfall in mm. p<0.05 if t value >1.96.

a) Fire seed
Null deviance = 112.5, 59.6% captured

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -1.531 | 0.424 | | | -3.6 |
| Fire 2 category (rec, rest ) | 0.927 | 0.205 | 27 | 35.0 | 4.5 |
| Substrate 2 category (lrfs:dc) | 0.502 | 0.201 | 26 | 13.0 | 2.5 |
| Rainfall antecedent in 6mths | 0.005 | 0.001 | 25 | 12.1 | 3.6 |
| Fire 2 cat. x Substrate 2 cat. | -0.527 | 0.203 | 24 | 6.9 | -2.6 |

b) Bulb
Total Deviance =128.8, 72.6% captured

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -0.0726 | 0.234 | | | -0.3 |
| Substrate: distance. to drainage | -8.697 | 2.172 | 27 | 84.5 | -4.0 |
| Fire distance to <2yr old | 0.222 | 0.0641 | 26 | 9.1 | 3.4 |

c) Total plant
Total Deviance =149.9, 34.0% captured

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -0.221 | 0.271 | | | -0.8 |
| Substrate: distance to drainage | 0.00435 | 0.00114 | 27 | 14.4 | 3.8 |
| Rainfall: antecedent in 6mths | -0.0198 | 0.00679 | 26 | 8.7 | -2.9 |

d) Termite
Total Deviance =60.7, 53.0% captured

| Variable | Estimate | Std. Error | df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -3.324 | 0.465 | | | -7.1 |
| Rainfall mean deviation in 12mths | -0.0123 | 0.00255 | 26 | 22.4 | -4.8 |
| Substrate: distance to drain/calcrete | 0.0259 | 0.00777 | 27 | 9.9 | 3.3 |

### *Temporal variation in the diet at the two sites with persistent activity*

#### The Tennant Creek latitude

At the Tennant transect (T1D), bilby activity was recorded and faecal samples were collected during six consecutive sampling periods between September 1995-March 1997. Sign of juveniles was recorded on three occasions (November 1995-June 1996) based on track or faecal diameter. No bilby sign was observed during sampling in November 1997 and March 1998. Part of the site had been burnt in 1993/4 and the remainder was burnt prior to 1983. Spinifex hummocks were well developed and commonly 70 cm high in the long-unburnt areas and 10-20 cm high in more recently burnt areas at the start of sampling. The dominant shrub was *Melaleuca glomerata* and spinifex cover was dominated by *Triodia pungens*. *Yakirra australense* was recorded during the food plant surveys conducted in autumn 1996 (1-5% cover) and 1997 (<1% cover) but was absent in 1998 and absent or recorded in trace amounts during the vegetation transects (2000 points) conducted in spring each year (1995-97). The cover of *Eragrostis eriopoda* declined from 8.7% to 0% over the same period and spinifex cover increased from 23.8 to 44.8%.

Over the 19 month period, the relative abundance of fire-weed seed in the faecal samples ranged from 23 to 72% (CV 65.6%) and non-fireweed seed ranged from 0 to 39% (CV 96.7%) (**Fig. 8.2**). *Yakirra australense* was the only fire-promoted seed recorded and *Eragrostis eriopoda* was the primary non-fireweed seed. No bulb material was recorded at the site. The overall amount of plant material ranged from 45-80% (CV 38.6%) with the least amount recorded during the last sample period. Fungal spore was present in low abundance ranging from 0.8-4% except in the final sample when it became relatively abundant at 12% (CV 139.8%).

Beetles contributed most to the invertebrate component of the diet over the sample period, ranging from 4.8-34% (CV 111.7%), with the last sample period containing the greatest relative abundance (**Fig. 8.2**). Termites contributed the next greatest relative abundance ranging from 3.2-15.2% (CV 180.8%). Least termite abundance was recorded in the autumn samples. Ants contributed less than 6% (CV 104.9%) of faecal material during each sample period except the last, when it increased to 19%. Overall, the amount of invertebrate was less than 30% (CV 71.0%) except in the last sample when it increased to 55%. The proportion of sand in faecal samples ranged from 24.3% to 43.7% (CV 53.9%) and was greatest in the last sample period. The combined proportion of plant (CV 38.6%) was less variable than the combined invertebrate component (CV 71.0%).

The Granites latitude

At the Sangsters long dune (SLD) site, faecal samples were collected on six occasions in the period June 1997- May 1998 and activity was observed again at this site in October 1998. Sign of juveniles was recorded on three occasions (June 1997, March and May 1998). Shrub cover at the site was dominated by *Melaleuca glomerata* with an understorey of *Triodia pungens* on the dune flanks with samphire on the lower lying areas. Large *Nasutitermes* termitaria, often over 2 m in height, were present in the region. The site had been burnt five years prior to the commencement of sampling in 1997 and spinifex cover was about 19% but there were other more recently burnt areas within a 5 km radius.

Over the 12 month sampling period, the faecal material was dominated by the bulb *Cyperus bulbosus*. This ranged in relative abundance from 43.2 to 76.8% (CV 36.1%) **(Fig. 8.3)**. Seed from *Yakirra australiense* was also present, but in small amounts, ranging from 0-12% (CV 211.8%). There was also a small amount of seed from non-fire-promoted plants (<2%). Overall, plant material ranged from 44 to 76.8% (CV 28.5%). The abundance of fungal spore ranged from 0-6.4% (CV 109.2%). Termites were the most abundant invertebrate recorded and ranged from 6 to 15.6% (CV 106.9%). Overall, the invertebrate component ranged from 20.8 to 28.8% (CV 67.9%) except in one sample when it reached 49.6% (**Fig. 8.3**). Faecal material collected from the SLD site contained relatively little sand, ranging in abundance from 11.5 to 23.1% (CV 61.5%).

*Comparison of diet at sites with persistent and transient activity*

Bilby activity was recorded at three drainage sites at the Tennant Creek latitude in August-September, 1995. While bilby activity continued to be recorded over the next 19 months at T1D site, feeding activity was not recorded again on site T2D or T3D during the study. The faecal composition at the T1D site was similar to the replicate site T3D and both were dominated by fireweed seed despite being located on drainage substrate. The composition at site T2D was dominated by bulb instead of seed. The proportion of summed plant material at the T3D site was not significantly different ($\chi^2$=2.92, df=1, p>0.05) to the T1D site. There was significantly more termite ($\chi^2$=34.4, df=1, p<0.001), ant ($\chi^2$=6.4, df=1,

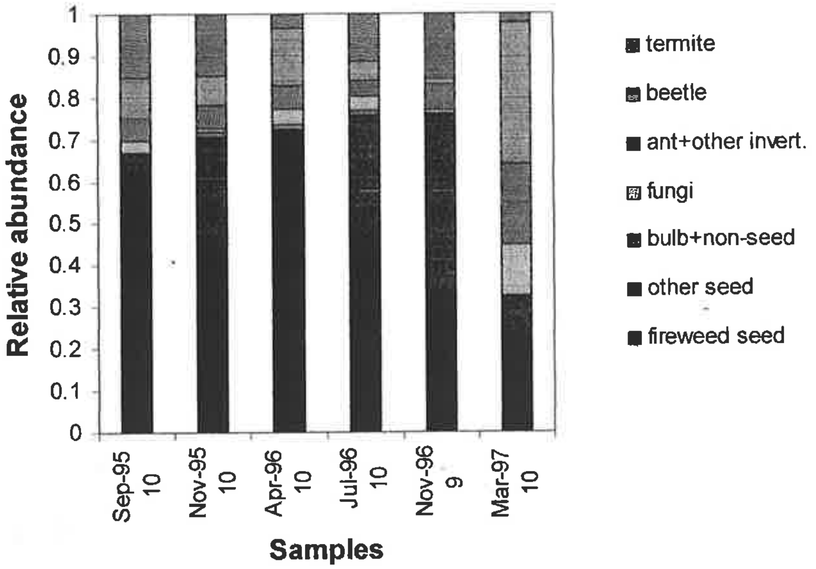

**Fig. 8.2** The proportional contribution of major food groups to the diet of the bilby over a 19 month period at the Tennant Creek transect T1D.

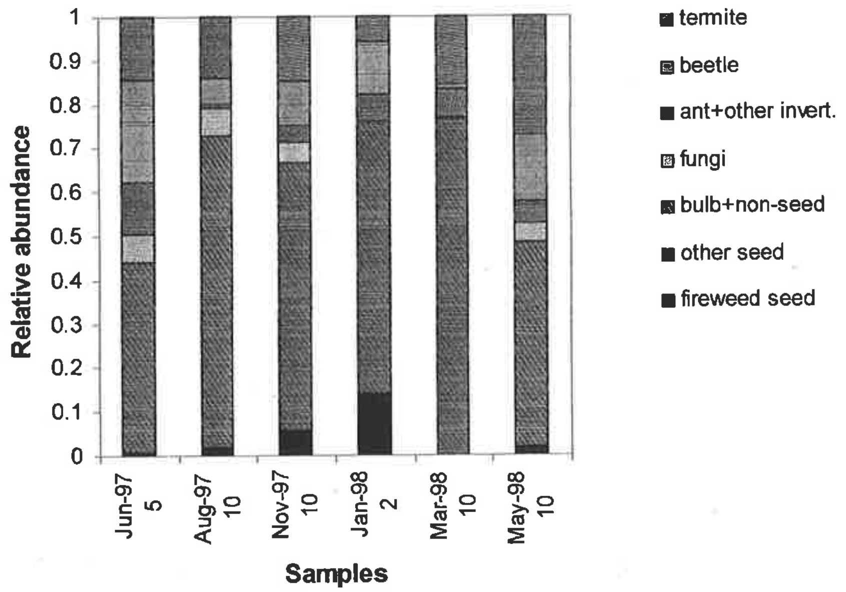

**Fig. 8.3** The proportional contribution of major food groups to the diet of the bilby over a 12 month period at site SLD at the Granites latitude.

$p<0.05$) and spore ($\chi^2=8.1$, df=1, $p<0.01$) but less beetle ($\chi^2=7.4$, $p<0.01$) and fireweed seed ($\chi^2=4.72$, df=1, $p<0.05$) at the T1D site compared to the T3D sites.

The SLD site lacked a contemporaneous sample site at the same latitude. However, the amount of bulb ($\chi^2=0.9$, df=1, $p>0.05$) and total plant ($\chi^2=0.001$, df=1, $P>0.05$) in the faecal samples collected at the SLD site was not significantly different to samples collected at T2D site at same time. There were significant differences in some of the less dominant dietary items with more beetle and fruit but less termite at the SLD: fruit ($\chi^2=17.1$, df=1, $p<0.001$), termite ($\chi^2=11.0$, df=1, $p<0.001$) and beetle ($\chi^2=21.1$, df=1, $p<0.001$).

The composition of samples collected from the long dune site (SLD) was also very similar to samples collected in October 1995 at G1D located in the same drainage system but 15 km away. The G1D site had greater spinifex cover (34%) and had remained unburnt for at least 11 years. There was no significant difference in the amount of bulb but significant differences in the amount of termite ($\chi^2=16.5$, df=1, $p<0.001$), spore ($\chi^2=8.9$, df=1, $p<0.001$) and beetle ($\chi^2=7.75$, df=1, $p<0.001$). There was more termite and spore at the SLD site but less beetle.

## Discussion

### *Dietary composition*

Both invertebrate and plant material occurred in almost all faecal samples analysed from the present study and the range of dietary items was similar to other studies that have now been conducted on the diet of the bilby in arid Australia (Gibson 2001; Smyth and Philpott 1968; Southgate 1990b; Watts 1969). As found previously, the plant material consumed was dominated by a few species (Gibson 2001; Southgate 1990b). In our study, seed from *Yakirra australiense* was a key plant food and the bulb from *Cyperus bulbosus* also formed a significant component of the diet at some localities. *Yakirra australiense* is a widespread and ephemerally common species in central Australia and is closely associated with spinifex grasslands (Jessop 1981). Ants are attracted to the seed because of an attached eliasome and the seed is carried back to their nests where the appendage is chewed off and the seed is discarded (Latz 1995). This acts to concentrate seed at ant nests for use by bilbies (Southgate, pers. obs.) and other species. On the clay downs in southwest Queensland, seed from *Dactlyloctenium radulans* forms the key plant food for the bilby (Southgate 1990b; Gibson 2001). Sparse sign of this plant species was recorded from only a few localities in our study and its seed was not encountered in any of the faecal samples.

Gibson (2001) has examined the relationship between food availability and the items consumed by the bilby, and she suggested that bilbies did not consume food items in direct proportion to their availability. Several potential invertebrate foods were avoided at her Queensland study sites while others were positively selected. Nevertheless, she found that seasonal trends in availability of the key foods consumed were reflected in the diet of bilbies. Therefore, it is likely that the absence of a key food in the diet eg. *Dactylocetenium*, *Yakirra* or *Cyperus* would indicate that this type of food was exceedingly scarce or absent at a locality.

