PREDATOR-PREY INTERACTIONS IN THE SPINIFEX GRASSLANDS OF CENTRAL AUSTRALIA

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CERTIFICATION

I, Rachel M. Paltridge, declare that this thesis, submitted in partial fulfilment of the requirements for the award of Doctor of Philosophy, in the Department of Biological Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Rachel M. Paltridge
10 May 2005.

ABSTRACT

Predation by exotic predators (cats *Felis catus* and foxes *Vulpes vulpes*) is believed to be one of the factors that has contributed to the decline of medium-sized mammals in arid Australia. Other factors include habitat degradation by introduced herbivores (rabbits *Oryctolagus cuniculus* and grazing stock) and altered fire regimes after Aboriginal people moved into permanent settlements. In general, the impact of exotic predators on arid zone mammals is believed to be significant only when predator numbers have been elevated by increased food availability from exotic prey species (rabbits, house-mice *Mus domesticus*, cattle carcasses) or when native prey populations have already been dramatically reduced by competition from introduced herbivores.

In much of the spinifex grasslands of the central Australian deserts, pastoralism never occurred, rabbit colonisation was extremely patchy and in some areas, traditional burning was still being practised when the extinctions commenced. None of the current models of mammalian extinctions adequately explain the declines in this environment. In this study I examined predator-prey interactions in two areas of the Tanami Desert to investigate whether predation by exotic predators may be a primary agent of extinction in its own right, capable of causing mass declines even in the absence of other human-induced perturbations. If this were the case then the following would be expected: (i) cats and foxes would eat medium-sized mammals when they are available, but be able to survive on alternative prey when mammals are scarce; (ii) populations of cats and foxes would be buffered against the declines of mammals during droughts, or would be able to recover more quickly than medium-sized mammals after droughts; (iii) medium-sized mammals would be more vulnerable to predation by cats and foxes than by dingoes *Canis lupus dingo* and other native predators, and (iv) there would be a correlation between the timings of the extinctions and the colonisation (or sudden increase) of cats and foxes.

These predictions were investigated by monitoring the diets and relative abundance of cats, foxes and dingoes in relation to fluctuating prey availability in two areas of the Tanami Desert at latitudes separated by approximately 400 km. Mean annual rainfall is higher and more reliable in the northern study area which was situated in the centre of bilby *Macrotis lagotis* distribution within the Northern Territory, whereas the southern study area was located on the southern edge of the bilby's range. Within each study area, monitoring occurred at three sites, approximately 20 km apart. Each site contained a sub-plot in each of two habitat types. Field work was conducted between September 1995 and December 1997. When the study began, the southern study area was experiencing drought conditions, however both study areas received significant rainfall in early 1997.

The population dynamics of a variety of potential prey groups were monitored to examine their resilience during droughts, patterns of recolonisation after rainfall, and use of two habitat types: the ubiquitous sandplain, and the moister, nutrient enriched palaeodrainage habitat which is believed to have provided a refuge for medium-sized mammals during droughts.

Native mammals were uncommon throughout the study period. Bilbies and macropods were significantly more abundant in the northern study area, and tended to occur more frequently in palaeodrainage habitat than sandplain. However, the palaeodrainage habitat did not appear to provide adequate refuge for the medium and large mammals during drought conditions in the southern study area, as they disappeared from the study sites altogether. Small mammals were significantly more abundant in the southern study area but densities remained low (< 2% trap success) throughout the study, and showed little response to improved seasonal conditions.

In contrast, the abundance and species richness of birds showed a marked increase following rainfall in the southern study area. Flocks of nomadic birds arrived within several months of drought-breaking rains, increasing the relative abundance of birds from 9.3 per km of transect in December 1996 to 49/km in July 1997.

Reptiles were the most resilient prey group during the drought conditions. Both varanids and smaller reptiles were equally abundant in the wet and dry years and showed no difference in abundance between study areas. However, reptiles showed marked temperature-related patterns in activity, with many species becoming inactive in the winter months.

A total of 142 cat scats, 126 fox scats and 75 dingo scats were analysed to investigate predator diets in the two study areas. Unlike cat, fox and dingo diets elsewhere in Australia (and the world), mammalian prey did not dominate. Reptile was the prey category that was most frequently consumed by cats and foxes in ‘summer’ (October-

April) and by dingoes throughout the year, and was identified as a “seasonal staple” prey type for all three predators in the Tanami Desert. When biomass of prey was taken into account, the varanids (predominantly the sand goanna *Varanus gouldii*) were the most important prey sustaining predators in the two study areas. Birds were an important part of the diets of cats and foxes in winter when reptiles were less active. Small mammals were consumed by cats and foxes throughout the study, in proportion to their field abundances. Invertebrates were a major component of the diets of foxes, representing 31% of prey items consumed. There was considerable overlap in the diets of the three predator species, but dingoes ate more medium (100-999 g) and large (>1000 g) prey than cats and foxes did.

The scarcity of medium-sized mammals in the study areas provided little opportunity to find evidence of predation events on such prey. However, bilby remains were found in two cat scats and one dingo scat in the northern study area, mulgara *Dasycercus cristicauda* remains occurred in several cat and fox scats from the southern study area, and there were fourteen occurrences of marsupial mole *Notoryctes typhlops* in predator scats during the study, primarily in fox scats. Elsewhere in Australia, there is ample evidence that cats and foxes regularly consume medium-sized mammalian prey (e.g. rabbits and ringtail possums *Pseudocheirus peregrinus*) when it is available.

Overall cats were the most abundant eutherian predators in the two study areas, and they were significantly more abundant in the northern study area than the southern study area. Surveys revealed that cats can persist into droughts by feeding on reptilian prey. When the study commenced, cats occurred on five of the six sub-plots in the southern study area, despite six consecutive years of below-average rainfall. However, by the end of the first year, they could only be detected on one sub-plot. Recolonisation of the sites rapidly occurred after significant rainfall (260 mm in 2 months), when nomadic birds colonised the sites and provided a plentiful food source.

Foxes also declined to very low densities during drought in the southern study area, but they had recolonised all sites by the winter of 1997. This coincided with the increase in abundance of birds, which became their most frequently consumed prey item. Overall, foxes were equally abundant in the two study areas, but statistical analyses revealed a significant interaction between latitude and habitat because in the southern study area foxes tended to utilise the palaeodrainage habitat more than the sandplain, whereas in the northern study area the majority of fox sign was detected in the sandplain habitat. This may have been due to the abundance of dingoes in the palaeodrainage habitat in the northern study area.

Dingoes were significantly more abundant in the northern study area than the southern, where they were usually only present at one of the three sites. The northern study area had higher densities of macropods (supplementary prey for dingoes) and more reliable access to drinking water, which persisted in the palaeodrainage channels for up to 6 months after significant rain events. Dingo numbers were relatively stable throughout the study and did not increase in response to improved seasonal conditions in the southern study area in 1997.

This study revealed that the distribution of foxes extends further north into the Tanami Desert than has previously been reported, and is not necessarily tied to the distribution of rabbits in the Northern Territory. Furthermore, discussion with Aboriginal people who lived a traditional lifestyle in the area until the 1940s, revealed that foxes were already present in the northern Tanami desert at that time, before the disappearance of many medium-sized mammal species. The patterns of medium-sized mammalian extinctions in the northern and western deserts between 1940 and 1960 is thus consistent with the colonisation of the fox.

Although cats had been present in central Australia for at least 50 years before the mammalian declines occurred, this does not discount them from contributing to the extinction process. It is postulated that during the early decades of their colonisation of the arid interior, cat populations may have been maintained at low levels by predation from dingoes and also Aboriginal people (for whom cats were a favoured food). But between 1920 and 1960 the western deserts were depopulated of Aboriginal people, and human hunting of cats diminished. This coincided with the introduction of the dingo bounty scheme, which encouraged many Aboriginal people to continue making regular excursions into the deserts to collect dingo scalps. In this study, cat remains occurred in 9% of dingo scats, suggesting that dingoes may be an important predator of cats. Thus, there may have been an increase in the cat population between 1930 and 1960, producing a more significant impact on native mammal populations than had previously occurred.

Information collected during this study was used to construct a new model of mammalian extinctions in the spinifex grasslands of central Australia that promotes predation by cats and foxes as the primary agent of extinction. The model proposes that cats and foxes will eat medium-sized mammals when they are available, but are capable of subsisting on naturally occurring alternative prey when mammals are scarce. Thus, cats and foxes can persist into drought periods by feeding on reptilian prey, which remains an abundant resource regardless of rainfall (at least during the warmer months). Predator populations eventually decline after a series of dry winters. When the drought breaks, the rapid response of nomadic birds provides a readily available food source for cats and foxes as they recolonise areas and commence breeding. Predation by cats and foxes thereby has the potential to exacerbate the declines of native prey populations during droughts and delay their recovery when seasonal conditions improve. In this way, introduced predators are capable of causing local extinctions of medium-sized mammals when populations contract during drought periods, even in the absence of introduced herbivores and altered fire regimes.

Although dingoes also prey upon medium-sized mammals, dingoes did not cause extinctions of medium-sized mammals in the spinifex grasslands because (i) they are more reliant on drinking water than foxes and cats, thus waterless areas would have provided some degree of predation refugia, and (ii) their social structure and territoriality prevent high densities accumulating, even when resources are abundant.

If further extinctions of medium-sized mammals (such as the bilby) are to be prevented, it may be necessary for wildlife managers to establish a series of predation refugia where fox and cat populations can be controlled without extinguishing local dingo populations. This could be achieved with a combination of predator-proof enclosures, zones in which foxes are killed through poison baiting and areas where Aboriginal people are employed to utilise traditional hunting methods to control introduced predators.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 EXTINCTIONS – A WORLD VIEW

The world is suffering an unprecedented rate of species loss as the human population escalates (Russell *et al*. 1998). Since 1600, the world has lost 85 species of mammal and 113 species of bird (Primack 1998). The majority of extinctions have occurred in the past 150 years and, based on information from the fossil record, current extinction rates are at least one hundred times the background rate of extinction (Primack 1998).

The current wave of extinctions is a side effect of human activity (Eldredge 1999), with habitat destruction, over-exploitation of species and introduction of exotic species the major causes of recent extinctions (Primack 1998). The impacts of exotic species are most severe on islands where species occupy small areas, and have evolved in the absence of significant predators, competitors and diseases (Primack 1998). Approximately 75 % of all mammal extinctions in the past 400 years have occurred on islands (MacPhee and Flemming 1999). Of the remainder, 74 % of mammal extinctions occurred on one continent: Australia (MacPhee and Flemming 1999).

1.2 EXTINCTIONS IN AUSTRALIA

Australia has a disproportionately high rate of mammalian extinctions compared with the rest of the world (Caughley and Gunn 1996). Of the 245 mammal species present when white settlement commenced in 1788, 16 species have become extinct and a further 26 now occur solely as remnant populations, having declined to less than 20 % of their former ranges (Short and Smith 1994). The majority of these declines and extinctions have been in the body mass range of 35 g to 5.5 kg (Burbidge and McKenzie 1989), referred to as the “medium-sized” range (Morton 1990). The areas that have been most affected have been the southern arid zone and the wheatbelt of Western Australia (Short and Smith 1994). Tasmania, the tropical north and certain mesic coastal areas have been least affected by the declines, although several species that have become regionally extinct elsewhere have recently declined in the monsoonal tropics of northern Australia (Woinarski 2001).

Birds have been less affected than mammals, with only one confirmed bird extinction from the Australian mainland since European colonisation (Garnett and Crowley 2000). However, 11.5 % of Australian bird species are considered threatened (Garnett and Crowley 2000). There have been no definite extinctions in the arid zone (Reid and Fleming 1992) but 30 % of the 230 species of arid zone birds have declined in at least part of their distribution (Woinarski 2001). In general, decline and regional loss of bird species has been greater in the temperate, highly modified, agricultural areas of southern Australia, where losses of up to 25 % of bird species have been recorded (Woinarski 2001).

Compared to mammals and birds, there is little historical information on the status of reptiles and amphibians at the time of European settlement of Australia (Woinarski 2001). Generally, reptiles appear to be remarkably resilient to changing land management practices (Morton 1990), but several arid zone lizard species are believed to have suffered considerable reduction in range in central Australia (Kerle and Fleming 1996, McAlpin 2001). Loss of frog and reptile fauna in arid Australia is clearly significantly less than in the more extensively cleared agricultural areas (Woinarski 2001).

1.3 HYPOTHESES FOR AUSTRALIA’S MAMMALIAN EXTINCTIONS

The declines in Australia’s mammal fauna were witnessed first hand by H.H. Finlayson, who conducted extensive field work in central Australia during two widely spaced periods: 1931-1935 and 1950-1956 (Finlayson 1961). He spent most of the early period in the south-western corner of the Northern Territory (and adjacent parts of South Australia and Western Australia), where discussions with Aboriginal people and comparisons with earlier collections revealed that the suite of mammal fauna that occurred there was still relatively intact. However, he noted that small numbers of foxes (*Vulpes vulpes*) had already started invading the area. When he returned to this region (which remained unaffected by pastoralism) in 1950, many of the mammal species had disappeared or severely declined.

Finlayson attributed the losses primarily to the increase of the fox, which was believed to outnumber the dingo (*Canis lupus dingo*) there at that time (Finlayson 1961). Frederick Wood Jones also identified the fox as a major reason for the disappearance of many mammal species from South Australia (Wood Jones 1923, 1924, 1925). However, many species of medium-sized mammals are believed to have disappeared from areas of the northern deserts before the arrival of the fox (Gibson 1986, Burbidge *et al.* 1988). The "fox predation" hypothesis was viewed as being too simplistic as the extinctions occurred during a period when many confounding changes were simultaneously occurring in arid zone ecosystems (Burbidge and McKenzie 1989, Morton 1990). For example, the invasion of the fox tended to follow the colonisation pattern of the rabbit (*Oryctolagus cuniculus*; Jarman 1986). These events were subsequent to the advent of pastoralism in central Australia, which generally coincided with a cessation in traditional Aboriginal land management practices including burning, hunting, and waterhole maintenance. A reduction in the available productivity of the land attributable to grazing by introduced herbivores and changed burning practices was seen as the primary cause for mammal declines (Burbidge and McKenzie 1989). Medium-sized herbivorous and omnivorous mammals were considered the most vulnerable fauna because of their limited mobility but relatively high daily metabolic requirements necessitating adequate access to nutritious vegetation (Burbidge and McKenzie 1989).

The "fire-stick farming" method of Aboriginal hunting (Jones 1969) was thought to be particularly important for the maintenance of populations of many species of mammals, because the small patchy burns produced a mosaic of vegetation in varying successional stages. This ensured that fire-stimulated food plants grew in close proximity to mature stands of vegetation which provided shelter (Bolton and Latz 1978). As Aboriginal people moved out of the deserts into permanent settlements, the fire regime changed from numerous relatively small fires occurring in a variety of seasons to a situation of infrequent but extensive summer fires (Latz and Griffin 1978, Kimber 1983). It has been suggested that the medium-sized mammals would have been left stranded after these large fires, in a mosaic of vegetation that was too coarse for them to readily move between the shelter-producing dense vegetation and the regenerating areas which had a greater diversity of food (Bolton and Latz 1978). The strength of the "altered fire regime" hypothesis is that it explains the loss of species from the northern deserts of Western Australia and the Northern Territory, where foxes are believed to have been absent at the time of the mammal extinctions (Short and Turner 1994).

The concept of more productive refuges amongst vast areas of infertility was brought into the habitat alteration model (Morton 1990) to explain how changes wrought by

European settlers could have had such a dramatic impact on Australia's vertebrate wildlife. This model was based on the assumption that medium-sized herbivorous mammals were dependent on refuge areas of more reliable productivity during drought periods. These refuge areas are believed to have suffered particularly severe degradation when high populations of introduced herbivores invaded the area, rendering them unsuitable for native species to retreat to during droughts. Populations thus became increasingly fragmented to the point where they became particularly vulnerable to local extinction by introduced predators. In the "degradation of refugia" hypothesis, predation by cats (*Felis catus*) and foxes was regarded as a secondary force in the extinction process whereas rabbits and grazing stock were seen as the major causative agents of decline (Morton 1990).

An alternative model of mammal extinction and decline implicated predation by cats and foxes as a primary agent of decline in conilurine rodents but also included rabbits as an important factor (Smith and Quin 1996). The "hyperpredation" hypothesis predicts that declines in rodent populations will be most severe in areas where predator densities are elevated by introduced species with superior reproductive rates such as rabbits and house-mice (*Mus domesticus*). The resulting effect can be likened to a permanent "predator pit" (see below). Native prey populations that may have contracted during drought conditions are unable to increase when seasonal conditions improve because of elevated predator populations that have already increased in response to exotic prey species with high reproductive rates (Smith and Quin 1996). Similarly, cattle carcasses and introduced water points are believed to sustain dingo populations during droughts, and even allow them to increase, which may have caused a suppression in populations of native prey in pastoral areas (Corbett and Newsome 1987).

The various hypotheses differ in the extent to which predation is responsible for the declines in Australia's native mammal fauna but, subsequent to Finlayson's early observations (Finlayson 1961), introduced herbivores (either rabbits or grazing stock) have been consistently regarded as central to the extinction process. However, many of the mammal species that disappeared from Australia's deserts had distributions that extended throughout the spinifex grasslands of the Tanami and Great Sandy Deserts in areas where pastoralism was never attempted and rabbits are extremely sparsely distributed, if they occur at all (Gibson 1986, Burbidge and McKenzie 1989). The assumption that rabbits may once have been abundant in these habitats and caused irreparable damage to the refuge areas (Morton 1990) is speculative and based on little evidence. Furthermore, traditional burning regimes were still being applied in the western deserts in the 1950s (Thomson 1975), when the extinctions were occurring.

In the simpler system of the spinifex grasslands, with fewer confounding variables, we can begin to investigate whether predation by introduced species may be a primary agent of extinction in its own right, capable of causing mass declines, even in the absence of other human-induced perturbations. The process by which introduced predators may have caused extinctions in arid Australia is the central issue investigated in this thesis. The following sections of this chapter introduce (i) predation and its various impacts on populations of prey and (ii) the cat, fox and dingo in Australia.

1.4 DEFINITION OF PREDATION

In this study, I define predation as the process of consumption of one organism (the prey) by another organism (the predator) in which the prey is alive when the predator first attacks (Begon *et al.* 1990). Of the four main types of predation (herbivory, parasitism, carnivory and cannibalism; Caughley and Sinclair 1994), only carnivory will be addressed here.

1.5 POTENTIAL IMPACTS OF PREDATION

At the level of the individual, the effect of predation is mortality. At the population level, however, the impact of a predator on a prey species may fall anywhere in the continuum of having no long term impact (if the affected individuals were soon to die anyway, or lost animals are readily replaced) through to extinguishing the species. Between these two extremes sit predator limitation and predator regulation.

There are many examples of introduced predators extinguishing native prey species on offshore islands. One of the worst cases was the accidental introduction of the brown tree snake (*Boiga irregularis*) to the island of Guam in the 1940s (Engeman and Linnell 1998). It is believed to have extirpated seven species of birds and four of the five remaining forest bird species are now critically endangered (Savidge 1987). Several species of lizards have also become extinct or endangered (Rodda and Fritts 1992). In another case, one domestic cat is believed to have extinguished a species of wren

(*Xenicus lyalli*) that was endemic to Stephen Island, New Zealand, within months of settlement on the island (Primack 1998).

In contrast to the situation on islands, evidence of exotic predators directly causing extinction of native species on continents anywhere in the world is harder to find (Frankel and Soule 1981, Burbidge and McKenzie 1989). While it is generally well accepted that predators can "limit" prey populations (i.e. reduce the population density below carrying capacity; Sinclair 1989), there is little evidence that predators can initiate declines in prey populations when densities are high (Trout and Tittensor 1989, Messier 1991, Macdonald *et al*. 1999).

Food supply is recognised as the primary factor determining population growth rate of vertebrate populations (Sinclair and Krebs 2002). For many populations, as the population density increases there is less food per capita, and the growth rate declines, either through increased mortality or decreased natality (Sinclair and Krebs 2002). This negative feedback mechanism is known as "regulation". Regulatory factors are a subset of limiting factors that have a density-dependent effect on population numbers. In other words, the negative effect of regulatory factors increases with population size, thereby causing the population density to return to its point of equilibrium (Sinclair 1989). While predators may be able to regulate populations of prey at low densities, few studies have found significant impact at high densities (Macdonald *et al*. 1999).

The impact of predation on the population dynamics of a prey species can be determined by studying the numerical and functional responses of predators to fluctuating prey densities. When combined a total response curve is produced, which gives the proportion of the prey population removed at different prey densities, and this can indicate the potential for predators to extinguish populations of prey.

1.6 FUNCTIONAL RESPONSE

Functional response involves changes in the foraging behaviour of an individual predator and is measured in terms of the number of prey eaten per predator at different prey densities (Holling 1959). The hypothetical Type I functional response depicts a linear relationship between prey density and number of prey taken by individual predators. This could only occur if predators had an unlimited appetite, and is therefore unrealistic for most predator-prey interactions (Caughley and Sinclair 1994).

Realistically, as a certain prey type increases in abundance, an individual predator may increase consumption of that prey, either linearly or curvilinearly in relation to prey abundance, but in either case reaches an asymptote set by satiation levels. The maximum number of prey that can be killed by an individual predator in a set period is usually dependent on the "handling time" required to find, subdue, kill, eat and digest a prey item. However, for predators prone to surplus killing and/or caching of prey (e.g. red foxes preying on sea-birds and spotted hyenas (*Crocuta crocuta*) preying on gazelles, Kruuk 1972), the prey density at which a predator cannot handle any more prey may never be reached in the field (Boutin 1995), and the number of animals killed may approximate a Type I functional response.