The invertebrates consumed were from several taxonomic orders. In our study, termites appeared to be a critical component of the diet when plant material was scarce, and continued to be eaten even when a large amount of plant material was consumed. Termite abundance in faeces increased with increasing rainfall deficit, distance from frequently burnt patches and distance from drainage lines, and it is suggested that this reflected primarily the decreasing availability of suitable plant foods and not a greater availability of termites. We argue that the availability of key plant foods is more labile than that of termites. The conditions suited for the production of *Yakirra* or *Cyperus* are short lived and occur infrequently. In contrast, termites feed on perennial plant species, unpalatable to most other animals; they store this food, and live underground or in mounds that are protected from potential predators and climatic extremes. Morton and James (1988) have argued that termites are extremely common and widespread in the spinifex deserts of Australia and account for the extremely rich assemblage of lizards in the spinifex grasslands of Australia. Furthermore, James (1991) stated that termites were probably more available than other taxa during all seasons, even during xeric periods when there is a reduction of invertebrates reliant on green herbage. The importance of termites in the diet of the bilby during dry periods has also been noted in other studies on the bilby (Newsome

1962; Smyth and Philpott 1968) as well as other arid-adapted bandicoots. For example, Southgate *et al.* (1996) found that the occurrence of termites in the diet of the golden bandicoot *I. auratus* increased during the dry season and Bradshaw *et al.* (1994) found that the diet of the golden bandicoot contained 50% termite during a drought but the volume fell to only 18% and other invertebrates increased 3-fold following a major cyclone. Redford and Dorea (1984) suggested that the nutrient value of termites does not vary greatly from other terrestrial invertebrates and predators select termites in terms of their availability rather than nutritional value alone.

The substantial use of plant material by the bilby is unusual compared to other perameloids that have been studied. The diet of species within *Perameles* (Heinsohn 1966; Quin 1992; Scott *et al.* 1999), *Isoodon* (Bradshaw *et al.* 1994; Broughton and Dickman 1991; Claridge 1993; Quin 1992) and *Echymipera* (Anderson *et al.* 1988) is dominated by invertebrates (~63-75%) and the plant foods used are mainly perennial plants that fruit or seed seasonally rather than annuals promoted by disturbance. Furthermore, the bilby appears to be the only extant mammal in Australia, apart from Aboriginal people (Latz 1995; Peterson 1978), that make substantial use of fireweed seed. Limited studies indicate that arid Australian rodents are omnivorous and that seed from dicots is far more commonly consumed than from monocots (Murray and Dickman 1994; Murray *et al.* 1997; Predavec 1994; Watts 1970). However, it is possible that fireweed seed formed an important part of the diet of a number of medium-sized mammal species such as *Chaeropus* and *Bettongia* spp. that are extinct or no longer present in the arid parts of Australia. The ability to burrow has made the bilby non-reliant on vegetation for shelter and has enabled the species to inhabit recently burnt or sparsely vegetated localities and to make use fireweed seed production following fire or drought (Southgate, unpublished data). However, this does not explain why monocot seeds appear to be under-utilised by semi-fossorial Australian rodents in studies to date and this issue warrants further investigation.

*Prevalence and persistence of the bilby and diet*

In this study, plant material dominated the diet where bilby activity was most prevalent and diminished where bilby prevalence was least. This suggests that bilby prevalence at the landscape scale is affected markedly by the availability of key plant foods. The use of plant foods such as *Yakirra* and *Cyperus* that can become temporarily abundant and easy to obtain, presumably allow individuals to aggregate and attain relatively high densities. This is comparable to the findings of Murray and Dickman (1994) who reported that two arid zone rodent species increased their abundance and the consumption of seed following high rainfall, despite a preference by the species for invertebrates. As key plant foods become scarce, it is suggested that bilbies revert to invertebrate prey, particularly termites which are more consistently abundant but demanding to obtain (Redford and Dorea 1984; Morton and James 1988). This is reflected in the greater amount of sand consumed with invertebrate items compared to that consumed with bulb or seed. Reliance on invertebrates as a food source would force the bilby population to become more highly dispersed and result in the diet becoming more diverse. Other studies of bandicoots have shown that the dispersion of food resources rather than social bonding affects the dispersion of individuals in the wild (Lee and Cockburn 1985).

The conditions that allow individuals to persist at a locality are less clear but may relate to the continued availability of key plant food plus a reliable supply of suitable invertebrate foods such as termites to supplement nitrogen requirements. Plant material dominated the diet at both sites where persistent bilby activity was recorded. At site T1D, where seed was mainly consumed, the amount of fireweed seed declined gradually over the monitoring period but greater inclusion of non-fireweed seed maintained the high proportion of plant material up until the last sample. At this point, the amount of plant material declined to 45%, termite declined to 2% and beetle (34%) and ant (19%) became more prominent. Following this sample, no further bilby activity was recorded at the site. At site SLD, where bulb was mainly consumed, the relative abundance of overall plant material was greater than 45% and the amount of termite recorded at this site was generally greater than 10%. Breeding activity based on the presence of immature animals was observed at both the sites with persistent activity and indicated that a diet dominated by either seed or bulb was suitable for the production of young. Where a comparison of diet could be made between sites with persistent bilby sign and sites where sign was transitory, there was no significant difference in the amount of plant consumed. However, there was consistently more termite (i.e. generally > 10%) at the most persistently occupied sites.

The diet of two persistent bilby sub-populations in southwest Queensland was similar to that found at the two localities in the Tanami Desert where bilby sign was persistent. At the Queensland sites, the diet was dominated by plant material (68%) and consisted mainly of seed (56%) from *Dactyloctenium radulans* (Gibson 2001). Termite which contributed about 11% of the relative abundance of dietary items dominated the invertebrate component. Bilby activity remained relatively constant at the two independent sites over an 18 month sample period (Gibson, pers. com.).

It should be noted that the localities that support an abundant supply of both plant and termite material are likely to be relatively uncommon in the current geographic distribution of the bilby. Of the 20 localities where nine or more faecal samples were collected in the Tanami Desert, only five sites contained >45% bulb or seed and >10% termite in the faecal samples. This is consistent with the proposition of Stafford Smith and Morton (1990) that the production of nutritious and easily digestible food in most of the arid zone is limited and spatially and temporally unpredictable.

### *Fire-promoted plant foods and habitat attributes*

Overall, fire-promoted plants dominated the plant material consumed by the bilby and greater amounts of fireweed seed occurred in the diet generally in closer proximity to recently burnt localities. However, fireweed seed was not limited to parts of the landscape where fire frequency was high, and the growth of *Yakirra* was found to be stimulated by other forms of disturbance. For example, a severe rainfall deficit resulted in the death of spinifex in parts of the Kintore region during the study and drought-breaking rain in summer resulted in a flush of *Yakirra* growth even within the dead spinifex clumps (Southgate, unpublished data). More localised growth of *Yakrira* was also observed where spinifex had been removed mechanically such as along graded road verges or where the soil surface had been disturbed by ant activity. Furthermore, the model describing the environmental variables that associated with dietary fireweed seed abundance indicated that both substrate and rainfall were significant variables in addition to disturbance from fire. Most rainfalls are too small and temporally isolated to have an immediate stimulatory effect on plant growth in the Australian arid zone (Stafford Smith and Morton 1990). A rainfall event of sufficient magnitude to stimulate germination, growth and seed-set could occur anywhere in the study area, but these events are less frequent in the southern part. Hence, the low probability of occurrence of fire followed by a large rainfall event make the production of abundant fireweed seed a relatively rare event in most parts of the Tanami Desert, particularly in the south. High dietary seed consumption did occur at some localities along drainage lines, but it was generally greater on sand and laterite substrates.

In contrast to dietary seed abundance, more bulb was consumed at sites in close proximity to drainage lines that had not been recently burnt. The different variables in the minimum adequate models for bulb and fireweed seed suggested that the factors controlling the availability of these plant foods (and possibly their production) were unrelated or, alternatively, the bulb was consumed only when the availability of fireweed seed had diminished. Either way, these results indicated that bilbies with access to both drainage substrate and sand and laterite/rock feature substrates would have a greater opportunity to maintain a diet high in plant food compared to bilbies located long distances from drainage substrates. Drainage and calcrete substrate occurs in less than 8% of the Tanami Desert and only a small proportion of this would have the local topographic and soil conditions suited for bulb production (Southgate, unpublished data). Drainage substrate is poorly represented in the northern part of the Tanami Desert and this may explain why bilby prevalence tended to be more variable and at times particularly low in the Newcastle Waters zone compared to the Tennant Creek and the Granites.

### *Implication for research and management*

Our research suggested that there was a reasonably strong, positive association between bilby prevalence and dietary plant food. At localities in closer proximity to recent fire, fire-promoted plants contributed significantly to the amount of dietary plant material. This linkage provides a coherent case that fire management could be used to improve the habitat suitability for the bilby and possibly improve the status of the species in some parts of its range. It is unlikely that the benefits of fire management would extend equally over the current extent of bilby occurrence. An increase in the spatial and temporal heterogeneity of fire ages would be most beneficial in areas where fuel production was greatest, particularly the northern part of the Tanami Desert.

A better understanding of the effect of fire, rainfall and substrate on the production of key food plants such as *Yakirra* would be necessary to assist the development of an adequate management plan. This would also require an understanding of the effect of rainfall and substrate on the accumulation of fuel from spinifex grasses and other plants to plan a management regime. A program to experimentally measure and validate the effect of patch burning and rainfall on fireweed plant abundance and the abundance of the bilby and other organisms, especially granivorous birds and mammals would also be important.

The high incidence of bulb and fireweed seed in the diet of the bilby has a number of other implications for management and further research. Firstly, bulb production is limited to drainage substrate and it is important to protect this habitat type against the impact caused by stock and introduced herbivores (Edwards *et al.* 2004; James *et al.* 1995). Secondly, the investigation of bilby diet provided no clearer indication why bilby occurrence was strongly associated with lateritic and rock feature substrates. While there was some indication that greater amounts of fireweed seed occurred in samples from sites on laterite, there was no significant difference between sand plain and laterite. It is possible that the availability of root-dwelling larvae and termites is greater and less variable on lateritic substrates but this requires further investigation.

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# Chapter 9

# Fire-promoted plant production and spinifex-fueled fires in the Tanami Desert[1]

*Preamble to Chapter 9*

In the previous chapter, I presented information on the diet of the bilby and showed that seed from a fire-promoted plant *Yakirra australiense* formed an important component of the diet of the bilby. Fire, rainfall and substrate variables associated with the amount of *Yakirra* consumed. In this chapter I examine the environmental variables that influence the production of *Yakirra* and the recurrence of fire in the Tanami Desert.

I aimed to develop a simple decision model to assist managers decide where and when to burn and what to expect regarding *Yakirra australiense* growth following fire and different amounts of rainfall. Ideally, existing fire history mapping and rainfall data would be adequate to parameterise the model. Such a resource would assist in mapping the broad-scale temporal change in total vegetation cover and in the identification of habitat suitability for the bilby.

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## Introduction

Fire is an important driving force in the arid zone of Australia, causing dramatic changes to the structure of the habitat and local environmental conditions (Griffin 1984; Stafford Smith and Morton 1990; Allan and Southgate 2002). Fire management has therefore been proposed as a means to improve or maintain habitat suitability for a range of plant and animal species (Christensen 1987; Friend 1993; Masters 1996). However, there is often little understanding of the conditions such as the timing and intensity of fire that result in a desirable outcome from fire management (Whelan *et al.* 2002). Even when this information is available, decision making is sometimes confounded by a perceived complexity about the importance of other environmental variables (Starfield and Bleloch 1986). Straightforward information is required to allow managers to determine whether there is sufficient fuel to conduct a burn, the parts of the landscape that most need fire management, when it would be best to burn, and the expected response of focal animal and key plant species to fire (Whelan 1995; Craig 1999).

Fires release scarce nutrients from perennial tissue, remove plants that compete for nutrients and water and affect soil temperature and air movement. These altered conditions allow a different mix of annual grasses and herbs and short-lived perennials that have persisted as seeds or dormant tubers to flourish in the time following fire (Griffin 1990). The bilby (*Macrotis lagotis*) is a threatened bandicoot that consumes seed from plants promoted by disturbance events like fire. In areas where the bilby is most prevalent in the Tanami Desert, its diet is dominated by plant material and a single fire-promoted species *Yakirra australiense* can contribute significantly to the diet (Southgate and Carthew 2006). Furthermore, one of the main environmental factors associating with bilby prevalence is proximity to recently burnt (<2 years) areas (Southgate *et al.*, unpublished). This suggests that fire and the promotion of key food plants is an important process affecting bilby distribution, and fire management presents an opportunity to improve habitat suitability and the status of the bilby. However, little is known about the factors that control the abundance of *Yakirra australiense* and other important plant species such as *Dactyloctenium radulans* and *Cyperus bulbosus* that contribute to the diet of the bilby. Similarly, there is limited information on the factors that affect vegetation cover, fuel production and fire frequency in spinifex (*Triodia* spp.) dominated grasslands of arid Australia (Craig 1999). Models of fuel production have been developed previously, but this work was limited to the lower rainfall parts of central Australia and limited to sand plain and lateritic soils (Griffin and Allan 1984; Burrows and Christensen 1990).

To better understand the relationship between fuel, fire and *Yakirra* production, it was considered important to examine the effect of substrate and rainfall on vegetation growth among the major spinifex alliances and determine whether readily available spatial data could be used to assist the development of prescriptive fire management. In this study, we aimed to determine 1) the variables significant to the production of ground and spinifex cover in the Tanami Desert, 2) the amount of ground and spinifex cover required to carry fire and 3) the variables significant to the production of key food plant species used by the bilby. It was expected to find greater production of cover associated with drainage substrates than on sand plain or laterite substrates because of the improved water recharge capacity (Stafford Smith and Morton 1990), and greater production of cover in the spinifex alliances dominated by *Triodia* species that resprout from rootstock. Finally, it was considered important to present information in a format that could be used easily by managers and stimulate adaptive management to clarify the patterns of fire response. A decision tree was developed to integrate the information relating to accumulation of fuel and indicate the expected production of *Yakirra* in response to rainfall and time since fire.

## Methods

### *Study area*

The study area was approximately 236,000 km$^2$ in size, bounded by the Northern Territory/Western Australian border and pastoral leases on the northern, eastern and south-eastern edges (**Fig. 9.1**). Most of the land is Aboriginal Freehold, sparsely populated and undeveloped. There are no major towns within the study area and few roads.
Summers in the Tanami Desert are very hot and winters are cold to mild. Mean daily maximum temperature during the hottest month ranges from 39.3°C in the northern part of the study region, to 36.2 °C in the south. Mean daily minimum temperature during the coldest month (July) is 11.3 °C in the north and 4.1 °C in the south (Bureau of

Metereological records). Rainfall in the region ranges from an annual average of 600 mm in the north to around 300 mm in the south. In the north, 90 % of mean annual rainfall occurs during summer compared with 77% in the south. Cyclonic incursions occasionally cause exceptional rainfall events, where more rainfall can occur within one month than the annual average. However, the frequency of these events decreases with increasing aridity and rainfall becomes more variable (**Table 9.1**).

The area is mostly flat to undulating and ranges in elevation from 200-600 m above sea level. Sand plains with earthy sands and dunes with red siliceous sands account for about 82% of the landscape. Skeletal soils and lateritic soils account for about 10% of the landscape, and drainage lines, calcareous soils and paleodrainage systems (van de Graaf *et al.* 1977) cover about 8% and are considered to be the most reliably productive substrate type (Stafford Smith and Morton 1990).

There are over 60 described species of *Triodia* (Lazarides 1997) but within the Tanami Desert, three species are most common: *T. basedowii, T. shinzii* and *T pungens*. In places, the three species can occur sympatrically (Griffin 1990). The vegetation overstorey consists of scattered shrubs and trees including *Eucalyptus*, *Acacia* and *Grevillea. Melaleuca* spp. are typically found in paleodrainage systems. Further description of the study area is given in Paltridge and Southgate (2001).

**Table 9.1** Annual mean and median rainfall (mm) at the study sites and the percentage of mean annual rainfall for the three years prior to the study and three years during the study. Rainfall information was derived from the splined rainfall coverage (1970-1997) using rain years (August-July). CV=coefficient of variation.

| | Decimal degree | | Annual rainfall | | Percentage of mean annual rainfall | |
|---|---|---|---|---|---|---|
| Location | Latitude | Longitude | Median | Mean (CV) | 1993-95 | 1996-98 |
| Newcastle Waters N1 | 17.30 | 130.84 | 539 | 578 (31.0) | 95 | 80 |
| Tennant Creek T3 | 19.10 | 132.77 | 433 | 455 (34.4) | 102 | 81 |
| Tennant Creek T1 | 19.48 | 132.88 | 430 | 447 (34.5) | 103 | 80 |
| The Granites G1 | 20.90 | 130.41 | 377 | 390 (41.7) | 96 | 70 |
| Kintore K1 | 22.83 | 129.62 | 288 | 323 (52.8) | 74 | 51 |
| Kintore K3 | 22.78 | 130.03 | 290 | 318 (56.2) | 70 | 52 |

*Random plot monitoring*

Vegetation composition and cover data were collected across the study area at 226 random plots stratified in relation to five substrate and three fire age categories between May 1996 to April 1998 (**Fig. 9.1**). The substrate types were categorised as calcareous (c), paleodrainage/drainage (d), laterite (l), rock (skeletal) features (r), sand plain and dune (s) and the fire ages were categorised as recently burnt (1-2 years old), intermediate (3-6 years old) and old (greater than 6 years old). Plots were spaced at least 4 km apart and at least five plots were sampled in each category. The point intersect method and a wheel point apparatus were used to collect 300 points of vegetation cover data at 1 m intervals (Griffin 1989). Plant species were identified and ground cover was categorised as spinifex, non-spinifex grasses, forbs and standing litter (>10 mm height). Flat litter (<10mm) was grouped with bare ground. Shrub cover (woody plants > 500 mm height) was recorded as a separate layer.

*Transect monitoring*

Repeated sampling of fixed transects was used to determine changes in vegetation structure and composition over time. Transects were located at eight sites within four latitudinal zones: Newcastle Waters 17-18.5° S, Tennant Creek 18.5-20° S, the Granites 20-21.5° S and Kintore 21.5-23.5° S. Three sites spaced about 25 km apart were located in both the Kintore and Tennant Creek latitudes and one site was located in each of the Granites and Newcastle Waters latitude. There were two transects at each site, one on sand plain/dune and the other on drainage/calcrete. Newcastle Waters lacked drainage substrate, and thus had two sand plain transects. Transects were 10 km long and marked at 500 m intervals. At each interval, 100 points of vegetation data were collected (using the wheel point apparatus) perpendicular to the transect, producing 2000 points of data per transect for each sample. Transects were sampled once per year, generally at the end of spring between May 1995 and May 1999. Vegetation data were categorised as described for the plots. Plots were resampled for key food plants (*Yakirra australiense*, *Dactyloctenium radulans* and *Cyperus bulbosus*) in autumn each year and cover was scored as absent 0%, trace <1%, present 1-5% and abundant >5%.

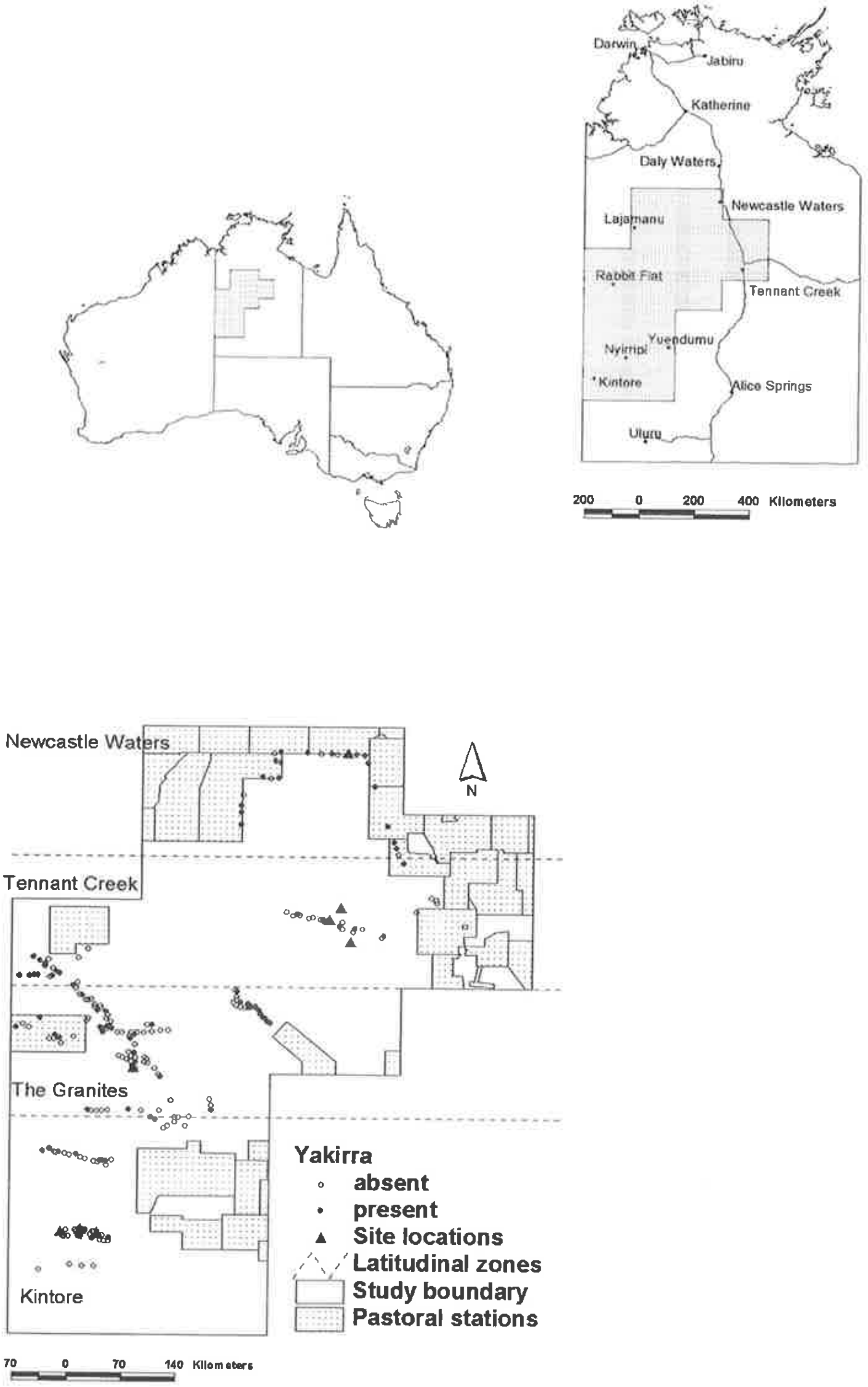


**Fig. 9.1** The study area in the Tanami Desert showing the location of plots, sites and the four latitudinal zones. The plots where *Yakirra australiense* was recorded are also shown.

Fire history mapping indicated that most transects had been burnt prior to 1985. Exceptions were the Tennant latitude where transects T1D and T1S were burnt in 1993/4 and transects T3S and T3D were burnt in 1994/5. Part of T3D burnt again early 1998. At the Granites latitude, part of the drainage (G1D) and the sand plain (G1S) transect was burnt in 1993/4 but most appeared to have been burnt in 1985 or earlier and this date was accepted for the entire transect.

### *Experimental fire plots*

Experimental fire plots were burnt near each of the fixed transects at the Tennant Creek and Kintore latitude to produce areas with known fire age and to investigate the response of fireweed plants to seasonal conditions. In most cases, plots were located on both drainage line and sand plain substrates. Attempts were made to burn sections of habitat during both cool and hot times of the year. Some burnt plots were sampled up to six times over the three year period but most were sampled only two or three times. Pre- and post-burn vegetation monitoring was conducted using wheel point apparatus and 300 points of data were collected per sample at each fire plot as described above. Fires were scored as: no burn (did not carry and <0.05 ha burnt); patchy burn (trickling movement of fire, spinifex clumps missed); or hot-clean burn (intense heat produced, virtually all ground cover consumed and rapid movement of the fire front).

### *Climatic variables*

Monthly gridded rainfall data for the region were obtained from the Bureau of Meteorology (BOM) as there were few rainfall stations in the vicinity of plots. Data were provided as a $0.25^{O}$ spatial grid (roughly 25 km resolution) and were derived using the Barnes successive correlation technique that links designated weather stations across Australia (Jones and Weymouth 1997). Mean annual rainfall, mean minimum temperature and the mean maximum temperature and elevation for each plot were derived by intersecting plot, site and transect locations with surfaces available from the Australian Natural Resource Data library. Data for annual rainfall and temperature used a spatial grid of $0.05^{O}$ (roughly 5 km resolution) complied between January 1979–December 1999. Monthly rainfall data were used to calculate cumulative rainfall since fire and cumulative rainfall prior to a specific sampling date. Rain years (August-July) were calculated to correspond with mapped fire history.

*Analysis*

Generalised linear modelling was used to determine environmental parameters associated with spinifex cover, total vegetative ground cover and *Yakirra* occurrence on plots. Explanatory variables included time since fire, rain since fire, amount of rainfall in the one, two, three, six and 12 months prior to sampling, cover of spinifex, shrub cover, spinifex species dominance, stoloniferous life-form, substrate type, mean annual rainfall, maximum and minimum mean temperature, latitude and longitude. A spinifex species was considered dominant if it contributed 90% or more to the spinifex cover (Griffin *et al.* 1990), otherwise the plot was specified as mixed. Fire age was determined from fire history mapping (Allan and Southgate 2002) and verified during the field assessment of vegetation cover. Plots were excluded from analysis if the mapped and the field estimates were substantially different. Total ground and spinifex cover expressed as a proportion were used separately as response variables. Modelling was performed as outlined by Nicholls (1989) using a forward stepwise procedure, with a logit link function. Plots that were long-unburnt (>12 years) were used to examine the effect of substrate on the maximum amount of spinifex cover and total cover.

The amount of long-unburnt total ground cover and spinifex cover on plots was compared among substrates, latitude and species using an analysis of variance with arcsine transformed cover data. The effect of substrate on the rate of increase of spinifex and total cover was examined on fire plots and fixed transects using in ordinary least square linear regression. The slope among regression lines on different substrates was compared using procedures outlined by Zar (1996).

## Results

### *Spinifex species and vegetation pattern*

Spinifex was present on all but four of the 226 plots sampled. Five spinifex species were recorded. *T. basedowii* was limited to the southern half of the study area and recorded at

25.7% sites. *T. schinzii* and *T. pungens* were distributed throughout the study area and were recorded at 36.2% and 70.8% of sites, respectively. *Triodia speciosa* and *Triodia* sp. were recorded at 3.6% and 0.8% of sites, respectively. Most plots had a single species of *Triodia* (63.1%) while two spinifex species were recorded at 35.1% and a mix of three spinifex species were recorded at 1.8%.