A Type II functional response can be depicted graphically by a simple convex curve (Holling 1959). The decreasing slope as density increases implies that the response is inversely density dependent at all densities, *i.e.* a decreasing proportion of the prey population is taken per predator as the prey population increases. In contrast, a Type III functional response curve is sigmoidal in shape: the number of prey killed per predator increases slowly at low prey densities, but fast at intermediate densities before leveling off at high densities (Holling 1959). The accelerating part of the curve at low densities represents a density-dependent response while the decelerating part implies predation is inversely density dependent at high prey densities. Thus individual predators kill a greater proportion of the prey population at low-to-intermediate prey densities than at high densities, but prey are not consumed in any quantity until they reach a certain threshold. This type of feeding behaviour by the predator is known as "switching." Switching occurs when a generalist predator shifts its focus from one prey type to another, concentrating its attacks on the more abundant prey type at a rate that is disproportionate to the relative frequencies of the two prey (Murdoch 1969). It may be caused by training (developing a search image for a prey species that is encountered more often, or becoming more practiced at obtaining a certain prey type) or if alternative prey live in different habitats or are active at different times, the predator may shift its hunting activity either spatially or temporally. Flocking behaviour may also cause switching, whereby predators are influenced by what their conspecifics are feeding on (Oaten and Murdoch 1975). Predators that engage in switching will have a tendency to ignore prey at low densities and thus should not cause local extinction of prey populations.

1.7 NUMERICAL RESPONSE

The effect of changes in prey density on the whole predator population in terms of survival, reproduction, immigration and emigration, is known as the numerical response and can be depicted by the trend of predator abundance against prey density (Solomon 1949). The rate of increase of the predator population depends on the species' reproductive potential, as well as its capacity for immigration. For example, resident non-migratory predators with a monoestrous breeding cycle may be slow to increase and show a considerable lag behind their prey, whereas highly mobile predators or those that can initiate breeding at any time of the year can potentially show a rapid numerical response to preferred prey types (Korpimaki and Nordahl 1991). Regardless of their rate of increase, predator abundance (as a proportion of prey density) tends to eventually reach a plateau, as social factors such as territoriality and interference become limiting for the predators. For example, at certain predator densities, the availability of suitable breeding sites may prevent further increases in the predator population, or interference interactions with conspecifics may take up excessive time, resulting in dispersal (Southern 1970). Thus a numerical response at low prey densities may or may not be density-dependent, but as it reaches an asymptote at high densities, the response becomes depensatory, or inversely density dependent.

The relationship between predator abundance and prey abundance at low prey densities depends on the ability of the predators to subsist on alternative prey and whether prey can escape to predator-free refugia (Pech *et al.* 1995). Thus, even a predator with a fairly broad diet may decline if all prey species show a similar response to major environmental changes (e.g. droughts and bushfires). However, if certain prey types persist or increase when the majority of species decline, predator abundance may be independent of particular preferred prey and remain stable when such prey have decreased in abundance.

1.8 TOTAL RESPONSE

Combining the number of prey eaten by one predator (functional response) with the number of predators (numerical response) yields the total prey mortality due to predation, as a proportion of the living prey population. This is known as the total response of the predators to the prey. If there is no density dependence in either functional or numerical response, then the proportional effect of the total response is uniformly inversely density dependent (Type II form). If there is some density-dependence then the shape of the total response is of Type III form, and shows density-dependence at low prey densities while remaining depensatory at high prey densities (Sinclair and Krebs 2002). Total response curves indicate whether predators can regulate prey populations, or send them to extinction.

Several studies (e.g. Newsome *et al*. 1989, Trout and Tittensor 1989, Messier 1991) have confirmed that although predators tend to have little impact on high densities of prey, carnivore predation can exacerbate population declines of mammalian prey, and delay their recovery for periods of up to several years.

In this type of situation, there may be two stable equilibrium points (where prey net recruitment is balanced by total mortality; Pech *et al*. 1992). A "boundary" density occurs between the two equilibrium points. Below the boundary density, predators are able to regulate the prey population and suppress abundance (Pech *et al*. 1992). It is not until exceptional conditions prevail, allowing a burst of recruitment by the prey (or alternatively predators are reduced by some other extrinsic factor such as human control) that the prey can increase beyond the boundary density. When prey levels exceed the boundary density they are no longer regulated by predation and their numbers fluctuate around a higher equilibrium point which may be dependent on intraspecific competition for resources such as food or breeding sites (Sinclair 1989). The range of densities below the boundary density is known as the "predator pit" (*sensu* Walker and Noy Meir 1982).

In Australia it has been suggested that a widespread environmental perturbation (such as drought or massive wildfire), which causes the decline of many species simultaneously (and provides carrion to buffer predators), is required before predator regulation can occur (Newsome *et al*. 1989). This is known as "environmentally modulated predation" and has been demonstrated for foxes and cats feeding on rabbits (Newsome *et al*. 1989) and inferred for dingoes preying on rabbits and red kangaroos (Newsome *et al*. 1983, Corbett and Newsome 1987). If mammalian carnivores are capable of regulating a species as fecund as the introduced rabbit, is it possible that "environmentally modulated predation" could have resulted in the extinction of some of Australia's native species of mammals?

1.9 CAN PREDATORS EXTINGUISH POPULATIONS OF PREY?

Predator-prey theory suggests that it is theoretically possible for a predator to extinguish small populations of prey, if the predator's total response is inversely density-dependent at all prey densities or if the total response is independent of the density of the prey species (Pech *et al*. 1995). Such situations may occur where prey are secondary or alternative prey species for a predator that is able to maintain high densities by feeding on other more abundant and persistent prey species, but continues to kill rare species either as a small consistent by-catch (i.e. a constant number of prey are taken) or a constant proportion of the prey population are consumed (Pech *et al*. 1995). If prey density declines below a certain threshold level, predation will drive the species to extinction if prey have no refuge from predation at low densities, and all age classes are vulnerable to predation. Only a burst of reproductive activity that swamps the predator's functional and numerical responses will ensure that extinction is avoided (Pech *et al.* 1995).

Analysis of field data from several Australian rare mammal populations produced predation curves that conformed to the predictions of predator-prey theory (Sinclair *et al*. 1998). For example, the black-footed rock-wallaby (*Petrogale lateralis*) was found to be a classic alternative prey species, vulnerable to extinction below a threshold population density. Other species' predation curves were more closely aligned to the Type III interaction, and appeared to have two stable states, however the lower state was of such low density that it would be subject to extinction due to stochastic events (Sinclair *et al*. 1998).

From this discussion of predator-prey theory it is apparent that the extent to which predators can regulate, cause significant declines to, or extinguish a particular species of prey depends on attributes of the predator species (ability to capture the prey, reproductive potential, capacity for immigration, tolerance of conspecifics, ability to subsist on alternative prey, propensity for switching, tendency for surplus killing) and attributes of the prey species (ability to evade predators, reproductive potential, ability to tolerate conspecifics, capacity to persist in refugia at low densities) as well as the relative availability of alternative prey species (i.e. whether the various prey species fluctuate in synchrony or independently so that there is always food available to buffer

Table 1.1: Attributes of a predator-prey system that may influence whether a predator can send a prey species to extinction

	Attribute	Prey populations may be extinguished	Predator unlikely to extinguish prey populations
Prey dynamics	1. **Prey population dynamics**	**Independently fluctuating prey:** some prey types remain or increase in abundance when most species are declining (e.g. during droughts)	**Synchronised fluctuations in prey:** prey show similar responses to environmental events (e.g. droughts and bushfires) leading to a food shortage for the predator
Predator diets and feeding behaviour	2. **Predator dietary requirements**	**Generalist:** can increase in response to one of many alternative prey species, meanwhile suppressing low populations of other species	**Specialist:** numerical response will tend to lag behind prey, therefore may regulate prey but won't extinguish it, or predator will starve
	3. **Feeding behaviour of predator**	**Non-switcher**: takes prey in proportion to encounter rate, therefore will occasionally prey on rare species even when populations are low	**Switcher:** tends to feed disproportionately on the most abundant prey type, therefore ignores prey at very low densities
	4. **Predator's propensity for surplus killing**	**High**: kills in excess of requirements; prey density at which functional response reaches asymptote may never be achieved in the field	**Low:** unlikely to have as much impact on prey populations as functional response will reach asymptote at lower prey densities
Numerical response of predator population	5. **Predator's reproductive potential**	**High:** can initiate breeding immediately, breed continuously and produce large litters, therefore can rapidly increase in response to increasing prey populations	**Low:** monoestrous, small litter size, social repression of breeding, resulting in a slower numerical response to increasing prey densities
	6. **Predator's capacity for immigration**	**High:** highly mobile predators can show a rapid numerical response to increasing prey populations	**Low:** numerical response to increasing prey is slower, as predator population can only increase by breeding.
	7. **Territoriality of predator**	**Non territorial or flexible territoriality:** can tolerate high densities of conspecifics when resources are plentiful	**Territorial:** interference from conspecifics will impose an upper limit to the numerical response which may prevent high enough densities accumulating to extinguish a prey population
	8. **Natural Enemies of predator**	**Few:** relatively free of predators, parasites and pathogens	**Many:** populations are kept in check by predators, parasites and pathogens
Refugia for prey	9. **Habitat requirements of predator**	**Ubiquitous** (with respect to prey): prey have no refuge from the predators therefore predators can extinguish local populations	**Specific** (with respect to prey): prey may have refugia where the predators do not occur, from which they can recolonise patches

predator populations). Table 1.1 lists some of the ecological attributes of a predator-prey system that may influence whether predation results in the extinction of a prey species.

In systems where predator and prey systems have coevolved, natural selection has operated on the characteristics of both predators and prey so that their interactions produce stability and the species can coexist (Krebs 1994). A specialist predator that evolves to be too efficient at harvesting its prey would eventually exterminate its food source and then suffer starvation (Krebs 1994). On the other hand, a "prudent predator" (*sensu* Slobodkin 1961) may avoid eating prey in peak reproductive condition or have developed territorial behaviour to prevent excessive densities from building up in response to prey. Alternatively, prey may use refugia where predators do not occur or have size classes that are inaccessible to the predators (Krebs 1994).

Specialist predators are more likely to act with prudence than generalist predators, which can shift their diet to alternative species if one species goes extinct. Also, specialist predators tend to track the abundance of their prey, and thus show time-lagged numerical responses; in a coupled predator-prey system where the predator is a specialist, the predator is more likely to be regulated by the prey, than the prey by the predator (Crawley 1992).

When prey are exposed to a new predator that they have not evolved any defenses against, they may be extremely vulnerable to surplus killing and overkill at both high and low densities (Short *et al.* 2002). If a refuge from the predator is not available the impact of the predator on the prey population can be rapid and catastrophic and may lead to major decline or local extinction (Short *et al.* 2002).

Thus, where there is no switching by predators (i.e. a Type II functional response), there is no refuge for the prey at low densities, and predators have an alternative prey source to maintain their population abundance when the first prey species is low, predation can potentially lead to extinction. Is this likely to have occurred when exotic predators were introduced to Australia?

In this thesis I examine the ecology of two recent invaders of the Australian continent, the cat and the fox, and one that colonised Australia several thousand years previously, the dingo. What do we know of the ecology of cats, foxes and dingoes that might enlighten us as to their impacts on native mammals in the spinifex grasslands?

1.10 THE STUDY ANIMALS: DINGO, FOX AND FERAL CAT

1.10.1 The dingo

The dingo evolved in Asia, from a primitive type of wolf, between six and ten thousand years ago (Corbett 1995a). Dingoes were subsequently transported to The Philippines, Indonesia, Micronesia, Polynesia and Australia by Asian seafarers, who presumably carried them as a source of fresh meat as well as for their assistance in hunting game (Corbett 1995a). It is unknown what the ancestral dingo evolved to feed on in its native environment, because the species has had such a long association with humans. Today, the major food of Asian dingoes is food scraps supplied by people or scavenged, but in rural areas of Thailand and northern Sulawesi, dingoes have been recorded hunting insects, rats and lizards along roadsides, rice paddies and in forests (Corbett 1995a).

Dingoes arrived in Australia approximately 3,500 years ago and rapidly colonised the entire mainland of Australia (Corbett 1995a). They have since been excluded from some agricultural areas of south-eastern Australia to protect livestock (Corbett 1995a). Throughout Australia, dingoes are primarily predators of medium- to large-sized mammals (Corbett 1995a) including macropods, rabbits and wombats (*Vombatus ursinus*), but they also eat a wide range of other prey ranging from invertebrates to water birds and cattle carrion (Newsome *et al.* 1983, Corbett and Newsome 1987, Marsack and Campbell 1990, Thomson 1992a, Corbett 1995b).

Dingoes tend to live in packs of between 3 and 10 individuals, with strong male and female hierarchies. Social dominance is maintained by aggression. Packs occupy territories, but the size of the territory varies with prey resources. Average home-range size ranges from less than 20 km^2 in eastern Australia to 77 km^2 in north-western Australia (Thomson 1992b, Corbett 1995a).

Female dingoes are monoestrous. Usually only a single litter of pups is produced by each pack per year (Thomson 1992c). Litter size varies from 1-10 with an average of five. Pups become independent when aged between six and twelve months; females commence breeding at two years of age. Humans are the only significant predator of dingoes, with many killed to protect livestock. They are considered a prized food source in north-east Thailand and were also eaten by Aboriginal People. Wedge-tailed eagles (*Aquila audax*) may take pups. Disease (Canine distemper: *Paramyxovirus*), hookworms (*Unicinaria stenocephala* and *Ancylostoma caninum*) and heartworm (*Dirofilaria immitis*) periodically cause significant mortality amongst dingo populations in northern Australia and south-east Queensland (Fleming *et al*. 2001).

1.10.2 The Fox

The evolutionary origins of the red fox are uncertain but it is thought to have evolved in North America (Saunders *et al.* 1995) and subsequently spread through much of the northern hemisphere. Staple prey for foxes in their native environment are either rodents (especially voles) or lagomorphs (Jarman 1986), and fox densities tend to fluctuate in accordance with the cyclic periodicity of their staple prey (but see Erlinge *et al*. 1984). The fox has few natural predators although cubs can be taken by birds of prey and dogs (Saunders *et al*. 1995).

Foxes may cohabit in pairs or larger groups consisting of a single male and several closely related vixens (Saunders *et al*. 1995). Pairs or groups usually occupy exclusive territories several square kilometers in area (Jarman 1986). Typical densities are less than two per square kilometer, but may be as high as eight per square kilometer (Jarman 1986). Not all vixens in a group produce cubs, but the proportion of barren females in a population is probably related to food availability (Englund 1970). Foxes are monoestrous, mating in winter and giving birth in spring (Coman 1995). Mean litter size is 4-6 but between 20 and 80 % of cubs die in their first year (Jarman 1986). Foxes become sexually mature at 10 months.

Australia is the only continent where foxes have been successfully introduced (Jarman 1986). They were released in Victoria for hunting in 1865 (Rolls 1969), and rapidly colonised areas where rabbits were present and dingoes absent, spreading more slowly through regions with high densities of dingoes (Jarman 1986). They crossed the Murray River into New South Wales in 1893 and had reached southern Queensland by 1910 (Jarman 1986). Foxes are believed to have entered South Australia in 1880 and were first recorded in the north-western corner in 1932 (Finlayson 1961), presumably crossing the border into the Northern Territory soon after this. In Western Australia, foxes have been present since 1915, and were first recorded around Broome in 1934 (Jarman 1986). After entering a district fox populations erupted, peaked within 5-15 years, then declined to lower levels (Jarman and Johnson 1977).

Rabbits constitute the staple prey of the fox in most areas of Australia and scavenged carrion also often dominates (Jarman 1986). Small mammals become important prey when they are abundant, and birds, invertebrates and fruits are supplementary prey (Jarman 1986). Foxes in Australia appear to suffer from few serious diseases, although there are occasional outbreaks of mange and distemper. Their only significant predators are dingoes and humans (Saunders *et al*. 1995).

1.10.3 The Cat

The domestic cat is believed to be derived from the African or Arabian wildcat (*Felis sylvestris lybica*) (Turner and Bateson 1990). Circumstantial evidence suggests that domestication began about 8000 years ago in the Eastern Mediterranean (Dickman 1996). Cats were fully domesticated and living in close association with humans in Egypt 3600 years ago. They spread from Egypt to Europe during the establishment of the Roman Empire and in the past 2000 years have subsequently been transported to most parts of the world (Dickman 1996).

Domestic cats were brought to Australia by the first European settlers in the late Eighteenth century (Dickman 1996), and feral populations had become established in eastern Australia by 1820 (Abbott 2002). They are now common and widespread throughout the entire continent, occurring in every habitat type (Wilson *et al*. 1992). It has been speculated that cats may have initially been introduced to the north-west coast of Australia by Macassan fisherman from Indonesia as early as the 15th Century (Baldwin 1980) or from Dutch Shipwrecks in the seventeenth century (Burbidge *et al*. 1988). However, a comprehensive review of historical sources found no evidence that cats were present in Australia prior to European settlement (Abbott 2002). It is now believed that cats colonised Australia from multiple coastal introductions during the period 1824-1890 (Abbott 2002). There are no records of their presence in unsettled areas until 1883 when one was sighted in south-eastern Northern Territory, but virtually the entire continent had been colonised by cats by 1890 (Abbott 2002).

Throughout the world, the diets of feral cats (*Felis catus*) are dominated by mammalian prey, with a mean prey size of 41.2 g (Pearre and Maass 1998). Birds are of secondary importance but cats are versatile predators and consume a broad range of prey (Fitzgerald and Turner 2000). In most areas of Australia either rabbits (*Orcytolagus* *cuniculus*) or other small mammals are the most frequently eaten prey items (Coman and Brunner 1972, Jones and Coman 1981, Catling 1988, Dickman 1996, Paltridge *et al*. 1997, Molsher *et al*. 1999, Risbey *et al*. 1999).

Feral cats are essentially solitary hunters, but are extremely variable in their tolerance of conspecifics. In some situations (usually where resources are in short supply) cats live alone and actively defend their territories from intruders (Langham and Porter 1991). However, where resources are plentiful, cats may live communally; an extreme example is an extraordinarily high density of up to 2,350 cats/km^2 coexisting in a Japanese fishing village (Izawa *et al*. 1982). Most feral cats are sedentary, occupying relatively stable home-ranges which vary from less than 20 ha in Scotland to greater than 2000 ha in central Australia (Edwards *et al*. 2001). However, cats have been recorded dispersing distances up to 200 km during periods of food shortage (Newsome 1995).

Female cats are polyoestrous and may raise up to three litters per year. However, usually only two litters are produced (Jones and Coman 1982). A litter may contain as many as eight kittens, but mean litter size is four kittens (Jones and Coman 1982). Kittens are weaned at about 2 months of age, and reach sexual maturity between 10 and 12 months (Martin and Bateson 1988).

The dingo is the most significant predator of the cat, but they have also been recorded in the diets of the fox, lace monitor lizard (*Varanus varius*) and wedge-tailed eagle (Brooker and Ridpath 1980, Weavers 1989, Brunner *et al*. 1991). Cats are also hunted for food by Aboriginal people (Rose 1995). Cats do not seem to be significantly limited by diseases or parasites in Australia; screening has revealed widespread immunity amongst Australian cats to the viral disease *Feline panleucopenia* (Moodie 1995), which caused significant mortality when introduced to Marion Island (van Rensburg *et. al.* 1987).

1.11 PREDATOR-PREY INTERACTIONS IN THE SPINIFEX GRASSLANDS OF CENTRAL AUSTRALIA

Despite the potential importance of predation in the decline of arid zone mammals, we have little information on predator-prey interactions in the Australian deserts. The dingo is the best studied of the three eutherian predators and we have a good understanding of its ecology in pastoral areas of central Australia (Corbett and

Newsome 1987, Corbett 1995a). The hypothesis of 'alternation of predation' describes how dingoes feed on sequentially larger prey as seasonal conditions become increasingly arid. In flush times dingoes feed on smaller prey (rabbits and rodents) which are easily caught by individuals, but as drought progresses, dingoes work in groups to bring down kangaroos and calves which are forced to concentrate their activity around water points. Severe droughts result in increased availability of cattle carrion. Introduced water points and cattle carcasses thus buffer dingo populations through droughts, allowing them to maintain a higher predation pressure on native animals than would have naturally occurred. The only information on dingo diet in the spinifex grasslands comes from a site where rabbits occurred, and were the staple prey for dingoes (Lundie Jenkins *et al*. 1993). Unless prey are particularly abundant, dingoes are thought to require drinking water (Green 1973) and thus for much of the time they are probably distributed quite sparsely through the desert areas.

There have been no specific studies on foxes in the Northern Territory and the only information available on the diet of foxes is restricted to the gut contents of 30 animals (Strong and Low 1983) and analysis of 30 scats (1995a), all from areas with rabbits. There is a similar dearth of information on foxes in the spinifex country of Western Australia. The colonisation of this area by foxes has not been documented (Jarman 1986) but it has been suggested that the distribution of foxes in the Northern Territory is linked to rabbit populations (Low 1984). After comprehensive fauna surveys of the Tanami and Great Sandy Deserts between 1977 and 1983, it was concluded that foxes were virtually absent from these regions (Gibson 1986, McKenzie and Youngson 1983). This has led authors to speculate that many of the declines and extinctions occurred prior to the invasion of foxes or in areas where foxes have never occurred (Burbidge and McKenzie 1989).

Cats are known to be distributed throughout the Australian deserts and are considered capable of surviving independently of fresh water (Johnson 1991), but factors affecting their abundance are unknown. A previous study of cat diet found small mammals to be their staple prey in desert areas where rabbits did not occur (Paltridge *et al.* 1997). Although there is evidence that predation by cats has thwarted reintroduction attempts of several medium-sized mammals including the mala (*Lagorchestes hirsutus*), golden bandicoot (*Isodon auratus*) and burrowing bettong (*Bettongia leseur*; Gibson *et al.* 1994, Christensen and Burrows 1994), the fact that cats coexisted with native species for at least 50 years before the declines occurred has discouraged the view that cats are a primary agent of extinctions (Burbidge and McKenzie 1989).