Of the 226 plots sampled, 174 were considered to have an accurate fire age and 131 of these were long-unburnt (>12 years). Of these, 95 were dominated (>90%) by *T. schinzii, T basedowii* or *T. pungens* with a total cover of 27.1, 22.3 and 29.2%, respectively. There was no significant difference in the amount of spinifex cover in each alliance ($F_{2,92}$=2.18, p=0.11). There was also no significant difference ($F_{2,92}$=2.75, p=0.07) in the amount of total ground cover among plots dominated by a particular spinifex species, although the ground cover of *T. basedowii* alliance (33.7%) was lower than that in the *T. schinzii* (46.4%) and *T. pungens* (40.7%) alliance. In general, 30-40% of ground cover was forb, non-spinifex grasses or standing litter material.

There were significant differences in the amount of total vegetative ground cover and spinfex cover on long-unburnt plots among the four latitudinal zones (ground cover: $F_{3,127}$=38.9, p<0.001; spinifex cover: $F_{3,127}$=15.5, p<0.001) (**Table 9.2**).Total ground cover was greater in the northern part of the study area and declined in response to greater aridity toward the south. In the northern part of the study area, non-spinifex grasses provided the dominant ground cover and spinifex contributed little. Spinifex dominance increased in the central and southern part of the study area, although total cover declined with increasing latitude as spinifex plants became smaller and more widely separated and non-spinifex vegetation cover diminished. Hence, there was a curvilinear relationship between spinifex cover and latitude (**Fig. 9.2**). Shrub and tree cover was also sparse in the south and central parts of the study area, increasing northward in association with higher rainfall.

**Table 9.2** Cover of spinifex and total ground vegetation in relation to substrate type and latitude on long-unburnt random plots.

| | Sand plain | Drainage line | Laterite |
|---|---|---|---|
| Newcastle waters | | | |
| Samples | 10 | | |
| Spinifex cover% ±se | 10.5±4.5 | - | - |
| Total cover% ±se | 45.6±4.9 | - | - |
| Tennant Creek | | | |
| Samples | 14 | 4 | 8 |
| Spinifex cover% ±se | 37.0±2.8 | 41.0±4.0 | 42.9±3.2 |
| Total cover% ±se | 47.6±3.3 | 55.6±4.9 | 53.4±3.6 |
| The Granites | | | |
| Samples | 15 | 22 | 7 |
| Spinifex cover% ±se | 32.4±2.2 | 31.9±2.4 | 37.3±3.2 |
| Total cover% ±se | 37.7±2.8 | 40.7±2.8 | 42.9±3.7 |
| Kintore | | | |
| Samples | 39 | 12 | |
| Spinifex cover% ±se | 20.7±1.3 | 20.9±2.7 | - |
| Total cover% ±se | 30.6±2.2 | 24.6±2.7 | - |

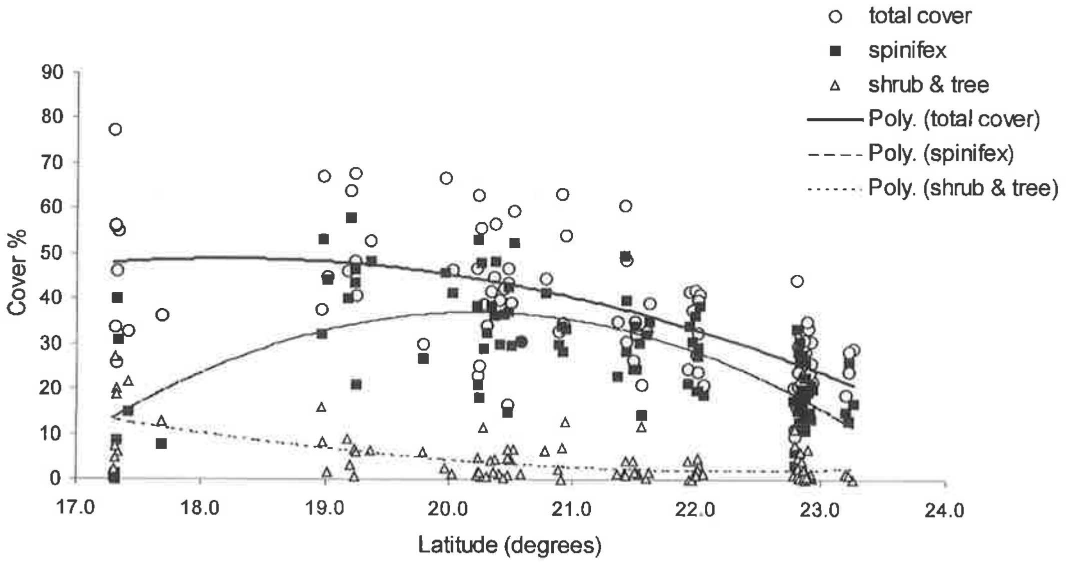


**Fig. 9.2** Total ground cover, spinifex cover and shrub cover in relation to latitude in the Tanami Desert. Data are from long-unburnt plots.

Generalised linear modelling indicated that ground vegetation cover was associated positively with mean annual rainfall, rain since fire, and cumulative rain in the previous three months. (**Table 9.3**). The linear predictor of total vegetation cover is given in eqn (1).

$$u = -1.829 + r_1 * 2.238 \times 10^{-3} + r_2 * 0.0994 \times 10^{-3} + r_3 * 0.945 \times 10^{-3} \qquad (1)$$

where $r_1$ is the mean annual rainfall, $r_2$ is the cumulative rainfall since fire and $r_3$ is the rainfall in the previous three months. The estimate $u$ can be transformed to estimate proportional total vegetation cover $y$ using eqn (2).

$$y = \exp(u)/(1 + \exp(u)) \qquad (2)$$

Spinifex cover was associated positively with mean annual rainfall and years since fire but negatively with the quadratic of mean annual rainfall (**Table 9.3**). The quadratic function indicated a curved relationship between annual rainfall and the spinifex cover. Substrate did not form a significant predictor variable for either ground cover or spinifex cover.

**Table 9.3** The minimum adequate model for (a) total vegetative ground cover and (b) spinifex cover using random plot data with an accurate fire age.

(a) Total vegetative ground cover
Null deviance = 139.6, 32.1% captured

| Variable | Estimate | Std. Error | Res. df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -1.829 | 0.218 | 173 | | -8.4 |
| mean annual rainfall | $2.238 \times 10^{-3}$ | $0.613 \times 10^{-3}$ | 172 | 22.9 | 3.6 |
| rainfall since fire | $0.0994 \times 10^{-3}$ | $0.023 \times 10^{-3}$ | 171 | 16.4 | 4.2 |
| rain in previous 3mths | $0.945 \times 10^{-3}$ | $0.404 \times 10^{-3}$ | 170 | 5.4 | 2.3 |

(b) Spinifex cover
Null deviance = 169.3, 26.7% captured

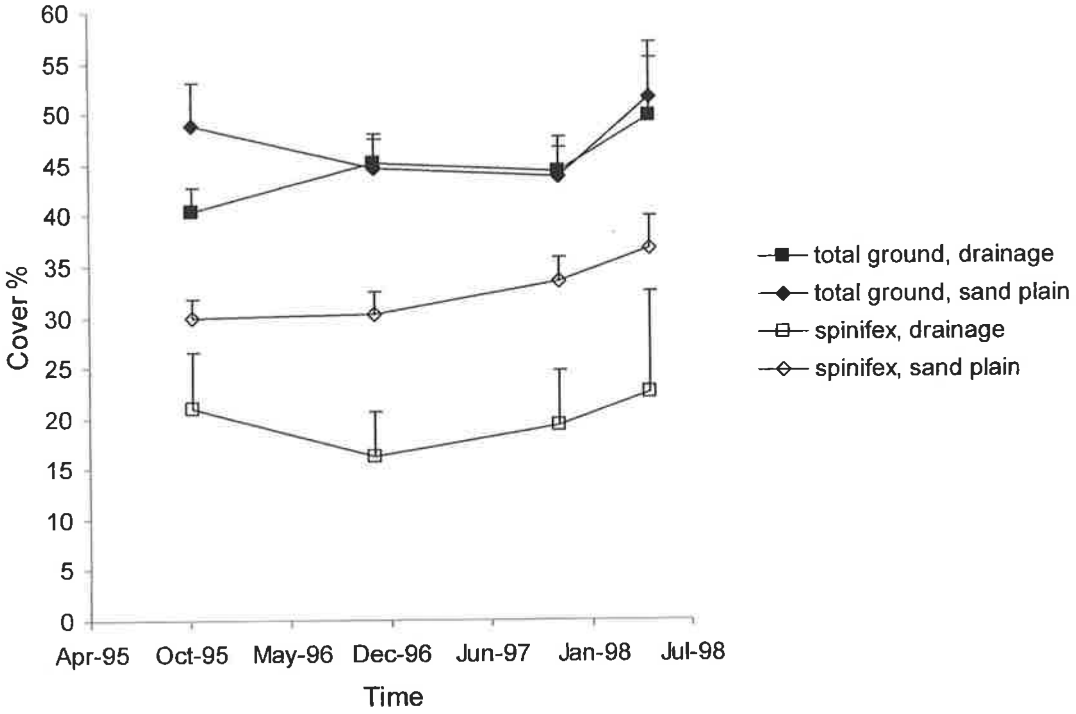
| Variable | Estimate | Std. Error | Res. df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -7.119 | 1.00 | 173 | | -7.1 |
| mean annual rainfall | $30.932 \times 10^{-3}$ | $5.471 \times 10^{-3}$ | 172 | 0.03 | 5.6 |
| I(mean ann.rain$^2$) | $-0.0413 \times 10^{-3}$ | $0.0075 \times 10^{-3}$ | 171 | 20.4 | -5.5 |
| years since fire | 0.055 | 0.010 | 170 | 29.1 | 5.3 |

Repeated monitoring of total vegetative ground cover and spinifex cover on the fixed transects indicated that the change in cover did not differ significantly among drainage and sand plain substrates. At Tennant Creek, 80% of the mean average rainfall was received over the sampling period (**Table 9.1**) and there was little increase in spinifex and ground cover (**Fig. 9.3a**) and no significant response of ground cover to substrate type (ground cover: t=0.76, 20 df, p>0.05; spinifex: t=-0.51, 20 df, p>0.05). At the Granites latitude about 70% of the mean annual rainfall was received during the sampling period and ground and spinifex cover remained fairly static in both habitats during the period (data not shown in **Fig. 9.3**). There was no significant difference in the response of ground cover or spinifex cover to substrate type (ground cover: t=-0.009, 2 df, p>0.05; spinifex: t=-0.02, 2 df, p>0.05).

At the Kintore latitude, about 50% of the mean annual rainfall was received during the sample period. Ground cover remained similar over time however, spinifex cover declined on both substrate types (**Fig. 9.3b**). This coincided with the broad-scale death of spinifex *T. basedowii* particularly at two sites at the Kintore latitude in 1997, presumably in response to the severe rainfall deficit. Although the decline of spinifex was most marked on the sand plain substrate, there was no significant difference in the response of spinifex cover or ground cover to substrate types (ground cover: t=0.12, 14 df, p>0.05; spinifex: t=1.8, 14 df, p>0.05).

Repeated monitoring of the fire plots indicated that the parameter rain since fire was better than time since fire in explaining increase in cover for both spinifex and ground cover, since it explained more than twice the variance (**Fig. 9.4a** and **b**). The rate of growth of spinifex and ground cover was similar. However, the rate of growth of spinifex was less variable than that of ground cover.

(a)



(b)

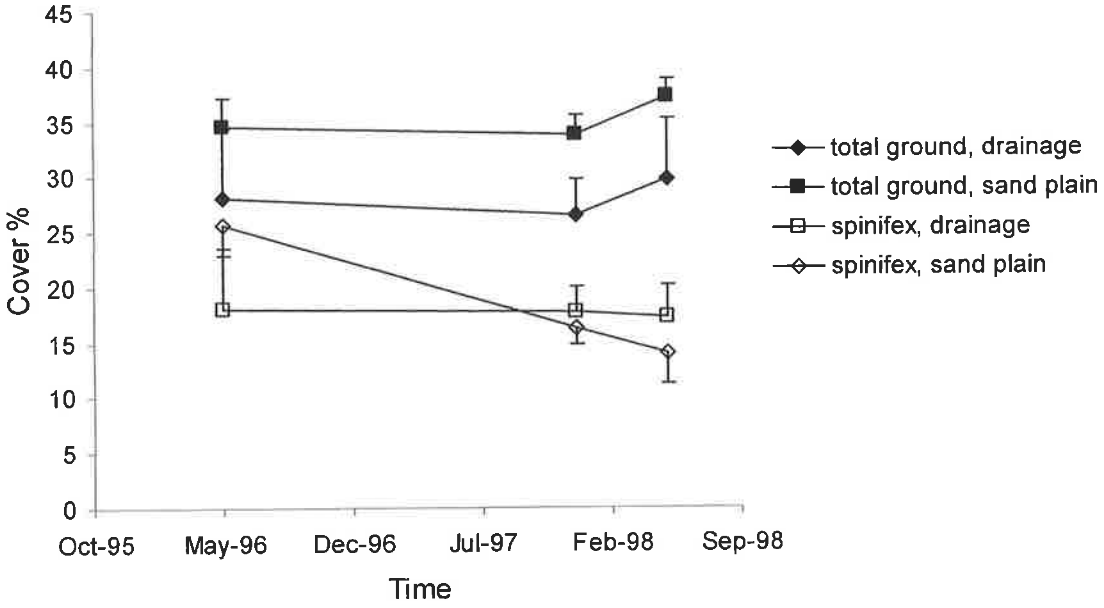
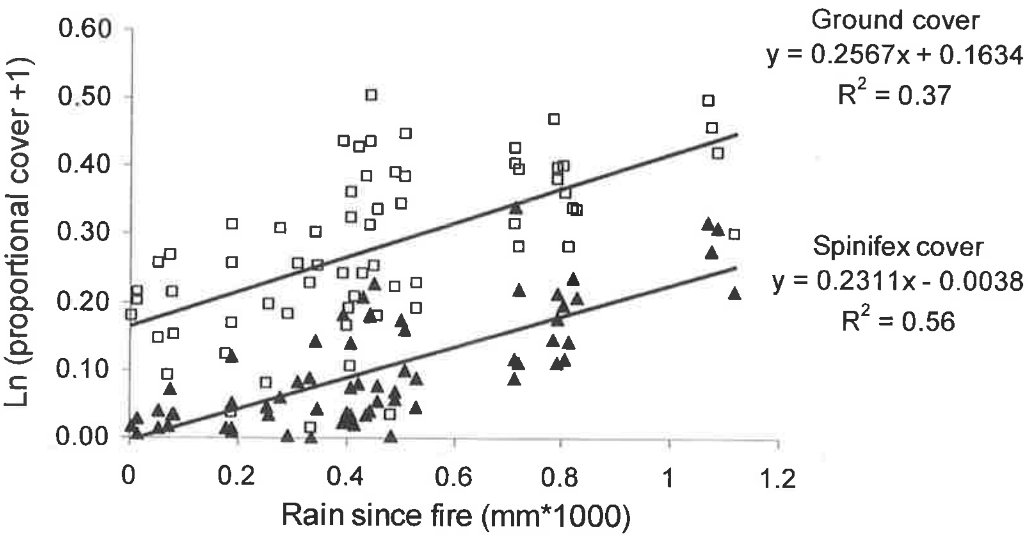


**Fig. 9.3** The change in vegetative ground cover and spinifex cover on fixed transects at the (a) Tennant Creek latitude and the (b) Kintore latitude over time. Error bars indicate one standard error.

(a)



(b)

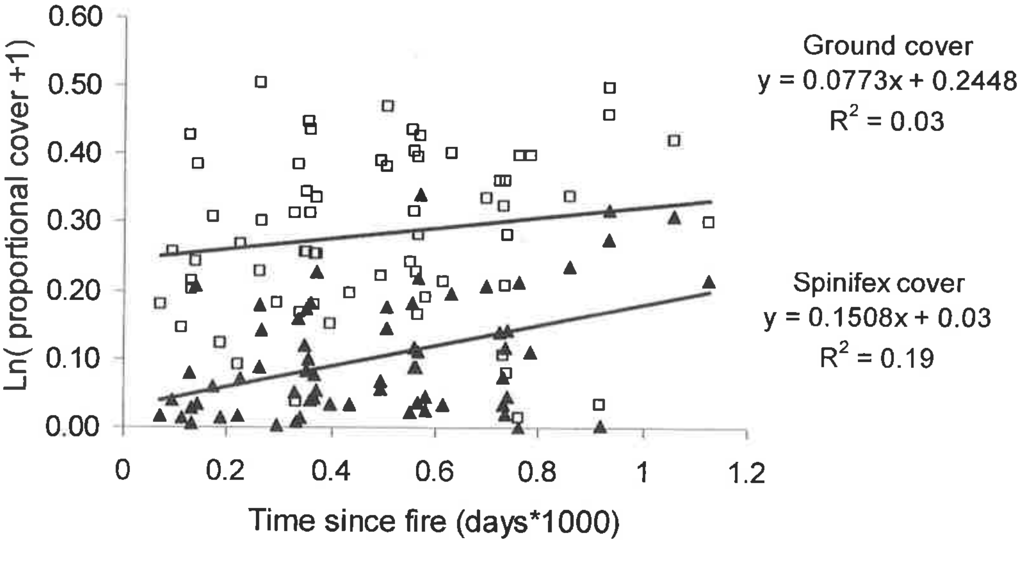


**Fig. 9.4** The rate of growth of total ground cover (open squares) and spinifex cover (closed triangles) on fire plots in response to (a) time since fire and (b) rain since fire. Values of cover are ln (proportional cover+1).

*Vegetation cover and fire*

There were 15 attempts to burn sections of habitat at the Tennant Creek latitude and 12 attempts at the Kintore latitude. This resulted in four hot-clean burns, nine patchy burns and one no-burn at the Tennant sites, and one hot-clean burn, four patchy burns and six no-burns at the Kintore sites. The total ground cover that produced hot-clean burns (50.5%±3.0) was greater than that for patchy burns (34.5%±3.4) or no-burns (30.2%±2.7) **(Fig. 9.5)**. Similarly, the spinifex component of total cover that produced hot-clean burns (37.4%±4.5) was greater than that for patchy burns (26.2%±3.4) or no-burns (22.5%±2.8). The minimum amount of total ground cover producing a hot-clean burn was 41.2%, which included 25.8% spinifex. Fires burnt less vigorously in the cool part of the year and there was an instance when a July fire did not carry with 42.9% total cover (including 37.2% spinifex). In terms of cumulative rainfall, a site would need to receive around 1200 mm of rainfall following fire to produce around 41% total cover including 26% spinifex, at which time fire could reoccur during hot windy conditions but may fail to spread during cool windless conditions.

**Fig. 9.5** The amount of total ground vegetative cover (black bars) and spinifex cover (open bars) in relation to three fire behaviour classes (clean burn, patchy burn and no carry) from fire plots at the Tenant Creek and Kintore latitudinal zone. The dashed line indicates the threshold cover required for fire reoccurrence.

### *Distribution of food plant species*

*Yakirra australiense* was the most widely distributed and abundant food plant used by the bilby in the Tanami Desert. It was recorded on a range of substrate types and at 36% of the 226 random plots, 10% of fixed transect samples and 34% of fire plots. *Dactyloctenium radulans* was encountered at only one of the Tennant sites on a drainage line transect, off-site at the Granites and Kintore latitude, on eight (3.8%) random plots (all at the Tennant latitude) and no fire plots. Of the eight random plot records, seven were located on the drainage substrate. *Cyperus bulbosus* was found only on drainage/calcrete substrate and recorded on 3.3% of the random plots and one fixed transect at the Granites latitude and two from the Tennant latitude. It was recorded off-transect at the Kintore latitude and on none of the fire plots. The examination of habitat parameters associating with occurrence of food plants was restricted to *Yakirra* because of the few records of *Dactyloctenium* and *Cyperus*.

### Yakirra *occurrence and growth*

Generalised linear modelling using data from 174 random plots indicated that *Yakirra* occurrence was associated primarily with rainfall- and fire age- related parameters. A substrate parameter became significant only when combined with rainfall and fire parameters. The strongest minimum adequate model included a negative association with years since fire and a positive association with rainfall in the preceding 12 months and with sand plain and drainage substrates (**Table 9.4**). In other words, low *Yakirra* occurrence associated with lateritic and rock feature substrates, localities that had received little rainfall or had not been recently burnt.

**Table 9.4** The minimum adequate model for *Yakirra australiense* occurrence using random plot data with an accurate fire age.

Null deviance = 224.2, 13.6% captured

| Variable | Estimate | Std. Error | Res. df | deviance | t value |
|---|---|---|---|---|---|
| (Intercept) | -1.574 | 0.630 | 173 | | -2.5 |
| years since fire | -0.099 | 0.031 | 172 | 15.34 | -3.2 |
| rain in previous 12mths | 0.0039 | 0.0013 | 171 | 9.93 | 2.9 |
| substrate (d+s). | 0.620 | 0.244 | 170 | 7.27 | 2.5 |

To identify conditions associated with *Yakirra* growth, actively growing *Yakirra* (i.e. with green leaves) were distinguished from those of senescent plants (i.e. with brown leaves). Only 26 of the 154 records of *Yakirra* sampled from the fixed transects and fire plots were plants with green leaves and the abundance ranged from trace to 35% cover. All were recorded during summer/autumn ($\chi^2_{,1df}=13.2$, $p<0.001$) with no significant difference in frequency of occurrence between sand plain and drainage substrates ($\chi^2_{,1df}=0.61$, $p>0.05$).

Green *Yakirra* occurred under a range of fire age conditions. Abundant cover (>1%) occurred at significantly more localities burnt within the previous 12 months ($\chi^2_{,1df}=16.2$, $p<0.001$) but it was also absent or in trace amounts at some more recently burnt localities. (**Table 9.5**). Where *Yakirra* failed to flourish, the recently burnt habitat had generally received little rain following fire and, at long-unburnt localities where *Yakirra* flourished, disturbance other than fire allowed the *Yakirra* to flourish.

The period of antecedent rainfall most significant to *Yakirra* growth was estimated by plotting *Yakirra* cover against cumulative rainfall in the previous one, two, three and six month period. Rainfall in the previous two months produced the best coefficient of determination ($r^2=0.163$) followed by three ($r^2=0.128$ ), six ($r^2=0.092$ ) and one ($r^2=0.085$ ) months , respectively. Abundant cover (>1%) occurred at significantly more localities with high rainfall (i.e. 100-300 mm and >300 mm rain) ($\chi^2_{,2df}=41.8$, $p<0.001$; **Table 9.6**).

Greatest *Yakirra* abundance occurred at localities that had been burnt within six months and had received >300 mm rainfall within 2 months (**Table 9.7**). *Yakirra* growth was substantially reduced when antecedent cumulative rainfall was less than 100 mm or when cumulative rainfall in the range 100-300 mm was received but the area had not been burnt recently (>12 months).

**Table 9.5** Abundance classes of *Yakirra* in relation to transects burnt less than 1 year old and greater than one year old. ns = not significant p>0.05, *** = p<0.001

| | >1% | <1% | absent | sum |
|---|---|---|---|---|
| localities with fire <1 year | 8 | 1 | 15 | 24 |
| Localities with fire >1 year | 7 | 10 | 113 | 130 |
| sum | 15 | 11 | 128 | |
| chi squared | 16.2 *** | 0.35 ns | 1.45 ns | |

**Table 9.6** Abundance classes of green *Yakirra* in relation to transects that received less than 100 mm rainfall, 100-300 mm and greater than 300 mm rainfall in two months prior to sampling. *** = p<0.001

| | | >1% | <1% | sum |
|---|---|---|---|---|
| Rainfall amount | >300 mm | 5 | 12 | 17 |
| | 100-300mm | 9 | 11 | 20 |
| | <100 mm | 1 | 116 | 117 |
| sum | | 15 | 139 | |
| chi squared | | 41.8 *** | 4.5 ns | |

**Table 9.7** Mean percent abundance of *Yakirra* in relation to time since fire categories and rainfall amount categories from fire.

| Rainfall (mm) in previous 2 months | | | <100 | 100-300 | >300 | n |
|---|---|---|---|---|---|---|
| Fire age | spring/summer | < 6mths | 0 | 1.2 | 13.9 | 9 |
| | autum/winter | 6-12 mths | 0 | 0.8 | 5.7 | 18 |
| | | >12 mths | 0 | 0 | 0.1 | 109 |
| | | n | 111 | 13 | 13 | |

## Discussion

Management of fire regimes to benefit biodiversity is challenging because species have different innate sensitivities to fire and particular response patterns are mediated by other factors such as landscape characteristics, weather and climate (Gill *et al.* 2002; Whelan *et* *al.* 2002). Furthermore, diverse land uses within a region has meant that fire management has to integrate multiple managers with varying goals (Keith *et al.* 2002). To deal with this complexity, fire management needs to be coordinated across land tenures at a landscape scale with explicit objectives defining both strategies and actions. To set clear objectives, the full range of the desired fire-responses need to be identified and an understanding of the outcomes of various fire regimes, given the range of possible conditions within a region (Whelan *et al.* 2002).

Spinifex grasslands cover over 22% of the Australian continent (Griffin 1984) and form some of the most remote and sparsely human inhabited landscapes on earth. Spinifex grasses have been described as perfectly designed for combustion (Pianka 1994) and in a state of cyclic development from fire to fire (Winkworth 1967). Prescribed burning has been conducted throughout this region for thousand of years by Aboriginal people to hunt, promote 'green flush' to attract animals and promote the abundance of food plants (Bowman 1998). Disruption in the patterns of traditional Aboriginal life has resulted in dramatic changes in the temporal and spatial pattern of fires. Fires have become larger and less frequent (Burrows *et al.* 1991). This is thought to have negatively affected some medium-sized mammal species that depended on a fine-grained mosaic of vegetation at different states of post-fire succession (Bolton and Latz 1978; Saxon 1983; Burbidge *et al.* 1988; Johnson *et al.* 1989). Despite the immense area covered by spinifex grasslands and the plausible negative impact of uncontrolled wildfire on threatened native fauna, there has been relatively little investigation into the response of focal species or communities to fire in the arid zone (Allan and Southgate 2002) or the range of conditions that can result following fire or achieved through prescribed burning (Craig 1999).