If predation by cats and foxes was a primary agent in the decline of medium-sized mammal fauna in central Australia (*i.e* capable of causing the declines in the absence of habitat change through spread of herbivores and changed burning patterns) we can make a number of predictions about predators in the spinifex grasslands, as follows.

1. Cats and foxes will eat medium-sized mammals when they are available, but be able to survive on alternative prey when mammals are scarce.

2. Populations of cats and foxes will be buffered against the declines of mammalian prey during droughts, or be able to recover more quickly than medium-sized mammals after droughts.

3. Medium-sized mammals will be more vulnerable to predation by cats and foxes than by dingoes and other native predators (due to differences in feeding behaviour, numerical responses to fluctuating prey densities and habitat usage by the predators).

4. There will be a correlation between the timings of the extinctions and the colonisation (or sudden increase) of cats and foxes.

Although the extinction debate is too late for many species, remnant populations of several species of medium-sized mammals persist in the central Australian deserts and serve to benefit from a better understanding of threatening processes. A variety of other mammalian species that have disappeared from the central Australian deserts have been maintained in captive colonies or on offshore islands and are available for reintroduction to their former habitats if threats can be identified and countered. These include the mala, golden bandicoot, burrowing bettong, brush-tailed bettong (*Bettongia penicillata*), western quoll (*Dasyurus geoffroii*) and greater stick-nest rat (*Leporillus conditor*). Understanding the relative importance of fire, introduced herbivores and exotic predators for mammal conservation is important for developing and prioritizing hypotheses that can be tested with manipulative field experiments.

The bilby (*Macrotis lagotis*) is one example of a species that suffered a massive decline in distribution during the same period that many other mammals disappeared, but persists in isolated colonies in the northern parts of its former distribution. At the time of European settlement, the bilby was common and widespread throughout 70 % of the Australian mainland (Southgate 1990a). It had apparently disappeared from Victoria by 1866 (Southgate 1990b), and was last recorded in New South Wales in 1912 (Dickman *et al*. 1993). By the late 1950s, it had virtually disappeared from South Australia (Southgate 1990b). The bilby is now patchily distributed across less than one fifth of its former range (Southgate 1990a). Historically foxes were implicated in the demise of the bilby (Wood Jones 1925, Finlayson 1961) and it appears that the areas where remnant populations of bilbies still occur (south-west Queensland, Tanami, Gibson and Great Sandy Deserts) are outside the normal range of the fox (Strahan 1995). However, the situation is complex because the distribution of foxes generally corresponds to that of rabbits, which may be destructive of bilby habitat. An altered fire regime is also believed to be a threatening process for the bilby, which includes the seed of several fire-induced plants as major components of its diet (Southgate 1990c). The bilby is currently classified as Vulnerable to extinction on a national scale (Maxwell *et al*. 1996).

Other medium-sized mammals that occur in the spinifex grasslands of central Australia include the echidna (*Tachyglossus aculeatus*), marsupial mole (*Notorcytes typhlops*), mulgara (*Dasycercus cristicauda*) and spectacled hare-wallaby (*Lagorchestes conspicillatus*; Gibson 1986). Of the original suite of medium-sized mammals to have lived in the deserts, only the echidna with its protective armor of spines remains widespread and common (Gibson 1986). Marsupial moles have been classified as endangered (Maxwell *et al*. 1996) due to a suspected reduction in area of occupancy and quality of habitat, but as there are currently no reliable methods for monitoring the distribution and abundance of marsupial moles, it is unknown whether the species has actually declined. The mulgara is classified as Vulnerable, having suffered a significant contraction in the southern and eastern parts of its range. Although it still has a large area of occupancy in the sandy deserts of Western Australia and the Northern Territory, populations are fragmented, surviving only in patches (Burbidge *et al*. 1988, Pearson 1991, Baker 1996). Predation by cats and foxes appears to be having a significant impact at the eastern edge of its distribution (Dickman 1996), but lack of fire management is thought to be the primary cause of decline in the spinifex grasslands (Masters 1997). The spectacled hare-wallaby remains common and widespread across northern Australia, but the southern limits of its range in the Northern Territory have contracted northwards by over 200 km during the last century, and the declines have been even greater in Western Australia (Ingleby 1991). The distribution of the spectacled hare-wallaby is now confined to areas free of foxes and rabbits (Ingleby 1991).

Until the impacts of predation on native animals in the remote spinifex grasslands can be quantified and further information is collected on the predator-prey and predator-predator interactions of this system, land managers will be loathe to fund expensive predator control programs, even if appropriate methods of control were available. Understanding the dietary patterns and population dynamics of the predators in relation to seasonal fluctuations in prey abundance is the first step towards understanding the potential for predators to extinguish localised populations of native species.

We also need information on what influences predator numbers so that we can predict when and where they might be a problem and target control programs accordingly. Knowledge of habitat preferences, hunting strategies and an understanding of when predator populations are likely to be most vulnerable will help managers to devise more effective and efficient control programs. Information on the extent of competition and predation between predator species will determine whether selective control of one species may affect numbers of the other predators.

1.12 AIMS AND SCOPE OF THIS STUDY

The overall objective of this study was examine the ecology of introduced predators in the spinifex grasslands of central Australia, in order to evaluate whether cats and foxes could potentially extinguish populations of medium-sized mammals. This information is critical to the conservation of threatened species that still occur in the arid zone, such as the bilby.

The predator-prey system attributes listed in Table 1.1 provide a framework of investigation for the thesis. Thus, information about prey population dynamics, predator diets and feeding behaviour, numerical responses of predator populations and habitat use (with respect to prey refugia) is compared between the two predators that recently colonised Australia (cats and foxes) and the dingo, which colonised Australia several thousand years earlier. Field data collected during this study will be synthesised with information from the literature pertaining to the attributes listed in Table 1.1.

The thesis has been written as a series of papers intended as stand-alone publications (Chapters 2-4) preceded by this General Introduction (Chapter 1) and followed by a General Discussion (Chapter 5). In Chapter 2, I set the context for the study by describing the study areas and seasonal conditions in which the study was conducted and presenting information on fluctuations in the abundance of potential prey for cats, foxes and dingoes. I also examine the importance of palaeodrainage habitat as a refuge for a range of species during drought. In Chapter 3, I assess the diets of cats, foxes and dingoes in relation to fluctuations in prey densities. I aimed to determine staple prey species in two areas of the Tanami Desert where rabbits do not occur and other mammalian prey are usually scarce. I was particularly interested in whether alternative prey would be available to sustain predators during droughts, and assist their recovery following droughts. In Chapter 4, I compare the relative abundances of cats, foxes and dingoes in two habitat types and two study areas over a two year period. I examine numerical responses of predator populations to fluctuating prey populations to determine whether these predator species can persist in the spinifex grasslands during droughts. I also compare use of the two major habitat types in the study area by the three predator species to determine whether prey are likely to have any refuge from predation. In this part of the study, I also investigated the premise that the medium-sized mammalian extinctions occurred in the northern deserts prior to the arrival of foxes to the area. Finally, in Chapter 5, I consider the role of predation in species declines in the Australian arid zone in light of information on predator-prey interactions collected during this study and discuss whether predation was a primary agent of decline or a secondary process finishing off fragmented populations that had already been decimated by other processes.

1.13 LIMITATIONS OF THE STUDY

The study was constrained by many factors, not least the remoteness and inaccessibility of the study sites. Because I wanted the sites to be isolated from the confounding factors of rabbit populations, pastoralism, artificial water points and other disturbances associated with people and also be situated in areas with extant bilby populations, it was necessary to work in very remote areas. The northern study area was approximately

700 km north-west of Alice Springs and 100 km from the nearest occupied habitation (an Aboriginal outstation) while the southern study area was approximately 450 km west of Alice Springs and about 80 km from the nearest occupied habitation (an Aboriginal community). The isolation of the study sites restricted the number of field trips that could be completed and the amount of food, water and fuel that could be carried limited the length of field trips to a maximum of 12 days.

Field work spanning less than 3 years is typical of PhD studies. It is of course too short to encompass the variation that can occur in Australia's deserts. The first two years of this study were at the end of a severe drought. Although considerable rain fell in the third year, it was by no means an exceptionally "flush" year, so important to the population dynamics of desert ecosystems. The two study areas obviously encompass only a tiny fraction of the spinifex grassland habitat that occurs in central Australia and I cannot extrapolate my results beyond my study areas to all of "spinifex grasslands," except to produce hypothetical models.

The predator species under investigation are notoriously difficult to study, being nocturnal and very cryptic, and in the spinifex grasslands they are generally in very low numbers making it difficult to collect sufficient data for statistical analysis. Also, there are currently no reliable methods for measuring the abundance of these predators which presented a major challenge for my study.

Because the study sites were situated on Aboriginal Freehold land (bilbies only occur on Aboriginal land in the Northern Territory), the project was very much constrained by restrictions imposed by the Central Land Council, particularly with regard to access to sites. Cultural sensitivities also prevented certain activities occurring. For example, poison baiting was not permitted, even as an experiment to manipulate predator densities. Traditional Owners consider cats to be a favoured food source and were therefore suspicious of poisons. However, the cooperation of Aboriginal people contributed enormously to the study and far outweighed any disadvantages of working on Aboriginal land.

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CHAPTER 2

THE EFFECTS OF HABITAT TYPE AND SEASONAL CONDITIONS ON FAUNA IN TWO AREAS OF THE TANAMI DESERT[1]

Preamble to Chapter 2

This chapter sets the context for the study, by describing the study areas and seasonal conditions in which the project was conducted. The population dynamics of a variety of potential prey species for cats, foxes and dingoes were monitored over a two year period, under fluctuating seasonal conditions.

I aimed to determine whether alternative prey species would have been available to sustain predator populations during droughts or facilitate their recovery after droughts prior to the recovery of the medium-sized mammal fauna that were dependent on green forage.

I also aimed to investigate the importance of palaeodrainage habitat in providing refuge for native prey species during dry periods, and to determine whether the increased moisture and nutrient levels of the palaeodrainage habitat resulted in a greater abundance and richness of potential prey species overall. If this were the case, then one would expect predators to target this habitat, particularly during dry periods.

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2.1 INTRODUCTION

The Australian deserts are typically infertile and unproductive (Morton 1990). The aridity of these deserts is not exceptional on a worldwide scale, but the temporal variability of rainfall is comparatively high (Stafford Smith and Morton 1990). Organisms must tolerate long periods of drought between occasional spells of plentiful rainfall. Amongst the vast areas of low productivity in the deserts, more fertile patches occur. Typically, these are depressions where water and nutrients are channelled during high intensity rain events, or areas where soils are derived from parent material with inherently higher nutrient levels (Morton 1990).

The Tanami Desert is located in central western Northern Territory (Fig. 2.1). Its northern extent borders the subtropics, and there is a gradient of decreasing mean annual rainfall from north to south (Table 2.1). The latitudinal gradient in rainfall has implications for plant productivity and frequency of fire. The higher growth rates of the northern spinifex grasslands result in their burning approximately every 10 years, whereas the southern spinifex grasslands only burn approximately every 30 years (Griffin 1990). Fire is an important determinant of community structure in the arid zone because it releases scarce nutrients from perennial tissue and creates space amongst perennial plants (Griffin 1990). Although many species of reptile and some birds and mammals require mature spinifex for shelter (Masters 1993, 1996, Reid *et al.* 1993) others, such as the bilby (*Macrotis lagotis*), rely on recently burnt areas for production of key plant foods (Southgate *et al.* 1997).

The Tanami Desert comprises vast tracts of spinifex sandplain, interspersed with more fertile habitats including salt and freshwater lakes, ancient drainage systems, water-courses, and calcrete areas (Gibson 1986). Because productivity in these more fertile patches is more reliable and of greater nutritional value, it has been postulated that they may form refugia for various herbivorous and omnivorous species during drought (Morton 1990). The palaeodrainage systems are thought to be important habitats for the mulgara, *Dasycercus cristicauda,* (Gibson and Cole 1992, Baker 1996), the mala, *Lagorchestes hirsutus* (Lundie-Jenkins 1993) and the bilby (Southgate 1990), and are probably breeding areas for burrowing frogs (Cogger 1992). However, there is little information on the significance of more productive habitats for other small mammals, birds and reptiles.

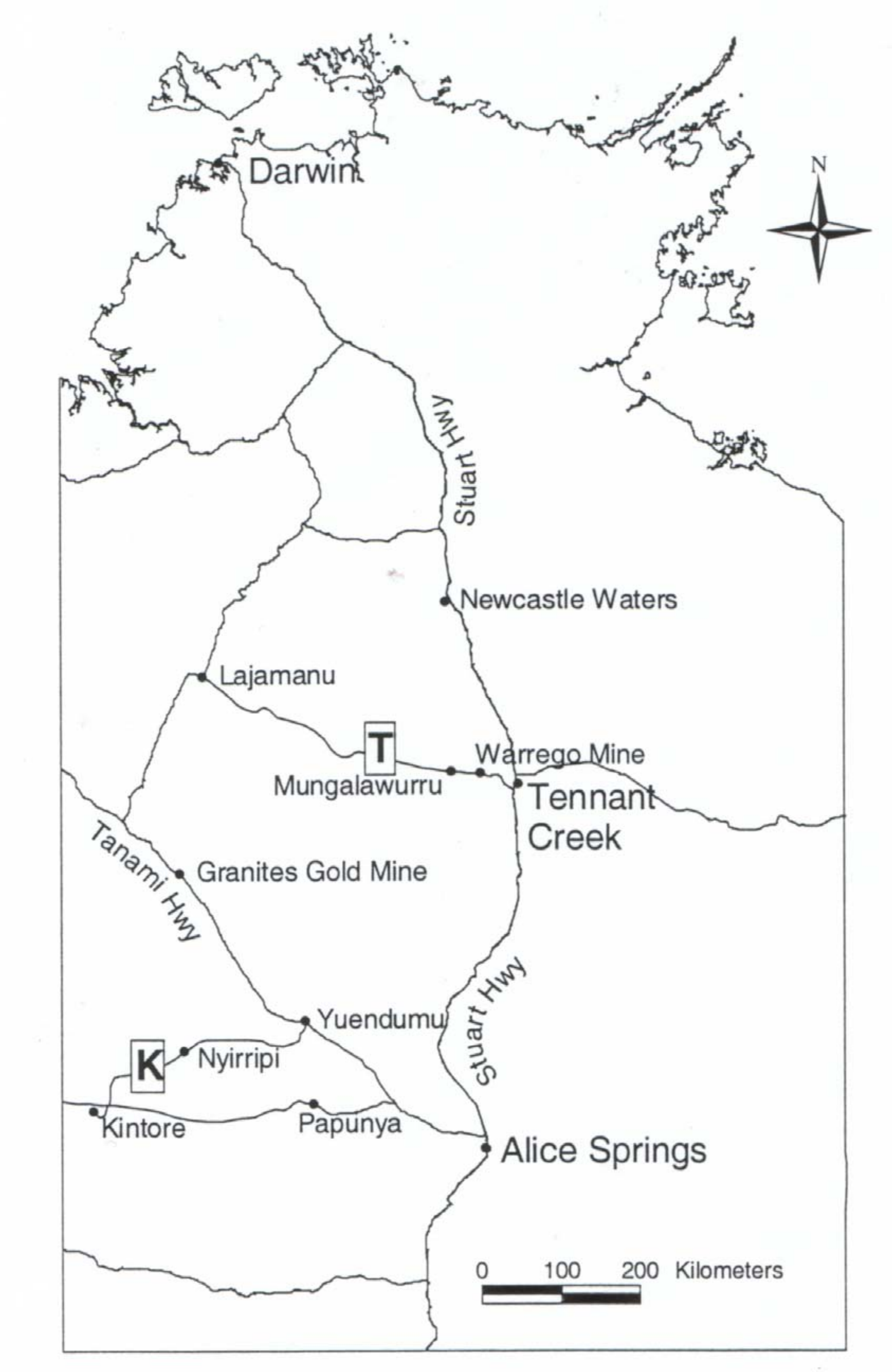

Figure 2.1 Map of the Northern Territory showing location of the two study areas: Kintore K and Tennant T .

The infertile spinifex sandplains have a high abundance of termites (Morton and James 1988), which have gut symbionts that enable them to utilise nitrogen-poor vegetation (Collins 1983). Termites are major prey for many invertebrate (Abensperg-Traun, 1994) and reptile species (Pianka 1986) in arid Australia and the high diversity of reptiles in the Australian spinifex grasslands has been attributed to the abundance and diversity of termites found in this system (Morton and James 1988). Termites may actually be disadvantaged by more nutritious vegetation (Braithwaite 1988, Collins 1983) and are probably less abundant and diverse in more fertile habitats (Stafford Smith and Morton 1990).

As part of a wider study into predator-prey interactions in the western deserts of central Australia, prey availability was monitored at four-monthly intervals over a 2-year period. In this chapter I compare faunal assemblages between palaeodrainage habitat and the surrounding sandplain, and between two study areas at latitudes approximately 400 km apart. I aim to test a number of predictions about the effect of habitat, latitude and seasonal conditions on the abundance and diversity of various taxonomic groups.

2.1.1 Effect of habitat

It was predicted that the higher nutrient and moisture levels of the palaeodrainage habitat would result in greater primary productivity in this habitat, thus supporting a greater abundance and diversity of mammals, birds and frogs than in the sandplain. However, invertebrates and reptiles, which are less dependent on plant productivity, were expected to be more abundant in the sandplain due to greater termite abundance.

2.1.2 Effect of latitude

It was expected that higher rainfall in the northern study area would result in greater productivity and therefore a higher abundance of mammals and birds than in the southern study area. More frequent recharge to soil moisture levels in the northern study area was also expected to result in higher densities of burrowing frogs. No difference in reptile abundance between latitudes was expected as I considered termite abundance would be similar in the two study areas.

Table 2.1. Climatic Gradients in the Tanami Desert

Data are shown for the two study areas as well as Newcastle Waters on the northern boundary of the Tanami Desert. Data for Tennant are based on information from Tennant Creek airport, 180 km SE of the Tennant sites, while data for the Kintore area are based on records from Newhaven Station, approximately 130 km E of the Kintore sites. The Newcastle Waters data include information from both Newcastle Waters Station and the township of Elliott, 24 km to the south. Data were provided by the Bureau of Meteorology (1999).

Please see print copy for Table 2.1

2.1.3 Effect of seasonal conditions

I predicted that significant rainfall events would cause an immediate increase in activity of frogs and invertebrates and result in a delayed increase in the abundance of birds and mammals as seed and nectar resources became available. Reptiles were expected to be affected more by temperature (because they are poikilothermic and active only at certain temperatures: Pianka 1986) than rainfall (because they can persist during droughts by becoming inactive and lowering their metabolic rates: Morton and James 1988).

2.2 METHODS

2.2.1 Study Areas

The study was conducted in two locations approximately 400 km apart (Fig. 2.1). The northern study area, ‘Tennant’ was situated in the northern Tanami Desert (19° 12′ S, 132° 40′ E), 200 km north-west of Tennant Creek. This area is classified as belonging to the Tanami Bioregion (Thackway and Cresswell 1995). The southern study area ‘Kintore’ was located approximately 450 km west-north-west of Alice Springs (22° 51′ S, 129° 57′ E), at the southern edge of the Tanami Desert. This study area is situated between Nyirripi and Kintore Aboriginal Communities (Fig. 2.1) and falls within the Great Sandy Desert Bioregion (Thackway and Cresswell 1995). The entire study region is Aboriginal Freehold land, and is sparsely populated and undeveloped.

The climate of the Tanami Desert is semi-arid, with very hot summers and mild winters but marked gradients in rainfall and temperature occur between the northern and southern extremes of the Tanami Desert (Table 2.1). Both study areas experience temperatures in excess of 40º C during the summer, but winter temperatures are generally warmer at Tennant than Kintore (Table 2.1). Mean annual rainfall is higher at Tennant, (428 mm), than Kintore (322 mm). Most rain falls during the summer months (Table 2.1), and summer rainfall is more reliable in the northern Tanami Desert than in the south, due to the monsoonal influence from tropical northern Australia.

Monthly rainfall during the study period (provided by the Bureau of Meteorology, 1999), is shown in Figure 2.2. When the study commenced, Kintore was experiencing drought conditions. Only 97 mm of rain fell in 1996, and in five of the previous six years annual rainfall totals were below-average. However, significant summer rainfall occurred in 1997, and the annual total for 1997 was 400 mm. Rainfall at Tennant was slightly below-average in 1996 (342 mm) but 1997 was a wet year (annual rainfall total = 706 mm). This was the first year of above-average rainfall since 1993.

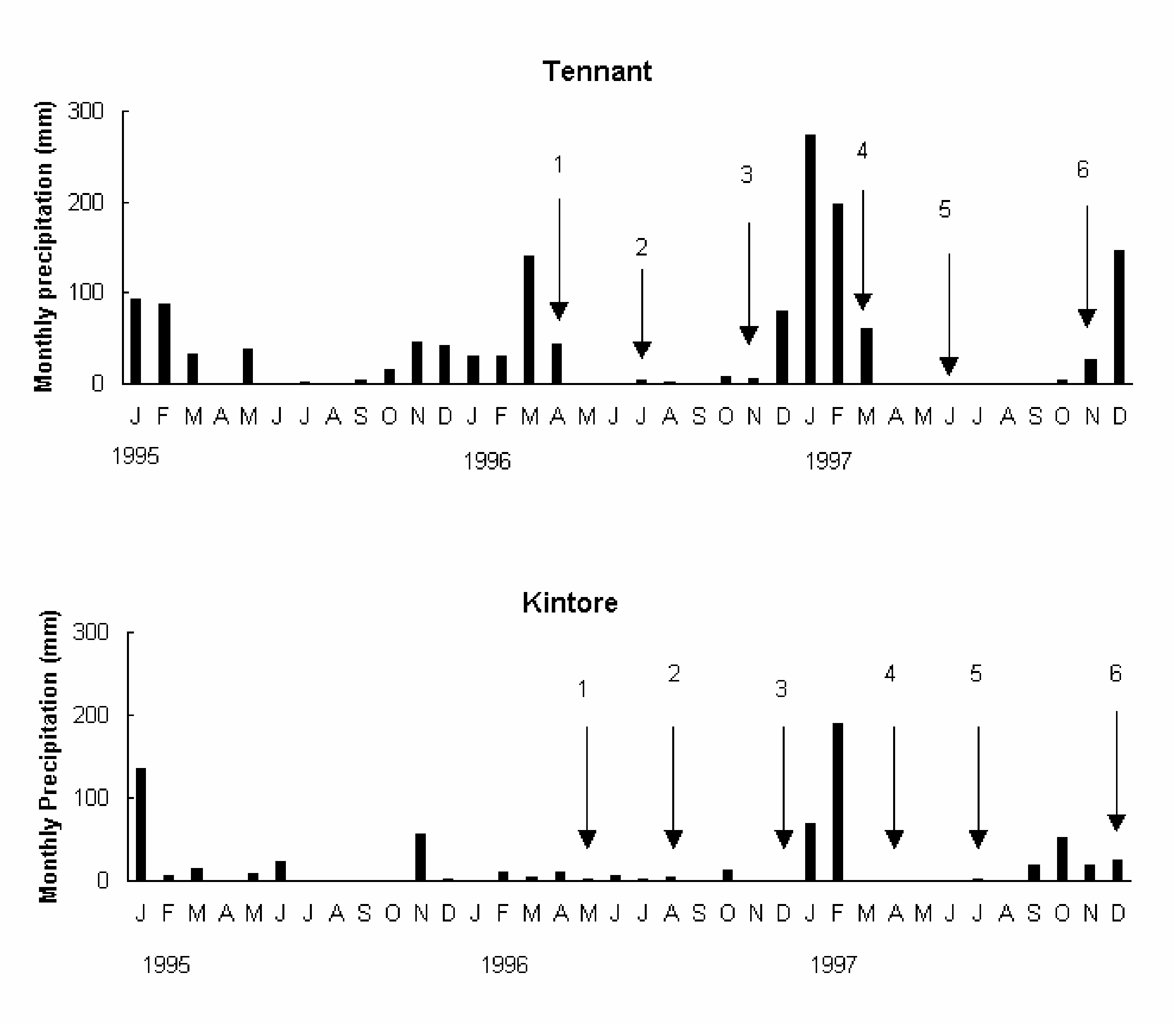

Fig. 2.2 Monthly rainfall in the two study areas, 1995-1997. Tennant data are based on rainfall data from Tennant Creek Airport. Kintore data are based on rainfall records from Newhaven Station. The arrows indicate sampling periods.

Both study areas comprise predominantly sandplain habitat, dominated by a mixture of spinifex species (*Triodia pungens and T. schinzii* at Tennant and *T. pungens* and *T. basedowi* at Kintore) with an overstory of scattered shrubs including species of *Grevillea, Eucalyptus* and *Acacia*. Low parallel sand dunes, approximately 1 km apart, dissect the sandplain at Kintore, but are infrequent at Tennant. Palaeodrainage channels, characterised by the presence of *Melaleuca* spp., also occur in both areas. The Tennant study area was situated around the Green Swamp Well palaeodrainage channel, which extends for over 100 km. The channel is of varying width, but in the vicinity of the study sites it was approximately 1 km wide. The palaeodrainage channel in the Kintore study area was approximately 80 km long and 2 km wide where it traversed the study sites.

Within each study area, I established three randomly chosen sites to conduct fauna surveys. These sites were at least 20 km apart. Nested within each site was a pair of study plots, approximately 4 km apart, one plot located in sandplain habitat and the other in palaeodrainage habitat (Fig. 2.3). All study plots were situated in mature (unburnt for >5 years) spinifex communities and remained unburnt throughout the study.

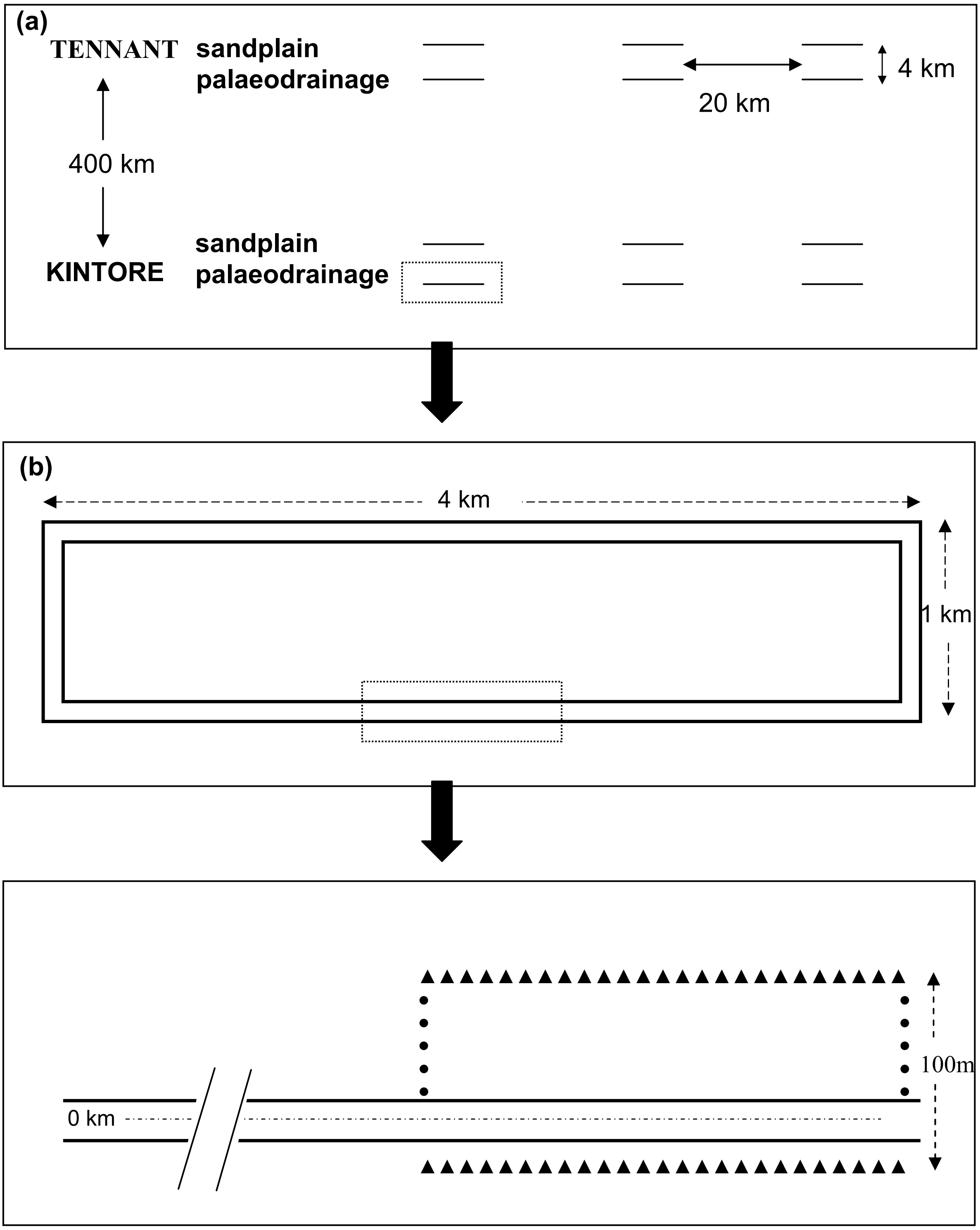

Fig. 2.3. The experimental design: (a) 3 plots per habitat in each study area, (b) a study plot showing the predator transect and (c) positioning of the pitfall traps ● Elliott traps ▲ and bird transect

2.2.2 Data collection

The broad range of fauna groups monitored required the use of a variety of survey techniques including trapping, counting individuals sighted along permanent transects and track counts along permanent transects. Monitoring occurred in both sandplain and palaeodrainage habitats at all three sites in each study area. Field surveys were conducted approximately every four months from April 1996 to November 1997 at Tennant, and May 1996 to December 1997 at Kintore. Monitoring was conducted for three consecutive days at each site. Only one site was surveyed during each three-day period, thus 10-day field trips were required to sample an area.

Small mammal and reptile abundances were monitored using pitfall traps and Elliott traps. Each study plot contained two lines of five pitfall traps and two lines of 25 Elliott traps (Fig. 2.3). Pit lines were 500 m apart, with the Elliott lines set perpendicular to the pit lines and running between them. Pits (25 L white plastic buckets) were situated 7 m apart and connected by a flywire drift fence standing 25 cm and partially buried into the sand. The fences were left standing for the duration of the study. Between surveys, plastic lids were fitted to the buckets. When the buckets were opened, the lids were propped up above the buckets, at fence height, providing shade within the pits. Extra shelter was provided for captured animals by small clumps of vegetation placed inside the buckets.

Elliott lines were set 100 m apart (Fig. 2.3). Traps were positioned at 20 m intervals and baited with balls of peanut butter and oats. Traps were opened in the late afternoon and closed early the next morning. The Elliott traps were removed from the sites between surveys.

The pit and Elliott traps were open for 3 days per survey, and cleared at sunrise each day. Basic measurements (mass, snout-vent length) were recorded from captured animals which were then temporarily marked with a marker pen and immediately released within 20 m of point of capture.

Invertebrates caught in pitfall traps were collected daily and stored in 70 % ethanol. This sampling method was a crude measure of invertebrate prey availability. It is unlikely to have adequately sampled flying or burrowing invertebrate species, and it is acknowledged that some individuals would have been lost to predation within the pits.

All invertebrates from one line of 5 traps were combined to comprise a single “sample”. Dry masses were obtained by drying samples at 70° C for 48 h in plastic petri dishes, (following the technique of Masters 1997) and then weighing the contents of the petri dishes on an electronic balance. No attempt was made to sort the invertebrates by taxonomic group.

The relative abundance of birds was assessed along 1 km walked transects (one transect per plot). Bird counts were conducted in the half-hour before sunset and each transect was surveyed once per field trip. All birds seen and heard within approximately 50 m either side of the transect were counted and identified to species where possible with the aid of 10 x 50 binoculars. As counts were usually too low to determine actual densities of birds (Buckland *et al*. 1993), only counts-per-km data are presented here. In addition to the transect counts, lists of all bird species and breeding behaviour observed at the study plots were compiled for each survey, and notes made of plants flowering or seeding.

The activity/abundance of macropods (red kangaroos, *Macropus rufus* and spectacled hare-wallabies, *Lagorchestes conspicillatus*) goannas (predominantly sand goannas, *Varanus gouldii*) bilbies (*Macrotis lagotis*) and bustards (*Ardeotis australis*) were monitored by track counts along 10 km “roads” cleared of vegetation (one transect per study plot). Roads were divided into 500-m cells and the proportion of cells with tracks present was recorded for 3 consecutive days during each monitoring survey. A heavy implement (e.g. chain attached to a piece of heavy steel 1.5 m wide) was dragged behind a four-wheel-drive vehicle prior to the first day of tracking at each site to clear animal tracks and vegetation from the transect. Inspection of the transects on subsequent days was done from an all-terrain-vehicle travelling at a constant speed of 10 km/h, and dragging a lighter implement (e.g. light steel bar with chain) to eliminate accumulated tracks and prepare a fresh tracking surface.

2.2.3 Data Analysis

For the purposes of data analysis, the fauna were classified into nine major groups: invertebrates, frogs, small mammals, small reptiles, birds, varanid lizards, bustards, bilbies and macropods. The effects of latitude (i.e study area), habitat and time (i.e. survey) on the relative abundance of each prey group were determined by 3 factor analysis of variance, where time was a repeated measures factor, latitude and habitat were fixed factors and the three sites in each study area were replicates. Where individual counts were collected for three nights (e.g. small mammals and reptiles), the data were pooled to give a total count for each plot, for each survey. Animals that were recaptured during a survey were counted only once. The data that were obtained from the tracking transects (varanids, bustards, bilbies and macropods) were normalised by the arcsine transformation, as proportion data form a binomial distribution (Zar 1996).

Species richness values (number of species present) for each of the major classes (reptiles, birds, mammals) were also calculated at each site during each survey. Species richness was compared between study areas, habitats and surveys using the repeated measures ANOVA described above.

2. 3 RESULTS

The results of the analysis of variance of the effects of latitude, habitat and time on the abundance and species richness of the fauna at the two study sites are shown in Table 2.2. A complete list of vertebrate species recorded during the study is presented in Table 2.3.

2.3.1 Terrestrial invertebrates

There was little effect of habitat on the biomass of invertebrates captured in pitfall traps (Fig. 2.4a). However, biomass fluctuated greatly between surveys ($F_{5,40} = 8.3$, $p < 0.001$). Invertebrate biomass was always low in winter, but varied in summer and autumn (Fig. 2.5a) probably depending on the local climatic conditions (temperature, humidity, rainfall) at the time of survey. Latitude was not a significant main effect but the time-latitude interaction was significant: in the summer surveys Kintore had greatest invertebrate biomass but in the autumn surveys Tennant had greater biomass ($F_{5,40} = 7.2$, $p < 0.001$).

Table 2.2. Results of the Analysis of Variance on the effects of latitude and habitat (fixed factors) and time (repeated measures fixed factor) on the abundance and species richness of fauna in two areas of the Tanami Desert.

The *P* values of significant results are highlighted in bold and the latitude or habitat (T=Tennant, K=Kintore, S=sandplain) with significantly higher abundances are shown in parentheses.

	Latitude		**Habitat**		**Time**		**Latitude*habitat**		**Latitude*time**		**Habitat*time**		**Latitude*habitat*time**	
	(df=1,8)		(df=1,8)		(df=5,40)		(df=1,8)		(df=5,40)		(df=5,40)		(df=5,40)	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Abundance														
Invertebrates	2.831	0.095	1.123	0.291	8.302	**0.000**	3.406	0.067	7.199	**0.000**	0.599	0.701	0.578	0.716
Frogs	5.656	**0.045 (T)**	0.917	0.366	2.004	0.098	1.023	0.341	2.256	0.067	2.221	0.072	2.186	0.075
Small reptiles	2.347	0.164	11.421	**0.009 (S)**	15.076	**0.000**	19.500	**0.002**	7.426	**0.000**	2.193	0.074	2.562	**0.042**
Goannas	0.035	0.856	0.090	0.772	15.238	**0.000**	3.529	0.097	8.627	**0.000**	0.589	0.708	1.879	0.119
Birds	0.913	0.393	0.030	0.870	5.634	**0.002**	0.176	0.696	4.386	**0.007**	2.582	0.059	1.378	0.274
Bustards	13.265	**0.006 (T)**	2.440	0.157	0.644	0.667	0.297	0.600	0.898	0.491	0.974	0.445	0.713	0.617
Small mammals	13.550	**0.006 (K)**	2.214	0.175	1.230	0.313	0.153	0.705	0.993	0.434	0.493	0.779	0.677	0.643
Macropods	18.367	**0.002 (T)**	3.559	0.096	1.300	0.283	0.448	0.522	1.624	0.176	0.735	0.602	1.684	0.161
Bilbies	6.35	**0.015 (T)**	3.13	0.082	0.527	0.754	3.137	0.082	0.527	0.754	0.213	0.955	0.213	0.955
Species richness														
Reptiles	0.001	0.971	1.389	0.283	7.395	**0.000**	4.713	0.073	2.958	**0.027**	0.122	0.986	0.741	0.599
Birds	3.087	0.139	0.082	0.786	6.300	**0.001**	1.760	0.242	1.338	0.281	1.144	0.364	0.889	0.503
Mammals	11.605	**0.009 (K)**	1.289	0.289	0.553	0.735	3.184	0.112	0.931	0.471	1.479	0.218	2.363	0.057

2.3.2 Amphibians

Frogs were trapped only during those surveys that coincided with rain events. *Neobatrachus aquilonius* was captured on only one of the Kintore surveys. *Notaden nichollsi* and *Uperoleia micromeles* occurred in both habitats in both study areas. Frogs were captured more frequently at Tennant than Kintore ($F_{1,8}$ = 5.6, $p < 0.05$) and at Tennant tended to be more prevalent in the palaeodrainage habitat (Fig. 2.4b).

Large aggregations of *N. nichollsi* and *U. micromeles* were found in communal burrows, approximately 1 m below the surface, by Aboriginal people at the Tennant study sites. The burrows were situated at the ecotone between the palaeodrainage and sandplain habitats. Frogs emerged from burrows within several hours of rainfall events exceeding approximately 8 mm.

2.3.3 Small Reptiles

Overall more small reptiles were captured in the sandplain habitat than the palaeodrainage habitat ($F_{1,8}$ = 11.4, $p < 0.05$). However, the habitat-latitude interaction term in the analysis of small reptiles was also significant ($F_{1,8}$ = 19.5, $p < 0.005$), because capture rates at Tennant were significantly greater in the sandplain than in the palaeodrainage habitat, but there was little difference in capture rates between habitats at Kintore (Fig. 2.4c).

The number of small reptiles captured during trapping sessions fluctuated greatly over time ($F_{5,40}$ = 15.1, $p < 0.001$). At Kintore small reptile abundance was greatest in summer and least in winter (Fig. 2.5c). There was an increasing trend in the abundance of small reptiles at Tennant with a large peak in autumn 1997.

Ten more species of small reptiles were found at Kintore (44 spp.) than Tennant (34 spp.; Table 2.3), but during most surveys species richness was very comparable between the two study areas. Capture rates and species richness were higher at Kintore than Tennant during the summer surveys but Tennant had the higher capture rates and species richness during the autumn and winter surveys. This resulted in significant latitude-time interactions in the analyses of both capture rate and species richness data. A greater percentage of small reptile species were active during winter at Tennant (72 %) than Kintore (48 %).

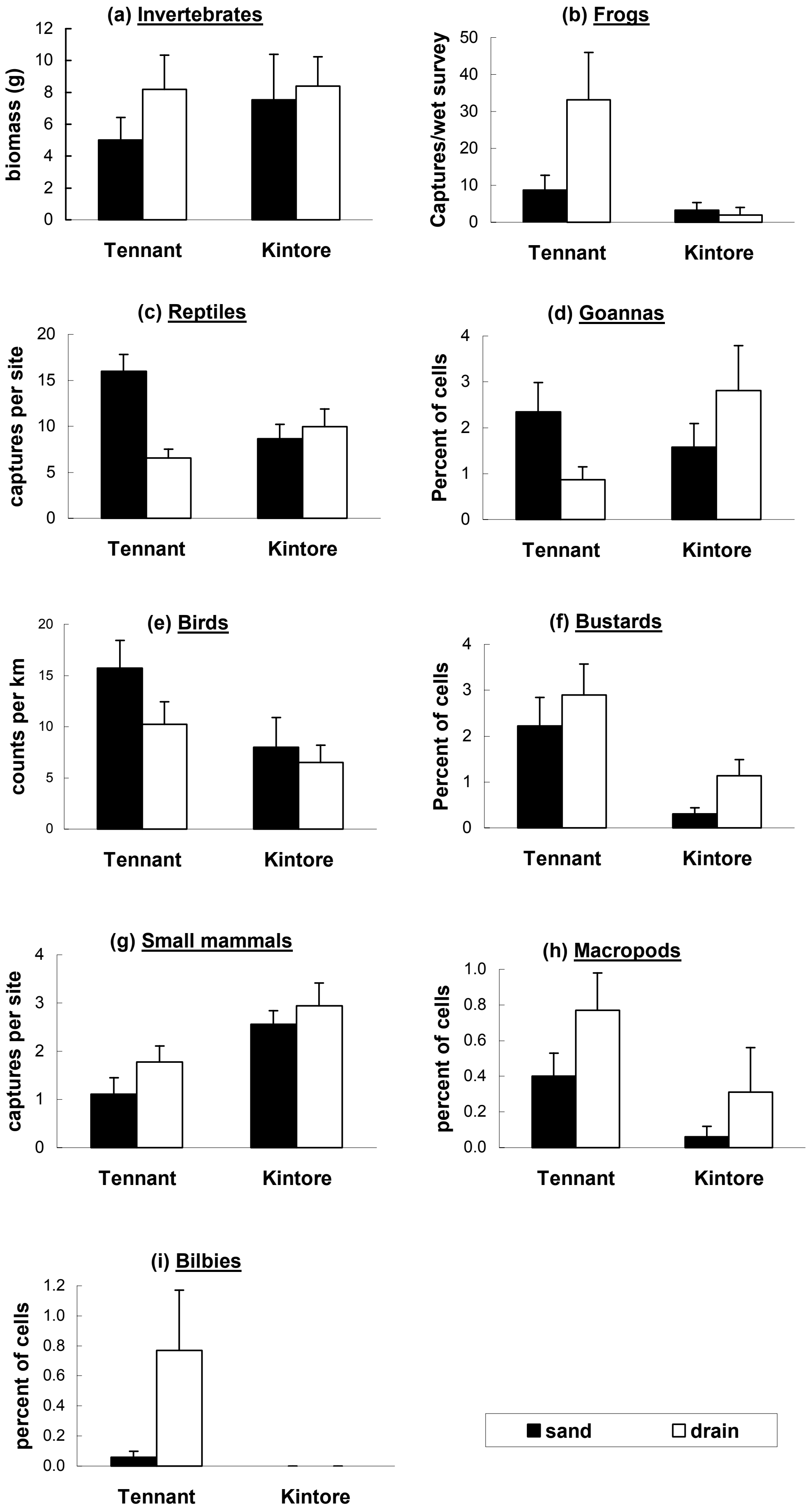

Fig. 2.4. The relative abundance of fauna (means ± standard error) in two habitats and two areas of the Tanami Desert, pooled over 6 surveys.