The bilby is one of the few native, medium-sized mammals that has been able to persist in the spinifex deserts (Burbidge and McKenzie 1989). It has catholic habitat requirements but shows a positive response to recent fire because of its use of fire-promoted foods (Southgate and Carthew 2006). Improving the availability of key food resources might offset the impact of predation from the introduced feral cat *Felis catus* and the red fox *Vulpes vulpes* and result in an overall improvement in bilby status. While there is strong evidence that predator control provides the most effective means of improving the status of medium-sized native mammals in Australia (Risbey *et al.* 2000; Moseby and O'Donnell 2003), the broad-scale control of introduced predators has yet to be achieved successfully in the arid zone (Gibson *et al.* 1994; Christensen and Burrows 1995). In contrast, the strategic use of fire offers a means to improve habitat suitability for the bilby and possibly a range of other species over a vast area with comparatively little effort. To better understand the mechanisms that affect the production of fire-promoted foods used by the bilby in the Tanami Desert, it was also necessary to determine the key conditions that affect fuel production and allow the recurrence of fire.

### *Determinants of vegetation cover*

The mean total ground cover in the study area ranged from 34%-46% and mean spinifex cover from 22-29%. This was within the range reported for long-unburnt sites from other studies in spinifex grasslands (Winkworth 1967; Griffin and Allan 1984; Burrows *et al.* 1991; Lundie-Jenkins 1993; Masters 1993). Between 60-70% of the ground cover was spinifex (alive) and the rest was litter, forb or non-spinifex grasses. The cover of non-spinifex material is more variable than spinifex, increasing quickly in response to rainfall and diminishing during periods with little rainfall (Allan and Southgate 2002).

The variables most significant to the production of vegetative cover in the study area were annual rainfall, cumulative rainfall since fire and three month antecedent rainfall. Differences in spinifex regrowth characteristics was not a significant factor and nor was the type of substrate. The three most common spinifex species in the Tanami Desert have distinctive regeneration capacities (Rice and Westoby 1999) and distinctive rainfall and soil requirements (Griffin 1990). Both *T. schinzii* and *T. pungens* have the ability to grow from seed or resprout from burnt root stock after fire while *T. basedowii* recovers almost entirely from seed (Westoby *et al.* 1988; Griffin 1990; Rice and Westoby 1999). *T. pungens* and *T. schinzii* occur mainly in the northern part of the Tanami Desert with *T. pungens* in richer parts of the environment, while *T. basedowii* occurs in the southern part of the Tanami Desert where there is less rainfall and on soils with a broad range of nutrient levels (Griffin 1990). However, no significant difference in cover was found among long-unburnt samples of each alliance.

Neither the amount of ground and spinifex cover nor the rate of spinifex growth varied significantly among drainage and sand plain substrate types. This indicated that ground cover did not correspond with the nutrient gradient between drainage lines and sand plains, or comply with the conceptual model regarding fertility and soil moisture proposed by Stafford Smith and Morton (1990). The lack of difference among substrates and spinifex alliances allowed the development of a relatively simple model to explain changes in total and spinifex cover in the Tanami Desert.

Mean annual rainfall was the most important parameter associated with ground and spinifex cover. Ground cover was higher in the northern part of the study area and diminished with increasing aridity. Non-spinifex grasses contributed most to cover at the Newcastle Waters latitude with greatest spinifex cover (and total cover) at the Tennant Creek latitude. Other factors that significantly affected ground cover were rainfall since fire and cumulative rainfall in a three month period. This highlighted the importance of short-term rainfall for the production of non-spinifex ground cover. This component of ground cover assists fire to spread across the gaps in between spinifex hummocks that would be otherwise too wide to allow fire to carry (Allan and Southgate 2002). During periods of exceptional rainfall, the growth of non-spinifex ground cover can result in sufficient fuel to allow areas to burn twice within three years (Griffin *et al.* 1983). Rain since fire was a more powerful variable than time since fire in the model for ground cover, although time since fire captured more deviance in the spinifex cover model. The quadratic function associated with mean annual rainfall accounted for the decline of spinifex cover at the northern edge of the study area. This decline possibly resulted from a higher density of shrubs and trees, and competition from tropical grasses. Although there was evidence from the fixed transects that a prolonged rainfall deficit would result in a reduction in spinifex cover, rainfall deficit did not form a significant component of the minimum adequate model describing spinifex cover.

Griffin (1992) suggested that about 6300 mm of cumulative rainfall was required over a number of years for a patch to accumulate sufficient fuel to burn again. The rate of increase in spinifex cover and ground cover calculated from regrowth on fire plots in the present study indicated that much less rainfall would be required to produce vegetative cover sufficient to carry fire. After 1200 mm of rainfall, ground cover was approximately 41% and spinifex cover was about 20%. This value is similar to the amount rainfall accumulated between burning rotations in parts of the Kimberley (Craig 1999). The reason for the large discrepancy between it and the value provided in Griffin (1992) is unclear.

### *Determinants of fire*

The factors that have been found to critically affect the ignition and spread of spinifex (hummock) grass fires include a fuel component and a weather component (Griffin and Allan 1984; Burrows *et al.* 1991; Cheney and Sullivan 1997). The weather component was limited to temperature and wind speed in fire spread models produced by Burrows *et al.* (1991) although Griffin and Allen (1984) also included relative humidity. The fuel component has focussed primarily on the amount of spinifex and non-spinifex cover but also included the patchiness of cover and moisture of spinifex. The poor success in starting fires at the Kintore latitude reflected the lack of fuel rather than weather conditions as fires were lit on hot windy days. Few of the sites had adequate cover and no fire carried cleanly unless there was greater than 20% spinifex cover and 43% total cover. Similarly, greater than 25% spinifex cover and 41% total cover was required at the Tennant latitude before a clean fire was achieved. However, a number of instances where there was no-burn or a patchy burn indicated the importance of weather component in the spread of fire in spinifex grasslands. Ground cover of greater than 48% would be desirable to achieve a clean burn.

The two sources of fire ignition in the spinifex grasslands are lightening and fire started by humans. Fires started by lightening can occur throughout the study area but occur mostly in the late dry season (Griffin *et al.* 1983). Fires following storms were observed on a number of occasions during fieldwork in November and December at the Granites and the Tennant Creek latitude (Southgate, pers. obs). Four fires were started within a radius of about 20 km during one thunderstorm. In comparison, the ignition of fire by humans occurs throughout the year but the distribution is non-random and linked primarily to roads and tracks. There is speculation that Aboriginal burning patterns in the past, although more diverse, would have been still aligned to particular travel or hunting routes between sources of water (Griffin and Allan 1986). The ability to ignite prescribed burns in remote locations is therefore a key consideration in the development of a fire management program in the spinifex deserts of northern Australia.

*Spatial and temporal determinants of food plants*

Seed from *Yakirra australiense* is the most commonly occurring plant component of the bilby diet in the Northern Territory and Western Australia, while seed from *Dactyloctenium radulans* is more common in southwest Queensland (Southgate 1990; Gibson 2001). Although the bulb from *Cyperus bulbosus* occupies a more limited range of substrates, it has been recorded in the diet throughout the bilby's current range (Southgate 1990; Gibson 2001). Herbarium records indicate that these food plants do not extend much further northward than the northern edge of the study area but they were broadly distributed to the east, west and south (Southgate and Nelson, unpublished data).

In the study area, *Yakirra* was the most widely spread food plant species and was distributed on sand plain, drainage and laterite substrate types. However, spatial modelling indicated that *Yakirra* occurred less commonly on laterite/rock feature substrates, but there was no difference among drainage and sandy substrates. The latter finding was supported by data from the fire plots and fixed transects. *Dactyloctenium* and particularly *Cyperus* were limited to drainage and calcrete substrates.

Season of burning, time since fire and the amount of rainfall were the variables most significantly associated with *Yakirra* abundance. The interactive effect of fire age and rainfall on *Yakirra* production was illustrated at three adjacent fire plots at Tennant T1S site. Each one received ~350 mm of rain in the two months prior to sampling when monitored in March 1997. The plots were burnt in July 1995, April 1996 and November 1996 and the amount of *Yakirra* recorded at each site was 0.7%, 2% and 32%, respectively. The amount of spinifex cover on each of the plots at the time of sampling was 22%, 17%

and 3%, respectively.

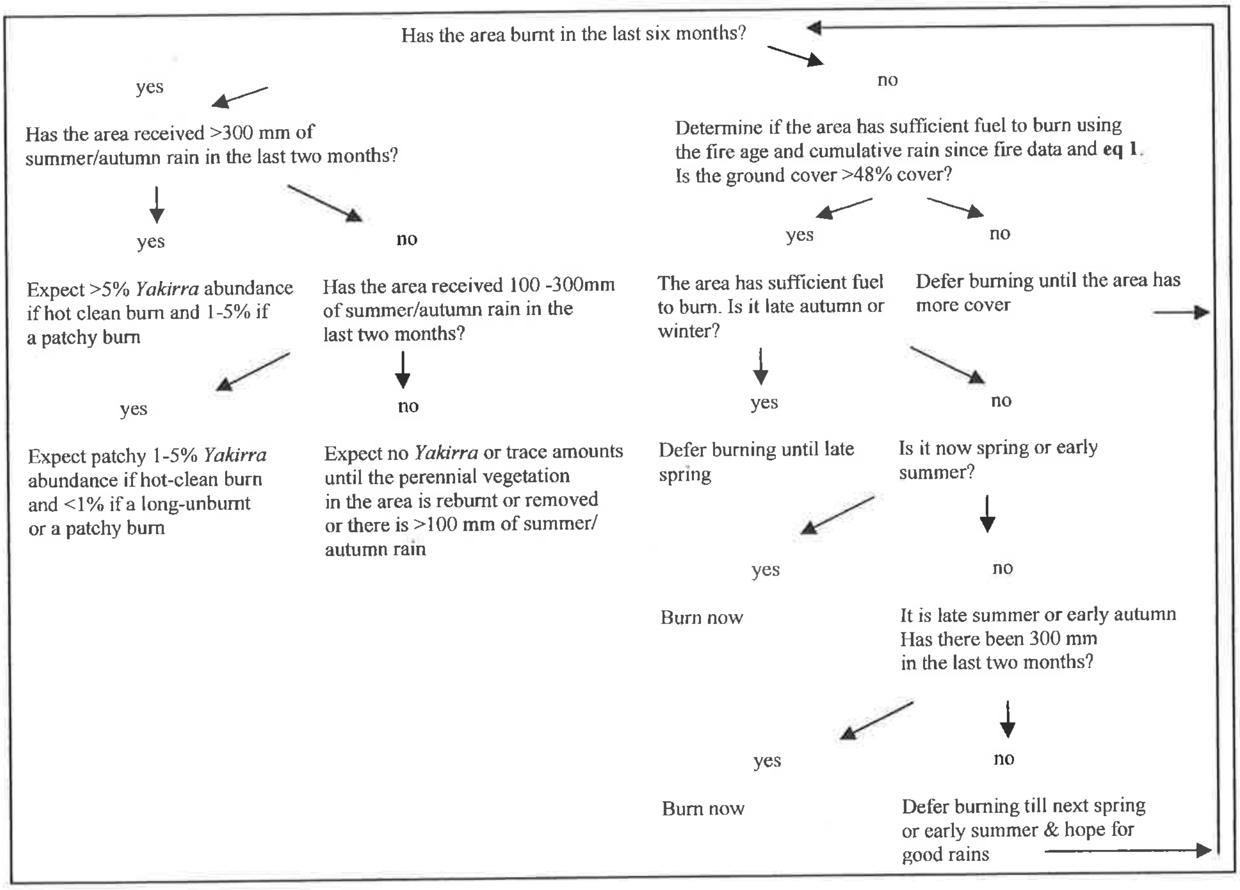
Although fire was the most common and widespread form of disturbance occurring in the study area, it was not the only type affecting the production of *Yakirra*. Following rainfall, *Yakirra* plants were observed at long unburnt localities either where vegetative cover had been removed mechanically (eg. around ant nests and along vehicle tracks) or where spinifex and other perennial groundcover had died as a result of drought. In this instance, *Yakirra* was observed growing through the gray, dead leaves of the spinifex plants (Southgate, pers. obs.).

No fresh sign of *Yakirra* was found outside summer and autumn and seed germination is probably limited to the warmer months. To promote *Yakirra* production, it would therefore be better to conduct burning in late spring or early summer compared to late autumn or winter with the expectation that adequate late summer or autumn rainfall would occur.

*Decision tree for fire management to promote* Yakirra *production*

Actions required to assess where and when it is best to burn to increase *Yakirra* growth are presented in **Fig. 9.6**. The model does not include consideration of issues relating to legality, safety and risk to property nor the sensitivity of other plant and animal species to the effects of fire. For example, the suggestion that burning be conducted in the early part of the wet season would generally require preparatory burning in the cooler conditions of the dry season to contain fires within prescribed areas (Craig 1999). Consideration of effect of fire on other species is also important because fire has been recognised as a threat to a large proportion of the declining bird species (Woinarski and Recher 1997) and a range of other vertebrates (Friend 1993; Masters 1993; Reid *et al.* 1993). In general terms, it is important to ensure that at any time there is a mosaic of successional states each of sufficient area to support successional-specific species (Richards *et al.* 1999).

Information on spatial and temporal patterns of rainfall and fire for a region is required to drive the decision tree. Foremost, it is the necessary to determine when parts of the landscape were last burnt and the size of these fires. The time since fire data are required to determine the season of fire because of its effect on *Yakirra* production and for the calculation of cumulative rainfall. The size of patches of a particular fire age and those of surrounding patches with a different age will affect the logistics of fire management. Fire mapping in central and northern Australia is currently being conducted using AVHRR NOAA satellite imagery with a pixel size of approximately 1 $km^2$ and a comprehensive spatial fire history has been developed for most of central Australia (Craig 1999; Allan and Southgate 2002).