Ctenotus calurus was captured only in the second year of monitoring, and was one of the few reptile species to respond to the better seasonal conditions at Kintore in 1997. Most species of skink were equally abundant in the first year as the second, however, geckoes and agamids tended to be more abundant in 1997.

2.3.4 Varanid lizards

Time was the only significant main effect ($F_{5,40} = 15.2$, $p < 0.001$) in the analysis of goanna track data, with post-hoc tests showing that the winter surveys had significantly less goanna activity than all the summer and autumn surveys. There was a significant time - latitude interaction ($F=8.6_{5,40}$ $p < 0.001$), because at Kintore goanna activity was greatest in summer whereas at Tennant Creek goanna activity peaked in autumn (Fig. 2.5d).

2.3.5 Birds

There was no consistent difference in total bird abundance between study areas or habitats (Fig. 2.4e), but time was a significant main effect ($F_{5,40} = 5.6$, $p < 0.005$). Bird counts remained very low at Kintore until winter 1997 when there was a significant increase in abundance (Fig. 2.5e), mainly due to an influx of nomadic birds including budgerigars, crimson chats, pied honeyeaters and masked woodswallows. Bird abundance during this survey was significantly higher than all the preceding Kintore surveys, but not significantly greater than any of the Tennant surveys. At Tennant bird numbers were generally highest in autumn and lowest in summer. Time was a significant factor in the analysis of species richness of birds ($F_{5,40} = 6.3$, $p = 0.001$), as there was a large peak in richness in winter 1997 in both study areas. There was no difference in species richness between the two habitats. However, a distinct assemblage of birds occurred at the Tennant palaeodrainage sites, dominated by splendid fairy-wrens and inland thornbills and when the melaleucas were flowering flocks of brown honeyeaters were present at these sites.

Sixty nine bird species were observed in the Tennant study area and 41 species were seen at Kintore (Table 2.3). The arrival of a large number of water birds after rain in early 1996 contributed to the high species count at Tennant. The first water birds arrived within 24 h of the appearance of surface water, and within 4 days eight species of aquatic birds had colonised the Tennant study sites. Although species richness was always slightly greater at Tennant, the effect of latitude was not significant, as there was usually only a small difference between the two study areas. Ubiquitous core species that were common in both habitats and both study areas in all seasons included singing honey-eaters, black-faced woodswallows, variegated fairy-wrens, white-winged fairy-wrens, brown falcons, willy wagtails and crested bell-birds.

2.3.6 Bustards

Bustards were consistently more abundant at Tennant Creek than Kintore ($F_{1,8} = 13.3$, $p < 0.05$). Although bustard activity appeared to be greatest in the palaeodrainage habitat (Fig. 2.4f), the effect of habitat was not significant. Bustards did not show a marked response to change in seasonal conditions during the survey period (Fig. 2.5f).

2.3.7 Small Mammals

Capture rates of small mammals remained low throughout the study period and no significant differences in abundance were detected over time. Both study areas showed a gradual decline in abundance of small mammals during 1996 followed by an increase in captures in Winter 1997 at Kintore and in Summer 1997 at Tennant (Fig. 2.5g), but these increases were not statistically significant. In both cases, the higher capture rates overall were due to an increase in rodents while dasyurid densities remained stable. The species richness of small mammals did not vary significantly between surveys.

More mammals were trapped at Kintore than at Tennant ($F_{1,8} = 13.5$, $p = 0.006$; Fig. 2.4g), and the species richness of mammals was also significantly greater at Kintore than Tennant. Distinct assemblages of small mammals occurred in the two study areas (Table 2.3). Rodents dominated small mammal samples from Tennant, whereas dasyurids were far more prevalent at Kintore. The native rodents *Pseudomys hermannsburgensis* and *Notomys alexis*, were captured in both study areas, but *Leggadina forresti* and *Mus domesticus* occurred only at Tennant. The only dasyurid common to both study areas was *Sminthopsis youngsoni*, but *Sminthopsis macroura* occurred at Tennant, and *Ningaui ridei* and *Dasycercus cristicauda* occurred at Kintore.

There was no clear effect of habitat on either capture rates (Fig. 2.4g) or species richness of small mammals in this study.

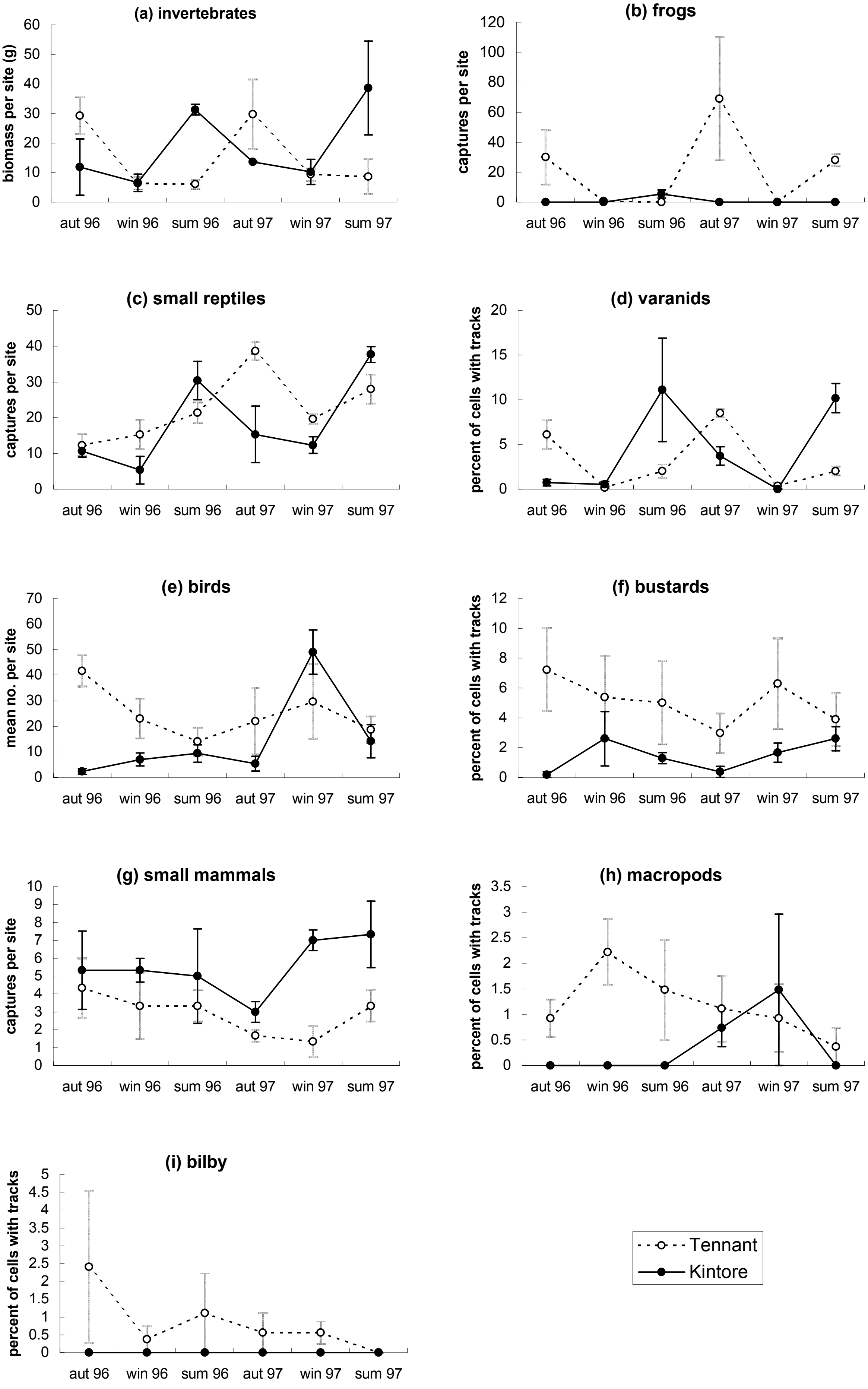

Fig. 2.5. Seasonal patterns in the relative abundance of fauna (means ± standard error) in two areas of the Tanami Desert, 1996-1997.

2.3.8 Macropods

Significantly more macropods occurred at Tennant than Kintore ($F_{1,8} = 18.3$, $p < 0.005$). Macropods (including red kangaroos and/or spectacled hare-wallabies) were recorded on every survey at Tennant but at Kintore, red kangaroos were only detected on the two surveys following significant rainfall in 1997 (Fig. 2.5h), and were the only macropods recorded. There appeared to be more macropods in the drainage habitat than the sandplain (Fig. 2.4h), however the difference was not significant due to the high variability between counts (indicated by standard error bars in Fig. 2.4h).

2.3.9 Bilbies

Significantly more bilby sign was found at Tennant than Kintore ($F_{1,8} = 6.35$, $p < 0.05$). Although bilbies were occasionally recorded in the wider region of Kintore during the study period, they were not recorded on the transects at all during the surveys. At Tennant, fresh tracks were recorded on at least one study plot during every monitoring trip except the final survey in November 1997 (Fig. 2.4i). The majority of records were from the palaeodrainage habitat at one of the Tennant sites, but they also occurred at the second site on one occasion and at the third site during three surveys.

2.4 DISCUSSION

The results of this study suggest that local seasonal conditions in the Tanami Desert are more important than the long-term effects of annual average rainfall or habitat attributes such as nutrient levels and moisture retention in determining the abundance and species richness of faunal assemblages. Although I did not actually measure the moisture content and nutrient levels in the soil, Foulkes *et al.* (1995) showed that such gradients occurred between palaeodrainage and sandplain habitats in the Tanami Desert and, although soil nutrient levels had a major effect on the distribution of vegetation communities, they had little influence on the distribution and diversity of fauna.

Table 2.3. Vertebrate species present in two areas of the Tanami Desert, 1996-1997, showing the number of surveys in which each species was recorded. Asterisks denote opportunistic captures during the surveys.

		TENNANT	KINTORE
AMPHIBIA			
Neobatrachus aquilonius		0	1
Notaden nichollsi	Desert Spadefoot Toad	3	1
Uperoleia micromeles	Tanami Toadlet	3	1
REPTILIA			
Varanus acanthurus	Spiny-tailed Monitor	3	0
Varanus brevicauda	Short-tailed Monitor	2	2
Varanus eremius	Desert Pygmy Monitor	4	2
*Varanus gilleni**	Pygmy Mulga Monitor	0	1
Varanus gouldi	Gould's Goanna	4	4
*Varanus panoptes**		2	0
Heteronotia binoei	Bynoe's Gecko	2	5
Diplodactylus ciliaris	Spiny-tailed Gecko	4	1
Diplodactylus conspicillatus	Fat-tailed Gecko	2	4
*Diplodactylus elderi**	Jewelled Gecko	0	1
Diplodactylus jeanae	Jean's Gecko	2	1
Diplodactylus stenodactylus	Crowned Gecko	5	2
Gehyra variegata	Tree Dtella	1	0
Nephrurus laevis	Knob-tailed Gecko	4	1
Nephrurus laevissimus		0	1
Rhyncoedura ornata	Beaked Gecko	5	3
Ctenophorus isolepis	Miltitary Dragon	6	6
Ctenophorus nuchalis	Central Netted Dragon	4	0
*Diporiphora lalliae**		0	1
Diporiphora winnecki		1	1
Lophognathus longirostris	Long-nosed Dragon	2	1
Moloch horridus	Thorny Devil	0	1
*Pogona mitchelli**	Mitchell's Bearded Dragon	0	2
Carlia triacantha	Three-spined Rainbow Skink	1	0
Ctenotus calurus	Blue-tailed Ctenotus	0	3
Ctenotus dux	Chief Ctenotus	0	3
Ctenotus grandis	Grand Ctenotus	4	4
Ctenotus hanloni	Hanlon's Ctenotus	4	4
Ctenotus helenae	Helen's Ctenotus	4	3
Ctenotus nasutus	Long-snouted Ctenotus	0	5
Ctenotus pantherinus	Leopard Ctenotus	5	6
Ctenotus piankai	Pianka's Ctenotus	2	3
Ctenotus quattuorodecimlineatus	Fourteen-lined Ctenotus	1	5
Ctenotus schomburgkii	Schomburgk's Ctenotus	2	0
*Egernia kintorei**	Great Desert Skink	0	1
Egernia striata	Nocturnal Desert Skink	1	1
Eremiascincus fasciolatus	Narrow-banded Sand-swimmer	4	2
Notoscincus ornatus	Ornate snake-eyed Skink	5	1
Lerista bipes	Two-toed Lerista	6	4
Menetia greyii	Grey's Menetia	6	2

Table 2.3 (cont.)

		TENNANT	KINTORE
Morethia ruficauda	Red-tailed Snake-eyed Skink	5	1
Tiliqua multifaciata	Centralian Blue-tongue	1	3
*Delma nasuta**		0	1
Lialis burtonis	Burton's Legless lizard	0	2
Pygopus nigriceps	Hooded Scaly-foot	1	2
Ramphlotyphlops enderotus		4	3
Pseudonaja nuchalis	Western Brown Snake	1	0
Simoselaps fasciolatus	Narrow-banded Snake	0	1
Suta punctata	Little Spotted Snake	2	0
AVES			
Tachybaptus novaehollandiae	Australasian Grebe	2	0
Ardea pacifica	Pacific Heron	1	0
Ardea novaehollandiae	White-faced Heron	1	0
Ardea sp.	Egret sp.	1	0
Anas gracilis	Grey Teal	2	0
Malacorhynchus membranaceus	Pink-eared Duck	2	0
Aythya australis	Hardhead	1	0
Oxyura australis	Blue-billed Duck	1	0
Milvus migrans	Black Kite	3	1
Hamirostra melanosternon	Black-breasted Buzzard	3	0
Accipiter novaehollandiae	Collared Sparrowhawk	1	0
Aquila audax	Wedge-tailed Eagle	1	0
Circus assimilis	Spotted Harrier	1	0
Falco longipennis	Australian Hobby	2	2
Falco hypoleucos	Grey Falcon	0	1
Falco berigora	Brown Falcon	5	4
Falco cenchroides	Australian Kestrel	3	4
Turnix velox	Little Button-quail	3	2
Gallinula ventralis	Black-tailed Native-hen	1	0
Ardeotis kori australis	Australian Bustard	6	4
Burhinus grallarius	Bush Thicknee	1	0
Vanellus miles	Masked Lapwing	1	0
Erythrogonys cinctus	Red-Kneed Dotterel	1	0
Himantopus himantopus	Black-winged Stilts	1	0
Stiltia isabella	Australian Pratincole	1	0
Geopelia cuneata	Diamond Dove	4	1
Geophaps lophotes	Crested Pigeon	2	0
Cacatua leadbeateri	Pink Cockatoo	4	0
Polytelis alexandrae	Princess Parrot	0	1
Nymphicus hollandicus	Cockatiel	0	1
Melopsittacus undulatus	Budgerigah	4	4
Cuculus pallidus	Pallid Cuckoo	1	1
Chrysococcyx osculans	Black-eared Cuckoo	1	0
Chrysococcyx basalis	Horsfields Bronze-Cuckoo	2	0
Ninox novaeseelandiae	Southern Boobook	3	0
Podargus strigoides	Tawny Frogmouth	0	1
Eurostopodus argus	Spotted Nightjar	2	2
Halcyon pyrrhopygia	Red-backed Kingfisher	4	2
Merops ornatus	Rainbow Bee-eater	6	0

Table 2.3 (cont.)

		TENNANT	KINTORE
Mirafra javanica	Singing Bushlark	0	1
Cheramoeca leucosternum	White-backed Swallow	0	4
Hirundo ariel	Fairy Martin	3	1
Anthus novaeseelandiae	Richards Pipit	2	0
Coracina novaehollandiae	Black-faced Cuckoo-shrike	2	0
Coracina maxima	Ground Cuckoo-shrike	0	1
Lalage tricolor	White-winged Triller	2	1
Melanodryas cucullata	Hooded Robin	2	0
Microeca leucophaea	Jacky Winter	1	0
Pachycephala rufiventris	Rufous Whistler	3	0
Colluricincla harmonica	Grey Shrike-thrush	2	0
Oreoica gutturalis	Crested Bellbird	4	6
Rhipidura leucophrys	Willy Wagtail	6	5
Psophodes occidentalis	Chiming Wedgebill	2	5
Pomatostomus superciliosus	White-browed Babbler	0	1
Cinclorhamphus mathewsi	Rufous Songlark	5	0
Cinclorhamphus cruralis	Brown Songlark	0	1
Malurus splendens	Splendid Fairywren	6	0
Malurus lamberti	Variegated Fairywren	5	6
Malurus leucopterus	White-winged Fairywren	6	6
Stipiturus ruficeps	Rufous-crowned Emu-wren	0	4
Smicrornis brevirostris	Weebill	1	0
Acanthiza apicalis	Inland Thornbill	3	0
Aphelocephala leucopsis	Southern Whiteface	1	0
Aphelocephala nigricincta	Banded Whiteface	0	5
Acanthagenys rufogularis	Spiny-cheeked Honeyeater	1	0
Manorina flavigula	Yellow-throated Miner	1	0
Lichenostomus virescens	Singing Honeyeater	6	6
Lichenostomus keartlandi	Grey-headed Honeyeater	5	2
Melithreptus gularis	Black-chinned Honeyeater	1	0
Lichmera indistincta	Brown Honeyeater	3	0
Phylidonyris albifrons	White-fronted Honeyeater	1	1
Certhionyx niger	Black Honeyeater	2	1
Certhionyx variegatus	Pied Honeyeater	0	2
Ephthianura tricolor	Crimson Chat	5	3
Dicaeum hirundinaceum	Mistletoebird	2	1
Pardalotus rubricatus	Red-browed Pardalote	0	1
Taeniopygia guttata	Zebra Finch	5	3
Grallina cyanoleuca	Australian Magpielark	1	0
Artamus personatus	Masked Woodswallow	4	4
Artamus cinereus	Black-faced Woodswallow	5	6
Cracticus nigrogularis	Pied Butcherbird	1	0
Gymnorhina tibicen	Australian Magpie	0	1
Corvus sp.	Corvid sp.	5	0
MAMMALIA			
Dasycercus cristicauda	Mulgara	0	3
Ninguai ridei	Wongai Ningaui	0	5
Sminthopsis macroura	Stripe-faced Dunnart	3	0
Sminthopsis youngsoni	Lesser Hairy-footed Dunnart	5	6

Table 2.3 (cont.)

Macrotis lagotis	Bilby	5	0
Lagorchestes conspicillatus	Spectacled Hare-wallaby	5	0
Macropus rufus	Red Kangaroo	6	3
Leggadina lakedownensis	Lakeland Downs Mouse	1	0
Mus musculus	House Mouse	6	0
Notomys alexis	Spinifex Hopping-mouse	5	2
Pseudomys hermannsburgensis	Sandy Inland Mouse	5	4
Canis lupus dingo	Dingo	6	6
Vulpes vulpes	Fox	6	6
Felis catus	Cat	6	6
Camelus dromedarius	One-humped Camel	0	4

2.4.1 Effect of habitat

Results of this study supported the hypothesis that reptiles would be less numerous in the richer palaeodrainage habitat than the surrounding sandplain, at least in the northern study area. This may be attributed to the findings that fewer termites and fewer species of termites occur in palaeodrainage lines than sandplain habitat in the Tanami Desert (Foulkes *et al*. 1995). My results did not support the suggestion of Stafford Smith and Morton (1990) that the diversity of reptiles would increase with decreasing fertility and soil moisture availability. I found little effect of habitat on the species richness of reptiles captured, with many species occurring in both habitats.

The hypothesis that mammals, birds and frogs would be more abundant and diverse in palaeodrainage habitat than sandplain habitat received little support from statistical analyses of the results. The density of frogs appeared to be greater in the palaeodrainage line habitat than in the sandplain, but the effect of habitat was not significant. Other studies have shown that where burrowing frogs occur in both habitats, capture rates decline rapidly in the sandplain habitat after the cessation of rain (Morton *et al*. 1993), but frogs continue to be caught for several weeks in palaeodrainage habitat, where surface water remains for a longer period (Foulkes *et al*. 1995).

Stafford Smith and Morton (1990 p. 272 fig. 9) suggest that diversity of birds will tend to increase with increasing fertility and soil moisture availability. However, no differences in species richness or abundance between sandplain and palaeodrainage habitats were found. Very few bird species are herbivorous (Morton 1990), and thus birds are unlikely to respond to an increase in vegetation greenness unless it is associated with higher concentrations of insects, prolonged flowering and seed production or greater provision of drinking water. I found no evidence that invertebrates were more abundant in the palaeodrainage habitat. Nomadic nectarivorous and granivorous birds respond to widespread rain events that cause reproduction of plants across all habitat types. There was greater availability of drinking water in the palaeodrainage habitat for periods of several months after rain, which allowed the persistence of aquatic birds in the palaeodrainage habitat. However, it had little influence on birds observed on the transects, except that Zebra finches (*Taeniopygia guttata*) were more abundant in the palaeodrainage habitat.

Overall, there was no clear effect of habitat on the abundance and diversity of small mammals, but palaeodrainage lines appear to be important for certain species of rodents and dasyurids. The introduced house mouse, *Mus domesticus,* was only found in palaeodrainage habitat and *N. ridei* was mainly caught in this habitat. This was in accordance with a previous study of palaeodrainage lines, where *M. musculus* as well as *P.hermannsburgensis* and two species of *Sminthopsis* were found to be associated with the palaeodrainage habitat (Foulkes *et al*. 1995). Palaeodrainage areas have also been demonstrated to be important habitat for the mulgara (Gibson and Cole 1992, Baker 1996), but in this study the mulgara was equally uncommon in both habitats.

Although macropods appeared to be more abundant in the palaeodrainage habitat, I did not detect a significant difference in the use of habitats by these species, and there was no evidence that the palaeodrainage areas provided a refuge for herbivores during drought conditions at Kintore during 1996. Rather, species such as the red kangaroo apparently moved out of the study area altogether, only returning after significant rainfall. Red kangaroos are capable of moving long distances in search of fresh plant growth and water (Denny 1982).

Bilby activity occurred more frequently in the palaeodrainage habitat, but only one of the Tennant sites showed recent bilby sign on a regular basis. The palaeodrainage habitat is thought to have originally provided refuge for a whole suite of medium sized herbivorous and omnivorous mammals that were dependent on higher quality forage than often occurs in the surrounding sandplain habitat (Morton 1990), but most of these species are now extinct.

It is possible that the lack of difference in abundance and diversity of fauna in the two habitat types was an artefact of the short-term nature of the study. However, if the palaeodrainage habitat was providing refuge for species during periods of drought, any differences in fauna abundance should have been evident during the time-frame of this research, as the study commenced during drought conditions.

If the palaeodrainage habitat is not providing adequate refuge for mammalian species, are there other habitats in the vicinity of the two study areas that may have higher moisture and nutrient levels? Several large rocky hills occur within 10 km of the Kintore sites, producing major run-on areas, which usually tend to be greener than the surrounding countryside (personal observations). Smaller rises occurred in the Tennant study area, and were again associated with country that was apparently more productive. Such run-on areas may provide refuge for some species during drought.

Other species may endeavour to find temporary refugia during dry times. Rainfall in the arid zone is particularly patchy (Fleming 1978). Most rain events in the summer are the result of thunderstorms, which often produce isolated showers of sufficient quantity to stimulate plant growth, but may only cover areas as small as 5-30 km^2 (Denny 1982). Newsome and Corbett (1975) suggested that the survival of nuclear populations of rodents between plagues was dependent on the geographic pattern of such isolated showers. In the Simpson Desert, both dasyurids and rodents have been recorded travelling distances of up to 10 km in response to isolated rain events (Dickman *et al*. 1995). Such rain events may increase the availability of food by stimulating invertebrate activity, enhancing the accessibility of buried seeds and promoting plant growth and reproduction (Dickman *et al*. 1995). Macropods and camels also seem to follow local rain events (Denny 1982, Grigg *et al*. 1995).

2.4.2. Effect of latitude

The hypothesis that birds, mammals and frogs would be more abundant at Tennant than Kintore, but reptiles would be equally abundant in the two study areas, was generally supported by results of the surveys. Significantly more frogs, bustards, macropods and bilbies occurred at Tennant than Kintore. Minimum densities of birds were also higher at Tennant due to a more diverse and abundant suite of resident bird species in the northern study area (but during flush times bird densities were at least as high at Kintore as Tennant).

The underlying difference between the study areas was the disparity in rainfall. During the 1996-1997 study period the Tennant study area received a total of 1049 mm whereas the Kintore study area received only 427 mm of rainfall. The higher annual average rainfall at Tennant probably results in more regular production of new growth and flowering of perennial plants, and more frequent emergence of ephemeral plants than occurs at Kintore. However, food availability resulting from plant productivity is not the only factor involved in the latitudinal gradient, with ensuing effects of differences in rainfall such as water availability, frequency of fire and predator densities also influencing the fauna (Masters 1997). Also, more frequent recharge to the soil moisture levels at Tennant would have created a more favourable environment for frogs.

The only taxonomic group that contradicted my predictions about the effect of latitude was the small mammals. Dasyurids were consistently more abundant in the southern study area than the northern study area. The reason for their dominance at Kintore is unclear, but is unlikely to be due to increased food availability, asIdetected no difference in the abundance of terrestrial invertebrates or reptiles between the two study areas. Dasyurids may have the competitive edge over rodents and birds in an unpredictable climate, with their ability to undergo torpor and utilise fat stored in their tails during unfavourable conditions (Morton 1978, Geiser 1994). Masters (1997) also found *Dasycercus cristicauda* to be more abundant at the southern, more arid of two sites in central Australia, despite an apparently greater food availability at the northern site. She suggested that the reduced productivity of the southern site was favourable for *D. cristicauda* because it resulted in lower predator densities and greater stability due to less frequent wildfires. In the current study, higher overall prey densities were associated with a more abundant predator population at Tennant than Kintore (see chapter 4), and increased predation may have contributed to the paucity of dasyurids in this study area.

In discussing the effects of “latitude” I am of course referring only to differences between the two study areas. Although there were three independent sites at both Tennant and Kintore, the area sampled represented a very small proportion of the spinifex grassland habitat of central Australia, and I cannot extrapolate the data beyond the two study areas. However, reference to the results of two other studies (Foulkes *et al*. 1995, and Masters 1997), may shed some light on whether the patterns observed between my two study areas are in fact due to a latitudinal effect. Both studies surveyed small mammals and herpetofauna at two central Australian spinifex grasslands sites: Sangsters Bore in the north-west Tanami Desert and Uluru National Park. Sangsters Bore occurs about half way between Tennant and Kintore and Uluru is several hundred kilometres south of Kintore. Foulkes *et al*. (1995) had a third site (Lander River) at approximately the same latitude as Sangsters Bore. Both studies found the abundance of reptiles to be very comparable between latitudes, lending support to the idea that a latitudinal gradient does not exist for reptiles. Much higher densities of frogs were recorded at Sangsters Bore than Uluru during significant rain events, which strengthens the argument for a latitudinal gradient in frog abundance. Dasyurids were consistently more abundant at Uluru than either Sangsters Bore or Lander River which is also in agreement with my findings that they are less common to the north, but there was no consistent latitudinal pattern for rodents.

2.4.3. Effect of seasonal conditions

My predictions regarding the effect of seasonal conditions on various taxonomic groups were largely supported by the results of the surveys, except that small mammals showed little response to changes in seasonal conditions during the timeframe of this study. Regardless of any underlying effects of latitude or habitat, the occurrence of significant rain events had a much greater impact on the abundance of frogs, birds and macropods than the mean annual rainfall or habitat type of the sites. Frogs and invertebrates showed an immediate response to rain events, and there was an increase in the activity of some reptiles (e.g. geckoes) on rainy nights. Within days of the appearance of surface water, aquatic birds began arriving. Red kangaroos arrived after fresh growth was produced, and a succession of nomadic bird species appeared in the ensuing months, as nectar and seed were produced.

Reptiles appeared to be less affected by rainfall than birds, with significantly higher abundances being recorded in the warmer surveys, irrespective of rainfall, habitat or latitude. There was no significant difference in reptile captures between the dry year and the wet year at Kintore. The low metabolic rates of reptiles and their ability to become inactive during periods of stress enables them to persist through drought conditions

(Morton and James 1988). Long term mark-recapture data for arid zone skinks have revealed high adult survivorship but little recruitment during poor to average years (James 1991, Read 1998), coupled with considerable reproduction followed by high adult mortality, during favourable years (James 1991). This may result in a relatively stable overall population density. Several of the most dominant species in the current study *(Diplodactylus conspicillatus, Ctenotus pantherinus and Lerista bipes*) are termite specialists (Pianka 1986). Termites are not generally dependent on green forage (Stafford-Smith and Morton 1989) and are probably always a plentiful food source. Nevertheless, there was a significant peak in the abundance of reptiles at Tennant in March 1997. Significant rain fell during this survey and the higher capture rates were probably due to increased activity, rather than recruitment, as very few juveniles were captured.

The abundance of small mammals remained low (≤ 2 % trap success) in both study areas throughout the duration of the study period. In spinifex grasslands elsewhere in central Australia, a succession of at least 18 months of above average rainfall following several years of below average rainfall is required for small mammal populations to increase significantly (Southgate and Masters 1996). Capture rates of small mammals may then increase to beyond 50 % trap success (Southgate and Masters 1996). Although small mammals may make small-scale migrations of up to 10 km to areas that have received rainfall (Dickman *et. al* 1995), their dispersive capabilities are relatively limited compared to birds and macropods, and they increase primarily by breeding.

The fauna of the Tanami Desert can thus be divided into three groups, depending on their strategies of response to seasonal conditions.

(a) the persistent stayers which remain at the sites, often with dormant phases. They include frogs, invertebrates and reptiles, and show an immediate increase in activity in response to favourable conditions by **emergence**.

(b) highly mobile nomadic species which increase by **immigration** (nomadic birds and macropods).

(c) the residents without dormant phases which may eventually increase after a succession of good seasons by **breeding** (small to medium sized mammals).

2.4.4. Conclusions

Results from this study provide little evidence that palaeodrainage systems are a significant refuge for vertebrate species in the Tanami Desert at the present time. I am not disputing the suggestion of Morton (1990) that such habitats originally provided refuge for herbivorous and omnivorous mammals. I agree that this was probably the case but, as Morton (1990) points out, most of the species that relied on such refuges were particularly susceptible to feral predators and competitors and are now extinct. Those that remain – the bilby and smaller macropods – tended to be more abundant in palaeodrainage habitat than sandplain in this study, but their rarity at the sites led to statistically insignificant results. However, the hypothesis of Morton (1990) cannot be expanded to include other mammalian or avian groups and there was no evidence that a more abundant and diverse faunal community occurs in palaeodrainage habitat than in the surrounding sandplain. Temporary refugia, resulting from isolated showers of rain, may be more important to the survival of desert mammals than habitats with inherently higher fertility and moisture retention capabilities.

Overall there was a greater abundance of vertebrate fauna in the northern study area than the southern study area and during this study minimum densities of birds and reptiles were lower at Kintore than at Tennant. However, during favourable conditions, the peaks in abundance were even greater at Kintore than occurred at Tennant. Local climatic conditions had an overriding effect that overwhelmed any differences attributable to habitat or latitude in structuring faunal communities in this study. The other major driving force influencing the biota of central Australia is undoubtedly fire, but this has been addressed elsewhere (Masters 1993, 1996, Reid *et al.* 1993, Southgate and Masters 1996, Southgate 1997) and was not a variable in this study.

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CHAPTER 3

THE DIETS OF CATS, FOXES AND DINGOES IN RELATION TO PREY AVAILABILITY IN THE TANAMI DESERT[2]

Preamble to Chapter 3

In the previous chapter I presented information on the availability of potential prey for predators in the Tanami Desert. I showed that reptile fauna were a readily available resource in the ‘summer’, regardless of rainfall, and nomadic birds rapidly colonised areas of the spinifex grasslands after significant rainfall.

But can such prey types be utilised by cats, foxes and dingoes, which are primarily predators of mammalian prey species in other parts of Australia and elsewhere in the world? In this chapter I present the results of the dietary analyses of cats, foxes and dingoes in two areas of the Tanami Desert, over a 2 year period, under fluctuating seasonal conditions.

I aimed to determine the staple, supplementary and opportunistic prey species for each predator and to consider the potential for these predators to prey upon medium-sized mammal species. I also aimed to use dietary information to gain some insight into the ecological interactions operating between predator species, by documenting intraguild predation and the level of dietary overlap between cats, foxes and dingoes.

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3.1 INTRODUCTION

Throughout the world, the diets of feral cats (*Felis catus*) are dominated by mammalian prey, with a mean prey size of 41.2 g (Pearre and Maass 1998). Birds are of secondary importance but cats are versatile predators and consume a broad range of prey (Fitzgerald and Turner 2000). In most areas of Australia either rabbits (*Orcytolagus cuniculus*) or other small mammals are the most frequently eaten prey items (Coman and Brunner 1972, Jones and Coman 1981, Catling 1988, Dickman 1996, Paltridge *et al*. 1997, Molsher *et al*. 1999, Risbey *et al*. 1999).

Foxes (*Vulpes vulpes*) are also opportunistic predators with a high proportion of mammals in their diets. Insects also feature prominently in fox diets during certain seasons (Ables 1975, Lloyd 1975). In areas of Australia where rabbits occur, they are staple prey for foxes (Jarman 1986). In areas not inhabited by rabbits, other small- to medium-sized mammals are the dominant prey (Green and Osborne 1981, Triggs *et al*. 1984), and foxes readily scavenge carrion when it is available (Martensz 1971, Bayly 1978, Croft and Hone 1978).

Dingoes (*Canis lupus dingo*) are primarily predators of medium- to large-sized mammals (Corbett 1995) including macropods, rabbits and wombats (*Vombatus ursinus*). Dingoes also scavenge cattle carrion during drought periods (Corbett and Newsome 1987).

In the Tanami Desert, in central-western Northern Territory, the medium-sized (35-5500 g) mammal fauna was once common and abundant (Burbidge *et al*. 1988). However, diversity and abundance of medium-sized native mammals throughout arid Australia have been severely reduced since European settlement (Finlayson 1961, Burbidge *et al*. 1988, Morton 1990). In many areas, they have been replaced by populations of rabbits, but in the spinifex grasslands of the Tanami Desert, rabbits are patchily distributed and generally uncommon (Low and Strong 1983). Fewer small mammals (< 35 g) have become extinct, but their abundance fluctuates dramatically in the arid zone, depending on rainfall, and for much of the time they are quite scarce (Carstairs 1974, Predavec and Dickman 1994, Southgate and Masters 1996). Carrion resulting from roadkills, kangaroo culling programs and death of livestock, which supplements the diets of predator populations elsewhere in Australia (Bayly 1978, Corbett and Newsome 1987), is not a common resource in the Tanami Desert.

Despite the frequent scarcity and unreliability of mammalian prey, populations of cats, foxes and dingoes persist in the Tanami Desert (Gibson 1986, Lundie-Jenkins *et al.* 1993, RP unpublished data). This chapter investigates the feeding habits of cats, foxes and dingoes in relation to prey availability, in two areas of the spinifex grasslands of the Tanami Desert. The study was conducted during a period when native mammals were relatively uncommon. It is the first comparison of the dietary habits of cats, foxes and dingoes in an area where rabbits do not occur. I examine the extent to which the diets of cats, foxes and dingoes are dominated by mammals in this environment and compare the size of prey items consumed by the three predator species.

3.2 METHODS

3.2.1 Monitoring prey availability

Field surveys were conducted approximately every four months from September 1995 to November 1997 at Tennant, and May 1996 to December 1997 at Kintore. Within the two study areas, prey monitoring occurred over three days at each of three sites. A 'site' comprised two 4 km^2 study plots situated approximately four kilometers apart (Further details on the layout of the study plots are provided in Section 2.2.1).

Abundance of invertebrates, reptiles and small mammals were monitored using pitfall traps and Elliott traps, which were open for 3 days per survey, and cleared at sunrise each day. Each plot contained two lines of five pitfall traps and two lines of 25 Elliott traps. Pit lines were 500 m apart, with the Elliott lines set perpendicular to the pit lines and running between them. Pits (25 L white plastic buckets) were situated 7 m apart and connected by a flywire drift fence standing 25 cm and partially buried into the sand. The fences were left standing for the duration of the study. Between surveys, plastic lids were fitted to the buckets and covered with sand. When the buckets were opened, the lids were propped up above the buckets, at fence height, providing shade within the pits. Extra shelter was provided by small clumps of vegetation placed inside the buckets.

Elliott lines were set 100 m apart. Traps were positioned at 20 m intervals and baited with balls of peanut butter and oats. Traps were opened in the late afternoon and closed early the next morning. The traps were removed from the sites between surveys.

Invertebrates caught in the pits were collected daily and stored in 70 % ethanol. All invertebrates from one line of 5 traps were combined to comprise a single ‘sample’. Dry masses were obtained by drying samples at 60° C for 48 h in plastic petri dishes and then weighing the contents of the petri dishes on an electronic balance. No attempt was made to sort the invertebrates by taxonomic group, but it was noted that beetles, scorpions, spiders, centipedes and crickets were commonly represented in the samples.

The relative abundance of birds was assessed along 1 km walked transects (one transect per plot). Bird counts were conducted in the half-hour before sunset and each transect was surveyed once per survey. All birds seen and heard within an estimated 50 m wide strip either side of the transect were counted and identified to species where possible with the aid of 10 x 50 binoculars. In addition to the bird transects, lists of all bird species observed at the study plots were compiled for each survey, and notes made of plants flowering or seeding and any breeding activity by birds.

The activity/abundance of macropods, goannas, bilbies and bustards was monitored by track counts along 10 km ‘roads’ cleared of vegetation (one transect per study plot) and swept of animal tracks each day between counts. Roads were divided into 500 m cells and the proportion of cells with tracks present was recorded for 3 consecutive days during each monitoring survey. When tracks were seen, the vehicle was stopped while the tracks were identified.

3.2.2 Scat Analysis

Predators scats were collected along the tracking transects to determine diet. In addition, approximately six person-hours per study plot (thirty-six person-hours per survey) were dedicated to searching for predator scats within the study plots. Cat, fox and dingo scats were distinguished on the basis of size, smell, shape and colour (Triggs 1996), and often the predator’s footprints could be used to confirm identification. A single scat was defined as one or more faecal pellets that appeared to have been deposited in one defecation event by one animal. The approximate age of scats was estimated according to colour, smell, apparent moisture content and surface deterioration, based on a 6 month ageing trial carried out in Alice Springs (Edwards and Paltridge unpublished data). Any scats that were judged to be older than three months were discarded. All remaining scats were retained in individual plastic bags and returned to the laboratory.

Scats were soaked in 70 % alcohol for a minimum of 72 h and then washed through graded sieves to break up prey remains into two size categories. The fragmented remains were then baked for 48 h at 80 ° C to rid them of viable parasite eggs.

Prey remains were initially sorted under a dissecting microscope and identified to the lowest possible taxonomic level. Reptiles were classified to the family level on the basis of scales and jaw-bones (i.e. skinks, varanids, agamids). Birds were lumped as a single category as only birds with very distinctively coloured feathers (e.g. budgerigars, *Melopsittacus undulatus*, fairy-wrens, *Malurus* spp. and zebra finches, *Taeniopygia guttata*) could be identified. Small mammals could often be distinguished using jaw-bones, but a representative sample of all hair was cross-sectioned and examined under a compound microscope. Identification of hair was then made using a reference collection of photographs of known material, made by the author. Medium and large mammals were usually classified to the species level, but small mammals were rarely identified beyond order (i.e. rodent or dasyurid).

All prey categories were assumed to represent one individual unless there was evidence to the contrary. For example, jaw-bones and feet of small mammals and reptiles, bird's beaks and head capsules of invertebrates could all be used to indicate the presence of multiple prey items in a scat.

3.2.3 Data Analysis

There are several ways of expressing scat data. Each method has its own biases and assumptions. 'Frequency of occurrence' is the proportion of scats containing a prey category. 'Numerical frequency' is the number of times a prey item occurs in a group of scats, divided by the total number of prey items contained in those scats. 'Biomass frequency' ((number of times a prey item occurs x estimated mass of prey item)/(total number of prey items x their estimated total mass)), takes the body mass of prey species into account. Body mass data were based on average masses of animals captured during the prey monitoring surveys where possible, but body masses in Strahan (1995) were used for some mammal species. A mass of 20 g was assigned to the lumped bird category, based on the average mass of five common bird species considered likely to be consumed by predators in the study areas (budgerigar = 28 g, crimson chat, (*Ephthianura tricolor*) = 10.7 g, zebra finch = 12.2 g, little button-quail, (*Turnix velox*) = 41.3 g and white-winged fairy-wren, (*Malurus leucopterus*) = 7.5 g; data were provided by the Australian Bird and Bat Banding Scheme, 1999). The biomass contribution of mammals considered too large to be consumed by a single predator in one day was adjusted based on the daily food consumption of each of the three predators, estimated to be 500 g for cats (Dickman 1996) and foxes (Marlow 1992) and 1000 g for dingoes (Newsome *et al*. 1983).

Frequency of occurrence is the simplest measure to calculate, and has been used in many predator diet studies (Croft and Hone 1978, Catling 1988, Jones and Coman 1992, Corbett 1995) but this method tends to overrepresent the importance of small prey items (Corbett 1989). However, to enable comparison with previous studies, frequency of occurrence data were calculated in this study, for the broad prey categories (mammal, bird, reptile, invertebrate). Numerical frequencies were used to determine the effect of prey availability on consumption of specific prey categories, as this method incorporates the additional information of actual numbers of prey items in scats. The problems with numerical frequency are that it is not always possible to determine the number of prey items represented in a scat, and again, numerous small prey items may overshadow a few larger ones (Pinkas 1971). Biomass frequency is based on the assumptions that all prey are adults and that prey are completely consumed (or consumed until satiation in the case of large prey), so this method may be biassed towards larger prey species.

Index of Relative Importance (IRI; Pinkas 1971) is a formula that integrates all three methods and thus provides a compromise, lessening the extremes of bias due to small or large prey. It traditionally uses the volumetric frequency of digested material (Pinkas 1971) but in this study, volumetric frequency has been replaced with the biomass frequency, based on the estimated fresh mass of prey consumed.

$$\text{IRI} = (\text{numerical frequency} + \text{biomass frequency}) \times \text{frequency of occurrence.}$$

The prey were classified into 13 categories: bilby, macropod, rodent, dasyurid, marsupial mole, cat, bird, small-skink, blue-tongue lizard, varanid, agamid, snake and invertebrate. A slightly finer level of categorisation was used for the IRI calculations than the numerical frequency charts to determine which taxa were most important in the diet of each predator. Although some categories are broader than others, they represent functional groups of similar sized species which cannot easily be further distinguished in scat analysis. Most categories include between one and three species with the exception of birds which is much broader, however the majority of birds consumed by predators would probably comprise 5 common species (listed above).