Has the area burnt in the last six months?

Has the area received >300 mm of summer/autumn rain in the last two months?

Expect >5% *Yakirra* abundance if hot clean burn and 1-5% if a patchy burn

Has the area received 100 -300mm of summer/autumn rain in the last two months?

Expect patchy 1-5% *Yakirra* abundance if hot-clean burn and <1% if a long-unburnt or a patchy burn

Expect no *Yakirra* or trace amounts until the perennial vegetation in the area is reburnt or removed or there is >100 mm of summer/ autumn rain

Determine if the area has sufficient fuel to burn using the fire age and cumulative rain since fire data and **eq 1**. Is the ground cover >48% cover?

The area has sufficient fuel to burn. Is it late autumn or winter?

Defer burning until the area has more cover

Defer burning until late spring

Is it now spring or early summer?

Burn now

It is late summer or early autumn Has there been 300 mm in the last two months?

Burn now

Defer burning till next spring or early summer & hope for good rains

**Fig. 9.6** A decision model to describe the expectation of *Yakirra* growth in response to fire age and rainfall conditions and directions to guide when to burn in the Tanami Desert to best promote *Yakirra* production.

Fire size is less critical to the bilby than it would be for some other animal species that are dependent upon infrequently burnt habitat and small tracts of mature vegetation for nesting and shelter (Bowman 1998). From bilby management point of view, prescribed burning should be used to even out the amount of landscape burnt each year prior to the arrival of substantial summer rains.

Data on monthly rainfall are required to determine cumulative rainfall-since-fire and antecedent rainfall in two and three month periods. These attributes are necessary to calculate vegetative cover and to assess expected *Yakirra* production. Monthly rainfall data are available from the Bureau of Meteorology for the entire Australian continent at a pixel size of approximately 25 $km^2$ (Jones and Weymouth 1997). These data provide course-grain indication of rainfall activity and do not account for variation caused by localised thunderstorms.

Ground validation to evaluate the adequacy of the decision tree in predicting spinifex cover and *Yakiira* abundance needs to be undertaken. It may be profitable for future work to investigate least-cost strategies to enhance the fire regime for the bilby as it changes from year to year in the spinifex deserts of northern Australia. Modelling using stochastic dynamic programming has been used by Richards *et al.* (1999) to examine when prescribed burns should be implemented in Ngarkat Conservation Park given the existing fire pattern in the park, the cost associated with different strategies and a management time frame. A model developed by Bradstock *et al.* (1998) may prove a means to test the sensitivity of other threatened species with different dispersal and demographic properties and dependencies on fire frequency to a fire regime derived as optimal for the bilby.

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# Chapter 10

# Conclusion

In this thesis, I have investigated the factors that limit and shape the current distribution of the bilby in the Tanami Desert and considered whether fire management could be used to improve the status of the species. A statistical modelling approach was used to make inferences about the processes that shape distribution and the environmental conditions that provide refugia for the species. The approach was also used to predict the species area of occupancy based on important environmental attributes.

Empirical models provide a way to derive a construct of the system and examine features affecting distribution at geographic scales that cannot be examined by experimentation (Elith *et al.* 2002; Mackey and Lindenmayer 2001; MacNally 2000; Manel *et al.* 1999). While it is not possible to determine causation from correlation, a description of functional relationships can be achieved and the reality of such relationships can be determined through internal cross validation using independent techniques, repeated studies or studies at different locations (Austin 2002).

The aim of statistical modelling is to understand the causes of variation in a response variable (Crawley 1993). Austin (2002) has argued that the development of a model requires the consideration of three components. An *ecological model* is needed that consists of the ecological knowledge, theory and assumptions to be used or tested in the analysis. A *data model* is needed that consists of the decisions made regarding how data are collected, measured and estimated, including issues such as scale of resolution and accuracy of data. A *statistical model* is needed that outlines the choice of a statistical analysis, error function and significance tests. In much of the thesis, I focus on issues relating to the *data model* and the *ecological model*. The investigation of a sparsely distributed species in a remote and relatively inaccessible part of Australia required the development of techniques that produced reliable and defendable data. Furthermore, although there is a growing body of work from arid regions, our understanding of the ecology of species and systems in arid Australia is still rudimentary because of the size of the region, the sparse human population and the dramatic changes to faunal communities that have occurred since European colonisation. Hence, the existing conceptual understanding of the ecological functioning of arid Australia still requires careful scrutiny.

The key findings in relation to the data model and the ecological model are outlined in the following section. I then revisit the hypotheses posed in the Introduction, and finally, identify consequences for management and areas of future research.

## Key findings

### *Data models*

#### Response variables

The scarcity of the bilby in the study area posed a number of methodological problems. Direct counts or capture of individuals on a broad scale was not feasible and there was little option but to rely entirely on sign and passive techniques to record occurrence. The traditional Aboriginal people with whom we worked encouraged this approach. These people demonstrated excellent skills in tracking and knowledge of the landscape and its fauna and flora. Although the use of passive survey techniques is gaining greater acceptance in wildlife science (Engeman 2005), there is still uncertainty about the accuracy and characteristics of the data produced. Track abundance does not necessarily translate to animal abundance but a linear relationship tends to occur when an animal population is at low density (Caughley 1977).

The use of tracking as the principal means to record bilby occurrence provided the opportunity to collect data on the occurrence of a range of other species that occupied habitat sympatrically. In Chapter 3, I compared three techniques used to collect information about bilby distribution, abundance and dynamics: fixed transects, random plots and aerial survey. Repeated sampling of the fixed transects provided an indication of the temporal changes in the population but produced little information on the spatial distribution of the species relative to effort. A combination of an aerial survey and a random plot technique proved to be the most cost effective means to produce repeatable baseline data. This approach allows the rapid and accurate collection of presence-absence data on bilby occurrence in the spinifex deserts of arid Australia.

The application of the three different methods to monitor bilby occurrence also provided an opportunity to cross-validate the pattern of distribution and habitat use for a range of cohabiting animal species. In general, the methods reflected similar regional patterns of distribution. Differences in the use of substrates and regional prevalence probably resulted from non-contemporaneous sampling and reflected the labile nature of populations.

Chapter 6 presents a technique for detection of sub-adult bilbies and large males based on the measurement of gait characteristics and faecal pellets. Need for the technique arose out of concern that few of the bilby prints encountered when sampling plots or transects were small. This suggested there was little recruitment of young occurring in large parts of the study area. A more systematic appraisal of print size was required to justify concerns. This led me to analyse information I had collected previously while conducting a reintroduction program where free-ranging bilby individuals were regularly recaptured and measured. Application of the age classification technique to the data collected in the Tanami Desert indicated that evidence of recruitment was limited to the central part of the study area where bilby prevalence was greatest.

### Explanatory variables

A large part of the thesis was devoted to describing and examining the explanatory variables. In Chapter 4, I outlined the characteristics of the raw spatial data used in analysis and derive a number of proximity and neighbourhood measures. These types of variables have often been found to serve as more useful predictors than the raw variables (Wintle *et al.* 2005). In Chapter 5, I used data on camel, fox, feral cat and dingo occurrence collected from the random plots to derive a probability of occurrence surface for each species. These spatial data were later used as explanatory variables to derive habitat association models for the bilby. The models for the feral cat and fox were not particularly strong and the models for the fox and the dingo did not perform well with evaluation data. This meant that the bilby models including these variables might contain substantial uncertainties.

The location of plots and sites were selected to cover the range of environmental gradients in the study area. Nevertheless, some areas received little attention and hence, model predictions would be less reliable in these regions. The minimum distance between two sampling locations was set at 4 km to reduce the chance of non-independence of bilby observations and avoid spatial autocorrelation (Legendre *et al.* 2002). While appropriate for the bilby, this distance may be inadequate to achieve independent samples for camel and dingo occurrence. The sampling of the plots was also used to validate the accuracy of the spatial data used for some of the explanatory variables. In general, reasonable accuracy was found, providing confidence that the existing spatial data could be used to evaluate some of the broad scale hypotheses about the ecology of arid Australia.

### *Ecological models*

In this thesis I examine six ecological models. Three relate to the ecological framework for arid Australia proposed by Stafford Smith and Morton (1990) and the remainders relate to the hypothesised causes of medium-sized mammal decline.

### 1. The adequacy of the Stafford Smith – Morton conceptual model

Stafford Smith and Morton (1990) presented a description of the substrate, variability and episodic nature of rainfall and fire pattern in arid Australia and proposed that the variables from indirect gradients (eg. geology, topographic position, slope) and resource gradients (eg. nutrients, water) were mainly responsible for the pattern of organisms. In Chapter 4, I compared the pattern of landscape features outlined in the Stafford Smith – Morton model with that present in the Tanami Desert study area. Reasonably good compliance was found. However, a strong climatic gradient was also evident in the study area, and this was clearly reflected in the change in vegetative cover from north to south. It was recognised that direct gradient variables such as rainfall and temperature had not been accommodated in the model proposed by Stafford Smith and Morton and it was suggested that this would make their conceptual model less adequate to identify key predictor variables shaping ecological relationships in the arid zone. Variables based on resource and direct gradients tend to make models more robust and widely applicable than those based on indirect gradients (Austin 2002; Guisan and Zimmermann 2000), especially in relation to a climatically changeable future.

2. Prevalence of medium and large herbivores is greater on localised patches of higher productivity

Stafford Smith and Morton (1990) suggested that introduced and native herbivores would be restricted to the moister, more fertile substrates. Therefore, it was expected that greatest prevalence of camel and rabbit activity would occur on the most continuously productive substrate types and least prevalent on the poorest substrates. The model can be abbreviated as:

*drainage+calcareous>laterite+rock features>sand plain+sand dune*

There was support for this proposition (Chapter 5). Rabbit sign was predominantly restricted to drainage and calcrete areas and, although camel sign was strongly associated with the climatic gradient, it also had a significant association with proximity to calcrete substrate in the statistical modelling.

3. Predator richness and abundance is greater on more productive parts of the arid landscape

Stafford Smith and Morton (1990) also proposed that the paucity of nutrients would have a cascading effect throughout food-webs in the arid Australian landscape and that endothermic predators would also be more abundant and diverse in the more productive parts of arid areas. Therefore, it was expected that the greatest prevalence of cat, fox and dingo activity would occur on the most productive substrates and least on the poorest substrates, abbreviated as:

*drainage+calcareous>laterite+rock features >sand plain+sand dune*

In parts of the study area there was an overlap of all three predator species but there was little support for the proposition (Chapter 5). Each predator species was found to associate with a slightly different set of landscape features. The dingo was the only species that showed a strong association with drainage substrates. Fox and cat sign was detected on the poorest and richest substrates in the southern part of the study area but there was proportionally less fox sign in drainage lines in the northern part of the study area, perhaps because of the greater dingo prevalence. Cats were widely distributed but were slightly less prevalent in the north and showed greater association with skeletal substrates located typically near rock outcropping and ranges. Foxes were absent in the northern quarter of the study area where mean temperature and rainfall were greatest.

The capacity of these predators to occupy substrates with low fertility lies evidently in their ability to use a wide range of foods, particularly reptile prey. Reptiles and invertebrates are highly abundant in spinifex grasslands (Morton 1988; Pianka 1988) and persistent during drought conditions (Paltridge and Southgate 2001). Paltridge (2002) found the diet of cats and foxes contained a large amount of reptile material even during winter and she suggested that the abundance of reptilian fauna has allowed populations of these predators to not only to occupy a broad range of habitats, but also to persist during dry conditions. This is significant because predators can theoretically extinguish a prey population if the prey form a secondary or alternative prey for the predators, and the prey population has no effective refuge from predation (Pech *et al.* 1995).

4. Productive substrates have been degraded by introduced herbivores

Morton (1990) proposed that introduced herbivores have destroyed the refuge areas associated with productive substrates leaving native mammal species vulnerable to predation during drought. If this form of refuge area degradation had occurred, it would be expected that bilby prevalence would be greater where introduced herbivore species were least prevalent, and greater use of productive substrate by the bilby would occur where introduced herbivores were scarce:

*low stock-camels-rabbits>low stock+camels-rabbits>stock+camels+rabbits*

The data presented in Chapter 7 indicated that bilby prevalence was least in parts of the study area where there was most camel and rabbit sign. However, the limited amount of bilby activity that occurred in this part of the study area was restricted largely to productive substrates, and further north where camel and rabbit sign was scarce, proportionally less productive substrate was used by the bilby, contrary to the expectations. Hence, there was contrary evidence and equivocal support for the Morton hypothesis. Robley *et al.* (2002) has also reported contrary evidence. They found that a reintroduced population of burrowing bettong continued to thrive in the presence of high rabbit numbers, even after the rabbits had caused widespread defoliation and death of vegetation.

### 5. The introduced predator suite limits native medium-sized mammal distribution

The suggestion that introduced predators, particularly the fox, were causing the decline of medium-sized mammals was provided initially by Jones (1923). Finlayson (1961) concluded similarly after finding dramatic changes in the composition of fauna between the 1930s and the mid 1950s. This hypothesis was dismissed as simplistic because some mammal declines were thought to have occurred prior to the invasion of foxes (Burbidge and McKenzie 1989) and it was considered inconceivable that predators could cause the extinction of a species without some other contributing factor like habitat degradation or drought causing fragmentation of populations (Morton 1990) or hyperabundant prey such as introduced rabbits or house mice keeping predator densities elevated (Smith and Quin 1996). However, the combined effect of predators has often been overlooked. The overall predation potential is broadened when a number of predator species of different size and with slightly different hunting techniques operate in concert (Begon and Mortimer 1986).