Scats from all surveys were pooled to determine an overall IRI score for each prey category in the diets of the three predators in each of the two study areas. Further IRI calculations were carried out to determine the importance of prey categories in predator diets during individual surveys.

Dietary overlap (Pianka and Pianka 1976) was calculated to determine the similarity between the diets of the three predators living sympatrically and also to compare diets of individual predator species between study areas.

$$\text{Dietary overlap (Do)} = \Sigma\, p_{ij}\, p_{ik} / \sqrt{\Sigma\, p_{ij}^2\, \Sigma\, p_{ik}^2}$$

where p_{ij} is the proportion of a prey category i in the diet of predator j and p_{ik} is the proportion of prey category i in the diet of predator k. A dietary overlap of 0 indicates no overlap whereas 1 indicates that the two diets are exactly the same.

The sizes of prey consumed by the three predators were compared to determine whether there was any evidence of prey-size partitioning between predator species. Potential prey species were arbitrarily divided into three categories: small (< 100 g), medium (100-999 g) and large (> 1000 g) based on their estimated biomass, as described above. Although the "small" prey size category encompassed many prey species, it was decided not to split this further (e.g. < 50 g / >50 g) as the only species that fell in the >50 g category were marsupial moles and mulgaras, which were infrequently recorded. The number of prey items in each size class found in scats were divided by the total number of prey items identified for each predator, to determine an overall percentage for each size class.

Seasonal patterns in food consumption were determined by pooling data from individual surveys into two ‘seasons’: summer (October-April) and winter (May-September). Within study areas, the frequency of occurrence of the four broad taxonomic groups (mammals, birds, reptiles and invertebrates) in each of the two ‘seasons’ were analysed using a test equivalent to the chi-square analysis for comparing two proportions (Zar 1996, p. 553). In addition, two-sample t-tests were used to compare consumption of prey categories between seasons. Proportional data from each survey in each study area were adjusted for normality by the arcsine transformation and used to calculate mean frequencies for each season that could be compared by t-tests.

Pearson correlation analysis in the Statistica computer package (Release 5, 1995) was used to determine the relationship between prey availability and consumption of prey by predators as indicated by numerical frequency.

3.3 RESULTS

3.3.1 Overall diets

A total of 76 cat scats, 53 fox scats and 77 dingo scats were analysed from Tennant and 70 cat scats and 70 fox scats were analysed from Kintore. No dingo scats were found at Kintore during the study, and I was unable to find cat scats at Tennant in March 1997 or fox scats in April 1996 and November 1997. The low numbers of scats found made it necessary to pool data between the three study sites and two habitats, within each study area. A complete species list of prey found in scats and their overall frequency of occurrence is presented in Table 3.1.

The diets of all three predators contained a combination of mammals, birds, reptiles and invertebrates (Fig. 3.1*a*-*c*). The t-tests did not reveal any overall effects of season on the consumption of prey types, however differences did occur within study areas.

Reptiles dominated the diet of cats in the summer surveys (Fig. 3.1*a*) but the increase in reptile consumption in the summer was only significant at Kintore ($z = 2.8$, $p < 0.05$). Birds tended to be consumed more frequently in the winter months than the summer months but this difference was only significant at Tennant ($z = 2.4$, $p < 0.05$).

Foxes consumed invertebrates more frequently than either of the other two predators (Fig. 3.1*b*). Birds were eaten the least frequently of the four categories by foxes, but appeared in the scats significantly more often in the winter than the summer at Kintore ($z = 2.9$, $p < 0.05$). Reptiles were consumed more frequently in the summer months than in the winter months, but again this was only significant at Kintore ($z = 2.1$, $p < 0.05$).

Dingo diet was consistently dominated by reptiles, regardless of season (Fig. 3.1*c*). Invertebrates were rarely eaten by dingoes.

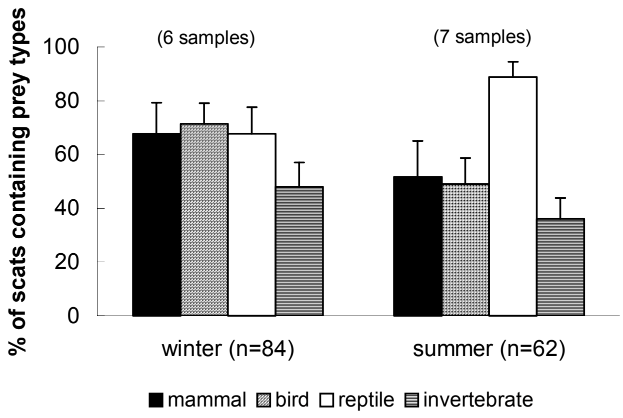
3.3.2 Numerical frequency of prey items in the diet in relation to prey availability

At Kintore, small mammal abundance remained relatively stable throughout the study period (Fig. 3.2). Birds were scarce during 1996, but became very abundant in the autumn and winter of 1997. Skinks and varanids were most abundant in the December surveys, and agamids apparently increased in abundance throughout the study period. Invertebrates were most abundant in the summer months (Fig. 3.2).

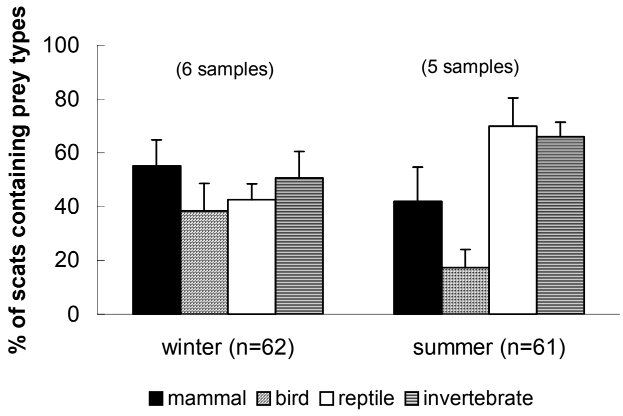
At Tennant, the abundance of small mammals declined throughout the study period, rising slightly in the final survey (Fig. 3.3). Bird abundance peaked twice during the study period, firstly in April 1996 and again in June 1997, both in response to good rain events. Captures of skinks and agamids fluctuated eratically, but varanids showed seasonal activity, being totally inactive during the winter months. Invertebrates were most abundant during the autumn surveys (Fig. 3.3).

In many cases, frequency of prey items in the diet followed a similar pattern to the relative abundance of prey, but few of the correlations were significant, probably due to insufficient data points. However, consumption of small mammals and skinks by cats at Kintore were strongly correlated with their field abundances ($p< 0.05$; Fig 3.2*a*). Small mammals were consistently eaten by cats, except in April 97 when birds became important in the diet. Birds continued to dominate cat diets at Kintore in July 97, but had decreased in the diet by December 1997 when skinks had the highest numerical frequency in the diet, as also occurred during the previous December (Fig. 3.3*a*).

(a) Cats



(b) Foxes



(c) Dingoes

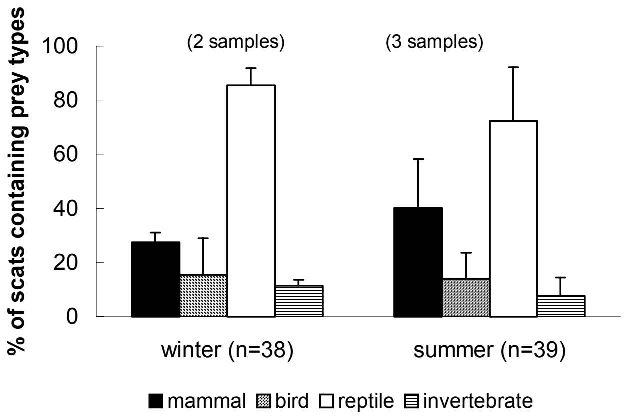


Fig. 3.1. Frequency of occurrence of prey types in predator scats collected during winter (May-September) and summer (October-April). Data are means (± std. error) of the results of multiple surveys conducted in both study areas. Number of samples refers to the number of surveys where at least five scats were collected, 'n' refers to the total number of scats collected in each season.

Table 3.1 Frequency of Occurrence of prey species found in cat, fox and dingo faecal pellets from two study areas in the Tanami Desert, 1995-1997.

ORDER, species	Tennant			Kintore	
	cat	fox	dingo	cat	fox
	n=76	n=53	n=77	n=70	n=70
MAMMALIA					
Tachyglossus aculeatus	0.0	0.0	2.6	0.0	0.0
Total Tachyglossids	**0.0**	**0.0**	**2.6**	**0.0**	**0.0**
Nigaui ridei	0.0	0.0	0.0	1.4	0.0
Sminthopsis spp.	0.0	0.0	0.0	2.9	0.0
Dasycercus cristicauda	0.0	0.0	0.0	4.3	2.9
Total Dasyurids	**11.8**	**7.5**	**2.6**	**47.1**	**21.4**
Notoryctes typhlops	2.6	5.7	2.6	1.4	7.1
Total Notoryctids	**2.6**	**5.7**	**2.6**	**1.4**	**7.1**
Macrotis lagotis	2.6	0.0	1.3	0.0	0.0
Total Peramelids	**2.6**	**0.0**	**1.3**	**0.0**	**0.0**
Macropus rufus	0.0	9.4	15.6	0.0	0.0
Lagorchestes conspicillatus	0.0	0.0	5.2	0.0	0.0
Total Macropods	**1.3**	**9.4**	**20.8**	**2.9**	**0.0**
Pseudomys hermannsburgensis	3.9	0.0	0.0	0.0	1.4
Notomys alexis	5.3	0.0	0.0	8.6	4.3
Mus musculus	1.3	0.0	1.3	4.3	1.4
Total Rodents	**38.2**	**22.6**	**6.5**	**32.9**	**38.6**
Felis catus	1.3	3.8	9.1	2.9	0.0
Canis lupus dingo	0.0	0.0	2.6	1.4	0.0
Camelus dromedarius	0.0	0.0	3.9	1.4	0.0
TOTAL MAMMALS	**59.2**	**45.3**	**50.6**	**77.1**	**80.0**
AVES					
Melopsittacus undulatus	9.2	7.5	2.6	27.1	14.3
Malurus spp.	5.3	0.0	1.3	17.1	10.0
Taeniopygia guttata	0.0	0.0	0.0	4.3	0.0
TOTAL BIRDS	**60.5**	**32.1**	**40.3**	**64.3**	**30.0**
REPTILIA					
Ctenotus spp.	52.6	18.9	13.0	51.4	30.0
Tiliqua scincoides	1.3	9.4	24.7	1.4	1.4
Total Skinks	**53.9**	**28.3**	**34.4**	**52.8**	**31.4**
Varanus acanthurus	0.0	0.0	5.2	1.4	0.0
Varanus gouldii	27.6	22.6	40.3	18.6	32.9
Total Varanids	**27.6**	**22.6**	**45.5**	**20.0**	**32.9**
Total agamids	**27.6**	**18.9**	**22.1**	**14.3**	**1.4**
Total elapids	**2.6**	**3.8**	**2.6**	**1.4**	**1.4**
TOTAL REPTILES	**72.4**	**49.1**	**76.6**	**62.9**	**65.7**
ORTHOPTERA	32.9	22.6	2.6	20.0	22.9
COLEOPTERA	11.8	43.4	7.8	11.4	31.4
CHILOPODA	0.0	1.9	0.0	0.0	4.3
TOTAL INVERTEBRATES	**35.5**	**60.4**	**9.1**	**38.6**	**64.3**

Fox consumption of invertebrates appeared to be correlated with invertebrate abundance at Kintore, but the relationship was not significant. The consumption of birds and varanids by foxes showed similar trends to the fluctuations in the relative abundance of birds and varanids respectively (Fig. 3.2*b*). Small mammals were eaten consistently by foxes, except in December 1996, when frequency of skinks in the diet peaked. Both cat and fox diets showed a marked increase in consumption of birds in April 1997, prior to the measured increase in bird abundance. However, it seems likely that birds had already started increasing at this time. Flocks of between 12 and 20 budgerigars were noted in the study area at this time (personal observations), but were not recorded during the actual bird transect counts, suggesting that the length of transects was not sufficient to monitor species with clumped distributions.

At Tennant, consumption of small mammals by both cats and foxes was strongly correlated with relative abundance of small mammals ($p < 0.05$; Figs. 3.3*a* and *b*). The relative abundances of the remaining prey categories were tracked more closely by cat diets than fox diets (Figs. 3.3*a* and *b*). Although none of the correlations between dingo diet and prey availability were significant, consumption of varanids tended to fluctuate in accordance with the relative abundance of varanids (Fig. 3.3*c*). When varanids were scarce, they were replaced in the diet by either blue-tongued lizards (*Tiliqua multifasciata*) or agamids.

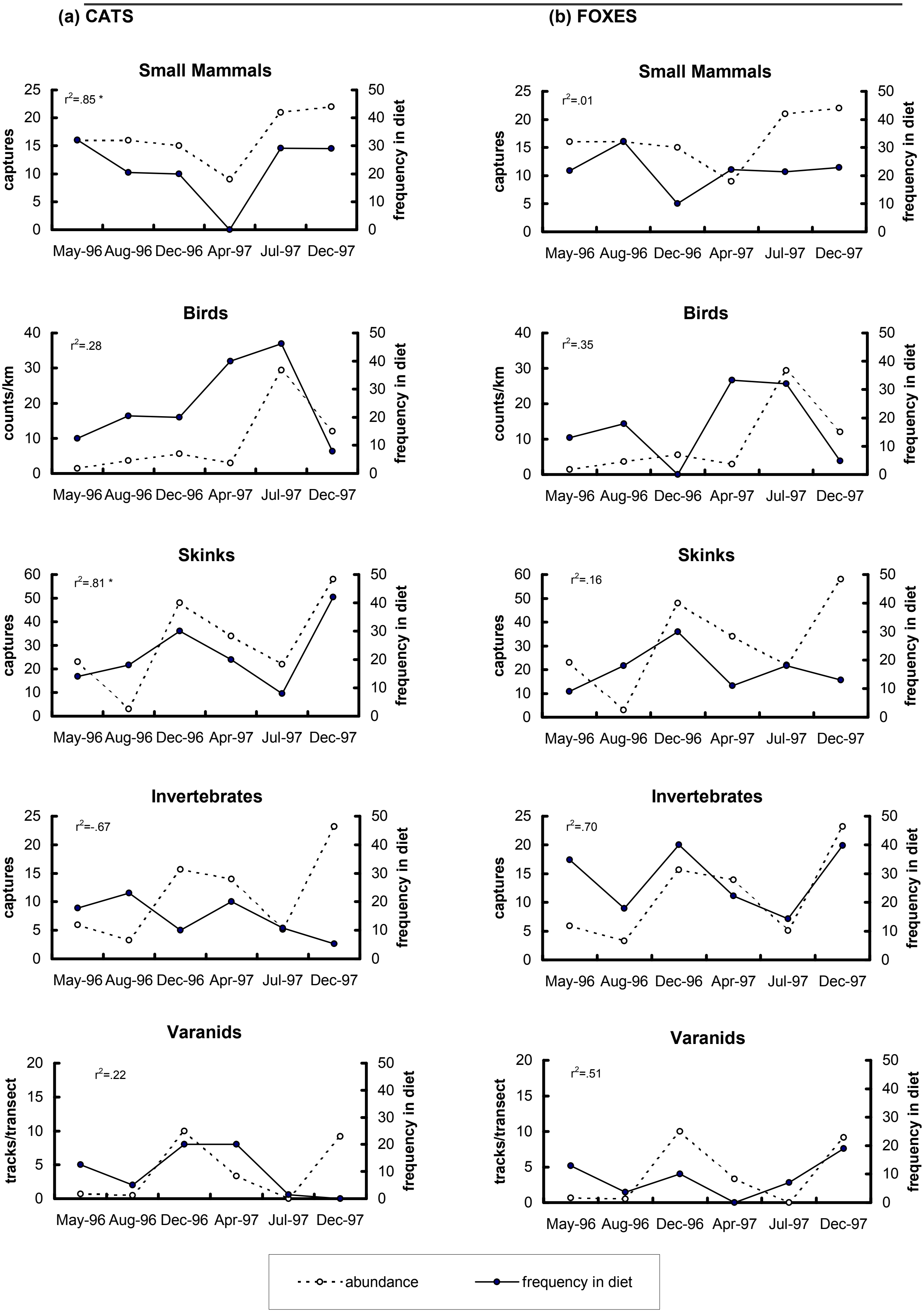


Fig. 3.2 The relationship between the relative abundances of the five most frequently consumed prey and their numerical frequencies in the diets of (a) cats and (b) foxes at Kintore. Consumption, shown on the secondary axes, is expressed as numerical frequency. Breaks in the lines indicate missing data. (Asterisk indicates that Pearson correlation coefficient r^2 is significant at 0.05; captures = animals caught per 1080 trap-nights; tracks/transect = mean proportion of 500m cells with tracks present.)

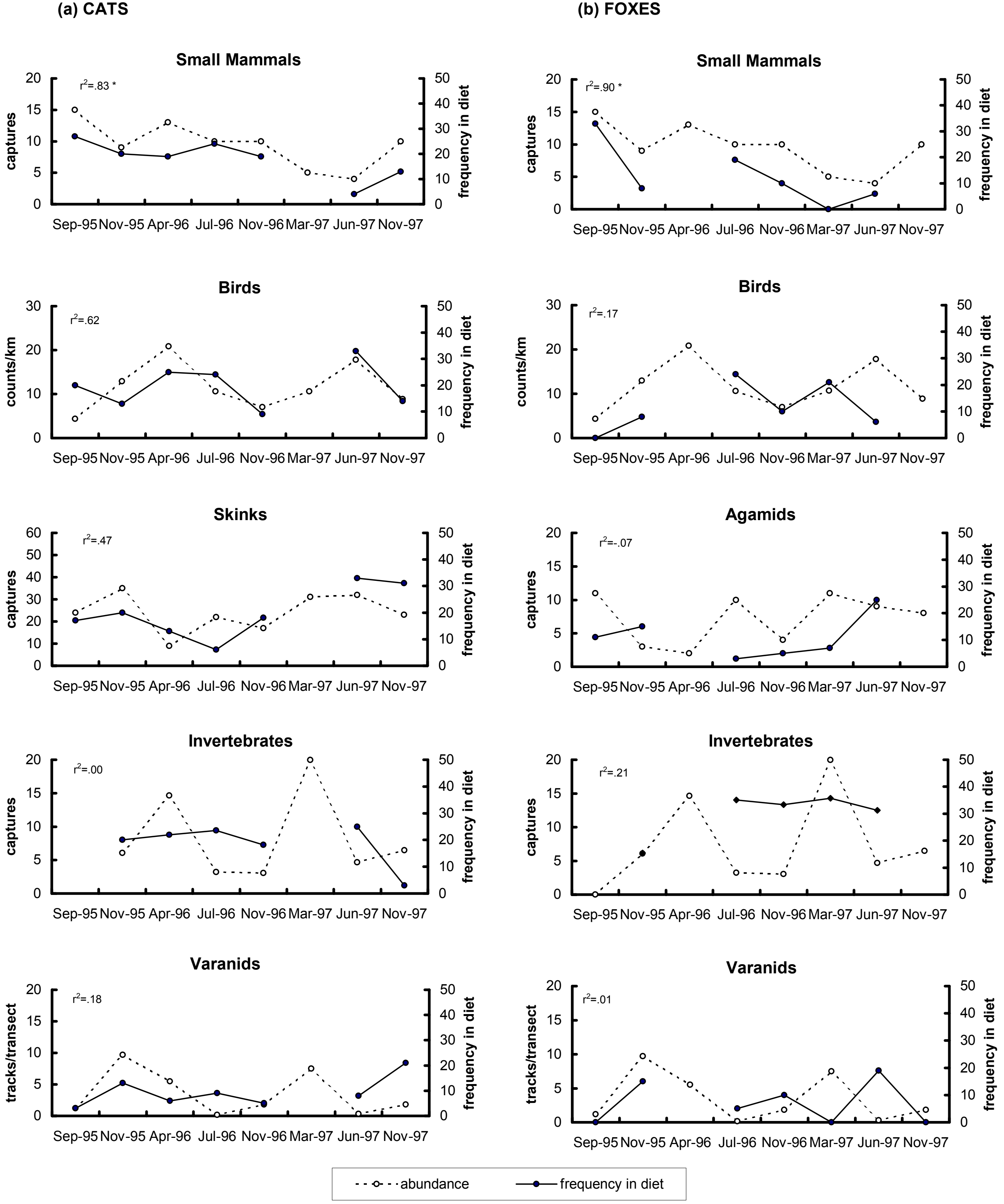


Fig. 3.3 The relationship between the relative abundances of the five most frequently consumed prey and their numerical frequency in the diets of (a) cats, (b) foxes and (c) dingoes at Tennant. Consumption, shown on the secondary axes, is expressed as numerical frequency. Breaks in the lines indicate missing data. (Asterisk indicates that Pearson correlation coefficient r^2 is significant at 0.05; captures = animals caught per 1080 trap-nights; tracks/transect = mean proportion of 500m cells with tracks present.)