If the combined effect of predators were a significant factor controlling bilby distribution, greater bilby prevalence would be expected to occur in areas where dingoes were present but both foxes and cats were scarce. Least bilby prevalence would occur in areas where all three predator species were present. Foxes occurrence was considered the greatest threat. The model may be abbreviated to:

*dingo-cat-fox>dingo+cat-fox>dingo+cat+fox*

There was good support for this hypothesis. Bilby prevalence was greatest in areas where fox and feral cat sign was least detected and dingo sign was prevalent. In areas where the three predator species were able to overlap, there was little chance of finding bilby activity, and refugia for the species had evidently been eliminated. The positive association between bilby and dingo prevalence that was found suggested that dingoes favour similar habitat attributes and may provide a rescue effect for the bilby (Chapter 7). The rescue effect provided by dingoes is a realistic proposition as dingoes were acting as an important predator of feral cats (Paltridge 2002) and evidently displacing fox activity within the study area (Chapter 5).

I suggest that bilby populations can withstand predation pressure from feral cats and dingoes. However, this might only occur where alternative prey is scarce and the density of both cats and dingoes is low and foxes are absent. An elevation in the abundance of these predators through provision of watering points on pastoral stations or from the availability of highly abundant alternative prey such as rabbits may create intolerable predation pressure on a bilby population. A similar situation may arise with the irruption of native prey species when a period of drought is followed by exceptional rainfall (Southgate and Masters 1996). Hence, the periods following exceptional rainfall may present as much a threat to a bilby population as periods of drought. This situation occurred at Watarrka National Park where a reintroduced bilby population collapsed in response to increased predation pressure following a two year period of exceptional rainfall (Southgate and Possingham 1995)

### 6. An altered fire regime has caused the decline of medium-sized mammals

The altered fire regime hypothesis was advanced because the disappearance of medium-sized mammals coincided with the movement of Aboriginal people out of the deserts and into permanent settlements, and it helped explain the loss of species from the desert areas of northern Australia where foxes were absent (Short and Turner 1994). The hypothesis was considered plausible because greater fire heterogeneity was found in some areas occupied by Aboriginal people in the 1950s compared to later (Burrows and Christensen 1991), and it was recognised that stands of mature vegetation in close proximity to recently burnt habitat provide medium-sized mammals access to shelter and nutritious food (Bolton and Latz 1978). Furthermore, previous work had indicated that fire-promoted foods were an important component of the bilby's diet (Southgate 1990).

If the fire regime was influencing bilby distribution, it was expected that greater bilby prevalence would occur in close proximity to recently burn habitat and possibly in parts of the landscape where fire age heterogeneity was greater, as per:

*recently burnt habitat>long-unburnt habitat*
*high fire age heterogeneity>low fire age heterogeneity*

There was support for both propositions. Bilby prevalence was greater where fire age heterogeneity was higher and in closer proximity to habitat that had been burnt within the previous year. This fire age variable also formed a significant component of the statistical models predicting habitat occupancy, but only in the central part of the study area (Chapter 7). However, the overall association between bilby prevalence and fire pattern was weak, particularly when data from the entire study area was considered, and this provided equivocal support for the hypothesis. Other findings cast doubt on the critical role that Aboriginal burning might have played in providing essential habitat for medium-sized mammals. In large parts of the study area that had remained unburnt for over 16 years, vegetation cover was found to be insufficient to carry a fire (Chapter 9). This indicated that the provision of a patch-burning regime over the more arid parts of central Australia would have been difficult to sustain. The accumulation of sufficient fuel to carry extensive fires can occur throughout central Australia but these events generally follow rare periods of exceptional rainfall (Griffin and Friedel 1985), as happened in the 1930s, 1950s, 1980s and 2000s. At a landscape scale, some patches of habitat always escape being burnt because of wind shifts, rain or substrate effects (Chapter 4). Hence, some fire age heterogeneity occurs without Aboriginal burning and this must have been sufficient to sustain medium-sized mammal populations prior to the arrival of Aboriginal people in Australia around 50, 000 years ago. In addition, there are a number of islands off the mainland of Australia where medium-sized mammal populations have remained intact without Aboriginal burning for at least 8000 years (Burbidge *et al.* 1997; Short and Turner 1994).

The results from the statistical modelling suggested that fire became an important process for the bilby only in the central and northerly part of the Tanami Desert where the accumulation of biomass was more rapid because of the greater and less variable rainfall. Here fire could play an important ecological role in clearing space, removing adult plants and recycling nutrients. It was found that a severe drought could also achieve this process in the more arid parts of the Tanami Desert (Chapter 9). This justified further and more detailed investigation of the functional relationship between the bilby and fire pattern, as was conducted in the final two data chapters.

### *A link between bilby prevalence, food production and fire pattern*

Faecal analysis was used to describe the diet of the bilby and test three predictions relating to composition of the diet near burnt areas, the contribution that fire-promoted plants made to the plant component of the bilby diet, and the relationship between bilby prevalence and the amount of plant material consumed (Chapter 8). In Chapter 9, a series of experimental fire plots and other monitoring was used to examine the factors affecting fire recurrence and the production of a key fire-promoted plant.

### Bilby prevalence, diet and the fire-promoted plant foods

The investigation of bilby diet confirmed the importance of plant foods, particularly the fire-promoted plant *Yakirra australiense*. Plant material formed a larger component of the diet in the central part of the study area where overall bilby prevalence was greatest. Furthermore, a single fire-promoted plant produced most of the plant material consumed by the bilby, and the amount of fireweed seed consumed increased with proximity to recently burnt localities. The study provided a coherent case for the proposition that fire management could improve the habitat suitability for the bilby. I identified that a better understanding of the effect of fire, rainfall and substrate on the production of key food plants such as *Yakirra* would be necessary to assist the development of a management plan to improve habitat suitability.

The bulb *Cyperus bulbosus* also contributed substantially to the plant component of the diet. This plant species was not promoted by fire and was restricted to drainage substrates. The results supported the proposition that seed and bulbs were exploited opportunistically by the bilby and invertebrates, especially termites, and were increasingly relied upon when plant food resources became more scarce. This presents a different view to that of Gibson (2001) who worked on the diet of the bilby in south-west Queensland.

### Conditions for the production of key fire-promoted plants and fuel

Monitoring of random and experimental fire plots was used to examine the factors associated with fire recurrence and the production of *Yakirra australiense* (Chapter 9). The work found that long-unburnt spinifex cover was mostly too sparse to carry a fire in the southern part of the Tanami and the growth of non-spinifex vegetation would be necessary to boost fuel load sufficiently to carry a fire. Generally, more than 41% vegetative cover was required to carry a fire but this was also dependent upon weather conditions.

Season and magnitude of rainfall and time since fire were the most important variables in the production of *Yakirra* seed. Total ground cover (i.e. fuel load) was related mainly to mean annual rainfall and time since fire, but not substrate type. This allowed the development of two relatively simple models, one to identify areas that would be suitable to burn and, the other that could be used to predict *Yakirra* production. Both could be parameterised using currently available fire history mapping and splined rainfall coverage.

Observations from the experimental fire plots indicated that managers should aim to burn some areas in late spring or early summer (end of dry season) to improve *Yakirra* production. This timing is consistent the recommendations for manageing spinifex pastures in northern Australia (Craig 1999). Fire management to enhance habitat suitability for the bilby would be of most benefit in the northern part of the Tanami Desert where growth rate of vegetation is greater and there is little existing fire age heterogeneity. Preparatory cool-season burning is required for creating protective firebreaks and to reduce the likelihood of uncontrolled, extensive wildfire

## Implications for management

Management may be identified as either custodial or manipulative (Caughley and Sinclair 1994) but it was argued that these forms of management need to also specify the amount or intensity of input required to sustain a desirable outcome (Chapter 1). Predator-proof enclosures are costly to establish and maintain and provide an example of high-intensity custodial management. These structures may provide a short-term safeguard against the extinction of selected species and offer opportunities to investigate aspects of a species' biology or ecology. However, they cannot be viewed as a long-term conservation solution for most species simply because ongoing running costs and security can not be assured over ecological time. Low intensity custodial or manipulative forms of management should be investigated exhaustively intensive forms of management are adopted because forms of low intensity management are more likely to be sustained over time and to not diminish a species' fitness.

The statistical modelling conducted in this thesis suggested that the bilby was not limited by a single threatening process and therefore, the delivery of a single management action would be unlikely to alter the status of the bilby subsantially. The study identified that both low intensity custodial and manipulative forms of management could be appropriate.

*Custodial management*

1. Laterite and rock feature substrates plus drainage line and calcrete substrates were identified as important for the bilby. These substrate types represent a small proportion of desert regions in Australia and need to be protected from the expansion and development of pastoralism in northern parts of the Tanami Desert and Great Sandy Desert.

2. Areas of laterite are currently targeted by mining operations for the placement of camps, air strips and extensive structures like tailings and over-burden dumps because of their lowered risk of inundation. A strategy to minimise the use of this substrate for mining operations needs to be developed.

3. Areas where dingoes and cats occur in low abundance in the northern part of the Tanami and Great Sandy Deserts need to be identified more clearly with finer-scale monitoring and these areas need to be secured as conservation reserves.

*Manipulative management*

1. Fire management needs to be implemented in the northern part of the Tanami and Great Sandy Deserts, focussing on areas where there is little substrate heterogeneity as a priority and in proximity to areas with existing bilby populations. This 'bottom-up' management approach should result in greater food availability for the bilby and improve recruitment if a proportion of the landscape can be burnt prior to the rainy season each year.

2. The hunting of foxes and cats by Aboriginal people should be encouraged with incentive schemes. Communities within the current area of occupancy of the bilby ($p>0.15$) should be given priority, followed by communities in the extent of occurrence (Chapter 7). Paltridge (2004) indicated that hunting by Aboriginal people within a 10 km radius of a communities would provide a buffer of 300 $km^2$ and this is an order of magnitude larger than most predator-proof exclosures.

3. Greater justification should be required before baiting and other measures are undertaken to control dingo populations.

## Implications for future research and monitoring

### *Innovative monitoring techniques*

Tracking as means of recording information on occurrence of fauna in the deserts of arid Australia has been neglected for far too long. The skills of Aboriginal people to track, observe and collect information have similarly been ignored and there is an urgent need to develop an employment model that recognises people with these abilities. This would require the development of some form of an accreditation scheme to ensure that people who engage in such work can meet specified standards, as has been done in southern Africa (Liebenberg, pers. com.). Realistic incentives that encourage people to collect information would be needed along with agreement regarding issues such as the ownership of data, sampling design, data collation and analysis. Once operational, and if applied consistently throughout arid Australia, valuable information on the occurrence of invasive and threatened species would emerge.

### *Evaluation and reformulation of species occupancy models*

The models to predict species occupancy presented here need to be evaluated with independent data collected in the Tanami Desert. It is likely that the models developed to predict species occupancy are portable and could be applied in the Great Sandy and Gibson Deserts. However, the outcomes would require thorough evaluation using field data. The models may need to be reformulated in the light of this information to better reflect the species-environment functional relationship. Examining the pattern of bilby and introduced species distribution in the Great Sandy and Gibson Desert should take foremost priority.

### *Assessment of status*

The finding that the estimated area of occupancy was much smaller than the extent of occurrence has significant implications for the assessment of bilby status. Much of the area within the extent of occurrence and covering most of the Tanami Desert might well be considered 'sink' habitat (Pulliam 1988), where mortality is likely to exceed natality. Hence, the extent of occurrence should not be used as a parameter to assess the status of the bilby. Regular monitoring of the population should be used to determine if there are changes to the current area of occupancy.

### *Climate change*

Rainfall and temperature variables were strong components of the statistical models for most of the animal species assessed. Hence, climate change is likely to affect the habitat suitability and distribution of each species studied, with the possible exception of the feral cat. The mid-range of expectations for climate change in Australia is approximately $3^{\circ}$ C warming by 2050-2100 compared with the 1990 baseline (Westoby and Burgman 2006). This means that the present day north-south temperature envelope will be dislocated pole-ward by about 300 km. It is predicted that variability and unpredictability of climate in arid and semiarid regions of Australia will also increase (Hughes 2003). Predicting what will happen to the distribution of the bilby and associated species is therefore a priority for research.

*Fox and feral cat control*

Research into the development of biological control of foxes and feral cats needs to be a priority. Species specific immunocontraception through baits or vectors offers great hope, but development of this technology is still its infancy (Barlow 2000).

*Ecological role of the dingo*

The role of the dingo as a trophic regulator needs more thorough investigation in an experimental framework. My work adds to the observational evidence that dingoes displace or limit the abundance of introduced predators like the feral cat and fox (Christensen and Burrows 1995; Lundie-Jenkins 1993; May and Norton 1996; Pettigrew 1993). The extent and the conditions under which a rescue effect might be provided by the dingo for species like the bilby need to be determined. The full cost of indiscriminate poison-baiting in the pastoral industry and for the purposes of conservation also needs to be rigorously assessed.

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## Statement of authorship

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