(c) DINGOES

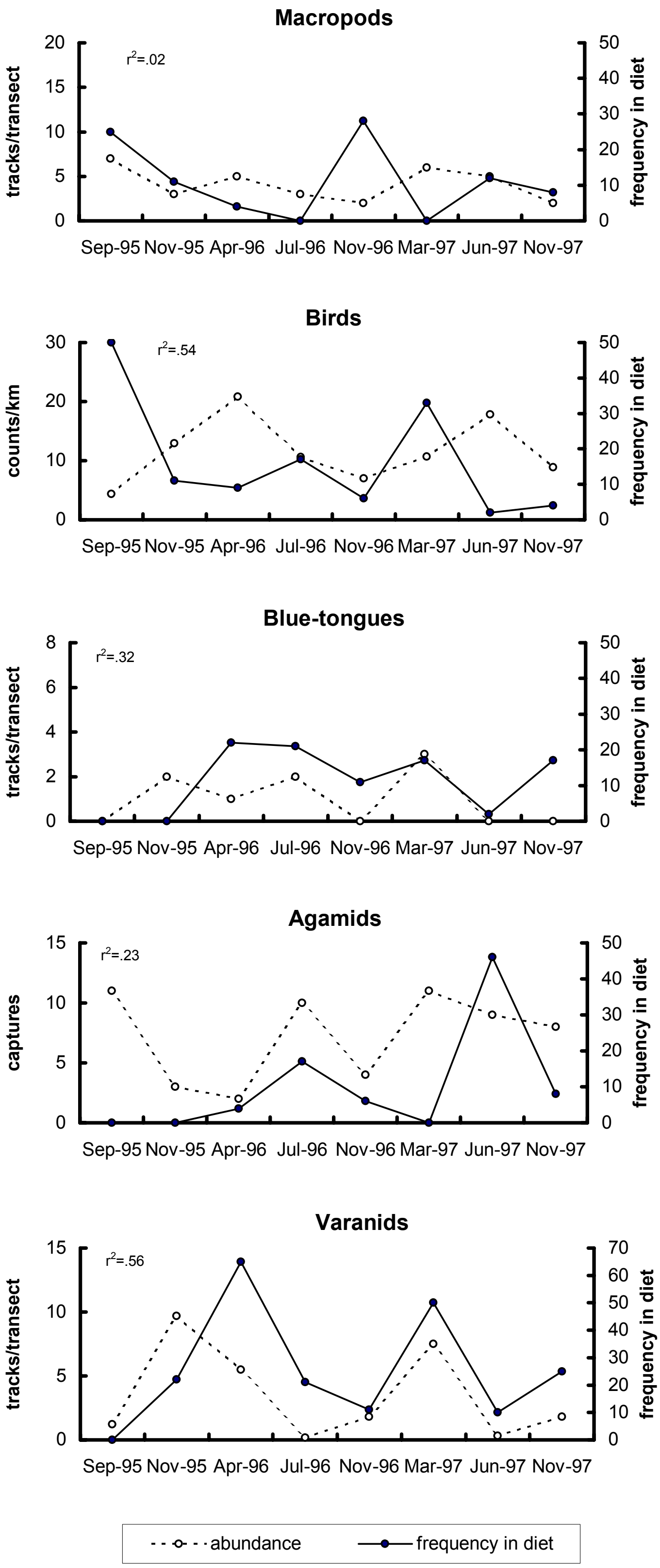


Fig. 3.3 cont.

3.3.3 Index of Relative Importance

Tables 3.2 – 3.6 list the eight major prey categories for the three predators at each study area, based on the Index of Relative Importance (IRI), therefore taking into account the biomass contributions of the prey to the diets. Overall IRI scores are shown for each prey category, based on the pooled data from all surveys in each study area. IRI scores were also calculated for individual survey periods, and these scores were used to rank the prey categories in order of importance, during each survey (Tables 3.2-3.6).

Birds contributed more to the diet of cats at Kintore than any other prey category (highest pooled IRI score), but ranked 1 only in the winter surveys (Table 3.2). Skinks ranked second overall, and varanids third. Varanids were very rarely eaten in the winter surveys, but were the primary prey during three of the four remaining surveys during autumn and summer (Table 3.2). Small mammals and invertebrates were also important in the diet.

The Index of Relative Importance revealed that varanids contributed more to fox diet at Kintore than any other prey overall, followed by invertebrates (Table 3.3). However, birds were the major prey species in the two winter surveys. Small mammals and skinks were also regularly eaten and marsupial moles were minor prey.

At Tennant, varanids, birds and skinks were the most important prey for cats (Table 3.4). As was the case at Kintore, varanids were ranked 1 during the summer surveys but birds became the most important prey during the winter surveys. Invertebrates, rodents and agamids were also regularly eaten by cats at Tennant.

Table 3.2. Importance of prey categories in the diet of cats at Kintore, based on the Index of Relative Importance (IRI). Overall IRI scores are given, based on pooled data from throughout the study period. Prey categories were also ranked during each survey according to the IRI values for that survey.

		Rank per survey					
Prey	IRI	May-96	Aug-96	Dec-96	Apr-97	Jul-97	Dec-97
bird	2368	5	1	4	2	1	3
skink	1165	4	3	2	3	5	1
varanid	998	1	5	1	1	7	-
dasyurid	675	2	4	3	-	3	6
invertebrate	631	3	2	5	4	4	7
rodent	585	6	7	-	-	2	2
agamid	131	7	6	-	-	8	5
macropod	34	8	-	-	-	6	4

Table 3.3. Importance of prey categories in the diet of foxes at Kintore, based on the Index of Relative Importance (IRI).

		Rank per survey					
Prey	IRI	May-96	Aug-96	Dec-96	Apr-97	Jul-97	Dec-97
varanid	2631	1	6	3	-	2	1
invertebrate	1805	2	5	1	-	4	2
rodent	702	3	2	-	-	3	3
bird	503	4	1	-	-	1	6
skink	486	6	3	2	-	5	4
dasyurid	168	7	4	5	-	6	5
mole	35	5	7	4	-	-	-
agamid	3	-	-	-	-	7	-

Table 3.4. Importance of prey categories in the diet of cats at Tennant, based on the Index of Relative Importance (IRI).

		Rank per survey							
Prey	IRI	Sep-95	Nov-95	Apr-96	Jul-96	Nov-96	Mar-97	Jun-97	Nov-97
varanid	1418	6	1	3	2	5	-	4	1
bird	1376	2	3	1	1	6	-	1	3
skink	1227	3	2	5	7	2	-	2	2
invertebrate	629	7	4	2	3	3	-	3	7
rodent	622	1	5	4	4	4	-	6	5
agamid	523	4	7	7	5	1	-	5	4
dasyurid	54	-	6	8	6	7	-	-	6
bilby	23	5	-	6	-	-	-	-	-

Table 3.5. Importance of prey categories in the diet of foxes at Tennant, based on the Index of Relative Importance (IRI).

		Rank per survey							
Prey	IRI	Sep-95	Nov-95	Apr-96	Jul-96	Nov-96	Mar-97	Jun-97	Nov-97
invertebrate	1846	1	3	-	1	1	1	1	-
varanid	897	-	1	-	4	2	-	2	-
bird	497	-	5	-	2	3	3	4	-
rodent	265	5	6	-	3	4	-	5	-
agamid	257	4	4	-	6	6	5	3	-
blue-tongue	160	2	2	-	-	5	4	-	-
skink	141	6	8	-	5	-	2	-	-
dasyurid	28	3	7	-	7	-		-	-

Invertebrates were ranked the most important prey in the diet of foxes at Tennant in all but one survey (Table 3.5). Varanids were the second most important prey category, followed by birds, rodents and agamids.

Dingo diet at Tennant was dominated by varanids (Table 3.6), with varanids ranked first in all but two surveys. Macropods were the other major prey and blue-tongued lizards, agamids, cats and birds also made important contributions to the diet. Skinks and invertebrates were minor prey (Table 3.6).

Table 3.6. Importance of prey categories in the diet of dingoes at Tennant, based on the Index of Relative Importance (IRI).

		Rank per survey							
Prey	IRI	Sep-95	Nov-95	Apr-96	Jul-96	Nov-96	Mar-97	Jun-97	Nov-97
varanid	2096	-	1	1	1	4	1	3	1
macropod	1081	-	2	-	5	1	-	2	3
blue-tongue	711	-	-	2	2	3	3	7	2
agamid	530	-	-	-	3	5	-	1	6
cat	252	-	3	3	6	2	-	5	4
bird	209	-	5	4	4	6	2	8	7
skink	61	-	6	6	-	7	-	6	5
invertebrate	52	-	4	5	-	8	-	4	-

There is potential for bias in calculations of the overall IRI scores because at Tennant, five out of the eight surveys were conducted in the summer months. However, this did not result in more scats being collected in the summer months at Tennant, except for cat scats, where 44 out of 76 scats were collected during summer. Similar numbers of dingo scats were found in both seasons, and more fox scats were found in the winter. At Kintore, there were three surveys in each season, resulting in similar numbers of fox scats being collected in each, but there were considerably more cat scats found in the winter (n = 52) than the summer (n = 18). This may partly contribute to the finding that birds were apparently the most important prey items overall in cat diet at Kintore.

3.3.4 Dietary overlap between species.

There was considerable overlap in the diets of cats, foxes and dingoes (Table 3.7), with greater overlap occurring between cats and foxes than cats and dingoes or foxes and dingoes. A comparison of fox diets between Kintore and Tennant showed that diets were very similar in the two areas. Overlap in cat diets between study areas was equally high (Table 3.7).

The majority of prey items consumed by cats and foxes weighed less than 100 g (Table 3.8). Medium sized prey, weighing between 100 and 999 g (varanids and blue-tongued lizards), accounted for between 7 and 16 percent of cat and fox diet. Less than 5 % of prey items weighed more than 1 kg. Dingoes consumed more medium and large prey than cats and foxes, however 48 % of prey items in dingo diet were in the small size class (< 100 g).

Table 3.7. Dietary overlap between cats, foxes and dingoes at Kintore $_{(K)}$ and Tennant $_{(T)}$

Species pair		Overlap in diets (%)
Fox_K	- Fox_T	0.94
Cat_K	- Cat_T	0.93
Fox_T	- Cat_T	0.86
Fox_K	- Cat_K	0.85
$Dingo_T$	- Cat_T	0.65
$Dingo_T$	- Fox_T	0.63

Table 3.8. Percentage of prey items taken by cats, foxes and dingoes in 3 size classes: small (< 100g), medium (100g - 999g) and large (> 1000g)

	Tennant			**Kintore**		
Size class of prey	cat	fox	dingo	cat	fox	dingo
small	87	80	48	92	86	-
medium	11	16	36	7	14	-
large	2	4	16	1	0	-

3.4 DISCUSSION

3.4.1 Staple, supplementary and opportunistic prey

In contrast to most dietary studies of predators in Australia, results from this study did not show an overwhelming dominance of mammalian prey in the diets of cats, foxes and dingoes. Reptiles apparently contributed more to carnivore diets in the Tanami Desert than has been found elsewhere in Australia. However, prey were consumed opportunistically, with the importance of most prey categories fluctuating in varying degrees of accordance with their abundance in the field.

Newsome *et al*. (1983) have defined three major prey categories for vertebrate predators: staple, supplementary and opportunistic. *Staple prey* are species that can usually be relied on over time to support predators, even though they may not necessarily comprise the highest average percentage occurrence. *Supplementary prey* may become the most important prey items when the staple prey decline in abundance, but are generally a regularly eaten but minor part of the diet. *Opportune prey* are those irruptive species that cannot be relied on but are occasionally very abundant (Newsome *et al*. 1983). This classification of prey categories was not adequate to satisfactorily describe the diets of predators in this study. A staple prey that large mammalian carnivores can consistently rely on does not exist in the spinifex grasslands of arid Australia. The abundance of birds and mammals fluctuates erratically, depending on rainfall (Chapter 2, Southgate and Masters 1996), and many species of reptiles show a marked reduction in activity during the winter months. However, seasonal changes in the availability of reptiles are highly predictable, being temperature dependent (Greer 1989) and skinks and varanids were generally abundant between October and April during this study. It is therefore appropriate to recognise another category of prey, the *seasonal staples*, to classify the significance of skinks and varanids in the diets of predators in central Australia. This category is similar to Corbett's (1995) 'seasonally predictable prey' but whereas Corbett's definition refers to the seasonal availability of prey, my definition implies that the prey are regularly consumed during the seasons that they are plentiful.

Cats, foxes and dingoes had very broad diets during the 2.5 years of this study. Varanids were seasonal staples for dingoes. Blue-tongued lizards, agamids and macropods were supplementary prey, which were eaten more frequently when varanids were scarce. Birds were eaten opportunistically by dingoes.

Invertebrates were the only prey category that were consistently consumed by foxes during this study, and may constitute a staple prey, particularly at Tennant. Varanids were seasonal staples for foxes. Small mammals were eaten fairly consistently, but were never in sufficient quantities during the study period to support these predators, so are best described as supplementary prey. Foxes also ate skinks as supplementary prey, and birds as opportunistic prey.

No one category could be designated staple prey for cats, but mammals were the most consistently eaten prey and skinks were seasonal staples. Varanids and birds were supplementary prey for cats, during summer and winter respectively.

3.4.2 Importance of reptilian prey

When biomass of prey was taken into account, the varanids (in most cases the sand goanna, *Varanus gouldi*), were the most important prey sustaining predator populations in the spinifex grasslands of the Northern Territory. The Index of Relative Importance ranked the varanids as the primary prey for cats and dingoes at Tennant and foxes at Kintore. In fox diet at Tennant, varanids were ranked second to invertebrates and although varanids were ranked behind birds and skinks in cat diet at Kintore, they remained the major prey category in 3 out of 6 surveys at Kintore.

Although the sand goanna is totally inactive between May and September, it is a useful food source during the rest of the year because it is reliably abundant, regardless of rainfall (Chapter 2), it is sufficiently large (300-400 g) for one goanna to sustain a fox or cat for one day (Marlow 1992, Dickman 1996) and its visceral fat bodies (Greer 1989) make it a rich source of food. Reptiles generally provide more kilojoules of energy per gram than mammals (Konecny 1987).

That reptiles are important prey for mammalian carnivores is an unprecedented result in dietary studies of dingoes and foxes. Reptiles occurred in 76 % of dingo scats and 58 % of fox scats collected during this study. In a review of eight dingo studies conducted throughout Australia (Corbett 1995), pooling 12,802 stomach and faecal samples, reptiles represented only 1.8 % of prey items. Reptiles (including goannas) were common and abundant at one study area in the Top End of the Northern Territory, but occurred in only 8 of 6722 dingo scats (Corbett 1995). At another study area in central Australia (inhabited by rabbits), reptiles accounted for only 11.9 % of prey items consumed by dingoes (Corbett and Newsome 1987). In a summary of 30 fox dietary studies conducted throughout Australia (Marlow 1992), frequency of occurrence of reptiles was usually less than 15 %. Even in arid areas where the sand goanna was apparently common, it was not recorded at all in 95 fox stomachs examined (Ryan and Croft 1974). However, previous studies have found reptiles to contribute significantly to the diets of cats (Bayly 1976, Paltridge *et al*. 1997), bobcats (*Lynx rufus*, Delibes *et al*. 1997) and coyotes (*Canis latrans*, Hernandez *et al*. 1994) in arid areas. The relationship between latitude of study site and frequency of occurrence of reptiles in the diets of cats has been examined by Fitzgerald and Turner (2000). At locations less than 35 ° north or south of the equator reptiles were usually present in at least 30 % of diet samples whereas at latitudes greater than 35 ° reptiles are rarely eaten by cats (Fitzgerald and Turner 2000).

3.4.3 Importance of avian prey

Birds were an important part of the diet of cats and foxes in the winter, when reptiles were less active, and birds tended to be more abundant (although they did not increase in numbers during the first year at Kintore). Fluctuations in the abundance of birds in central Australia are due largely to the movement patterns and breeding of nomadic birds, which periodically travel large distances in search of food resulting from good rain events (Schodde 1982). Significant summer rainfall in central Australia has the potential to produce an abundance of nectar-producing flowers and grass-seed in the autumn and early winter (Davies 1984, Jacobs 1984, Latz 1996), providing a food source for the nomadic birds. This enables predators to switch from a predominantly reptilian diet in the summer to a winter diet of birds. During years of low rainfall, however, the winter bird community comprises only resident insectivorous species, usually in low abundance (Chapter 2) and it is during these times that predators may struggle to meet their nutritional requirements.

3.4.4 Importance of mammalian prey

The proportion of small mammals in the diets of cats and foxes was correlated with the relative abundance of small mammals and it seems likely that this prey category would dominate the diets of cats and foxes during an irruption of small mammals. Previous analysis of cat diet in the Tanami Desert region revealed that the Spinifex Hopping Mouse (*Notomys alexis*) was the most frequently consumed prey item (Paltridge *et al.* 1997). This was not reflected in the current study, probably because small mammal numbers were low during the study period, despite considerable rainfall occurring in the second year. In spinifex grasslands elsewhere in central Australia, it has been shown that a succession of two to three years of above average rainfall is required for small mammal populations to increase significantly (Southgate and Masters 1996).

Macropods form the staple prey for dingoes in many other areas of Australia (Whitehouse 1977, Robertshaw and Harden 1985, Thomson 1992). The consumption of macropods (including the Red kangaroo *Macropus rufus,* and the Spectacled Hare-wallaby *Lagorchestes conspicillatus*) by dingoes at Tennant did not seem to be influenced by the relative abundance of macropods, which appeared to be fairly consistent during the study period. The peaks in consumption of macropods were during periods when most other prey species appeared to be scarce. As red kangaroos are a very mobile species (Denny 1982), it is possible that their numbers did rise and fall between the July 1996 and November 1996 surveys, which is the study period represented by scats collected during the November survey.

3.4.5 Importance of invertebrate prey

Invertebrates were a major component of the diet of foxes in this study, representing 31 % of prey items consumed. They were consistently eaten by cats, comprising 16 % of their diet, but only accounted for 6 % of prey items eaten by dingoes. Beetles were the invertebrates most commonly consumed by foxes, whereas cats ate more grasshoppers than beetles (Table 3.1). Most studies of cat diet have shown invertebrates to be a consistent but overall fairly minor dietary item (Fitzgerald and Turner 2000, Pearre and Maass 1998), although their importance may increase when other prey types become scarce (Hubbs 1951, Fitzgerald and Veitch 1985, Paltridge *et al.* 1997). Invertebrates tend to be more commonly eaten by cats in low latitude areas (Pearre and Maass 1998).

They are useful prey items in the desert as they have a higher proportion of water per unit nitrogen and a higher proportion of fat per gram of body mass than vertebrates (Konecny 1987). Invertebrates are also important prey for canids, both in the Namib and Sonoran Deserts (Bothma *et al*. 1984, Hernandez *et al*. 1994).

3.4.6 Comparison of diets between predator species

This is the first study to simultaneously monitor the diets of cats, foxes and dingoes in relation to prey availability. There was considerable overlap in the diets of all three species but fox and cat diets were more similar than fox and dingo or cat and dingo diets. Dingoes ate fewer small prey and more large prey (including macropods, cats and echidnas) than foxes or cats. Some degree of prey size partitioning was also evident when comparing the diets of foxes and dogs in eastern Australia (Brown and Triggs 1990), a suite of four mammalian carnivores in South Africa (Avenant and Nel 1997) and cats, ferrets and stoats in New Zealand (Alterio and Moller 1997).

The main cause of overlap between predator diets in this study was the consumption of reptiles, (particularly varanids and agamids) and also the combined bird species category. My inability to identify bird species in the scats may have led to an overestimation of the proportion of small prey items in the diet of dingoes however, if some of the birds consumed by dingoes were larger species, such as the Australian Bustard (*Ardeotis kori australis*). The main differences between cat and fox diets were greater consumption of birds and reptiles by cats and increased importance of invertebrates in the diet of foxes. Small mammals were equally important to cats and foxes although dasyurids were ranked above rodents in cat diet at Kintore whereas foxes ate more rodents than dasyurids at these sites, despite many more dasyurids being captured than rodents (Chapter 2).

In order to fully determine the degree of niche partitioning, and therefore the potential for interspecific competition, it is necessary to identify prey items to the species level, which is not often possible in scat analysis. Further identification of birds, in particular, could provide much more information on selective use of prey. Interspecific competition only occurs when a resource is in limiting supply (Begon *et al*. 1990), and it may be that cats, foxes and dingoes can all coexist eating similar prey in the summer months because the abundance of reptiles is not a limiting factor. Competition is probably greater in the winter. Like studies elsewhere (Bayly 1978, Triggs *et al.* 1984, Catling 1988, Risbey *et al.* 1999), that have shown cats and foxes and/or wild dogs to share a relatively abundant staple prey species (rabbits or ringtail possums *Pseudocheirus peregrinus*), the niche differentiation may be more evident in consumption of supplementary prey.

Cat remains were found in 3.3 % of fox scats and 9.1 % of dingo scats in this study. Intraguild predation has been observed in other studies (Rau *et al.* 1985, Palomares *et al.* 1995, O'Donoghue *et al.* 1995) and it has been suggested that carnivores that prey on competing predator species when prey availability is low, may serve to take the pressure off the depleted prey species (O'Donoghue *et al.* 1995).

3.4.7 Predation on vulnerable species

Cat and fox predation has been implicated in the demise of medium sized mammals in the Australian arid zone (Kinnear *et al.*1988, Morton 1990, Short *et al.* 1992, Gibson *et al.* 1994). In this study, three threatened species of mammal were found in predator scats: the bilby, mulgara and marsupial mole. Despite the dominance of small prey in the diet of cats, it appears that they are also capable of preying on larger species, such as the bilby, even if they are only taking young animals. Bilbies and mulgaras were both rare occurrences in the scats, but this is to be expected given their low densities in the study areas. Marsupial moles were recorded in scats on 14 occasions, all during the first year of the study. This may represent a significant level of predation on this relatively unknown species (Paltridge 1998), as no sign of marsupial moles was observed at the study sites at all during the surveys. All three predators were recorded to consume marsupial moles, but fox scats contained the highest proportion of this species.

Given the predator diet information we have from elsewhere in Australia where rabbits or native mammals are plentiful, it seems likely that when medium sized mammals were abundant in the central Australian deserts, they would have been important prey for cats, foxes and dingoes. When mammal populations declined during drought periods, varanids and other reptiles would have helped to buffer predator populations from starvation, at least during the summer months. Even if predator numbers eventually declined, when seasonal conditions improved the arrival of the highly mobile nomadic bird species would have preceded the build up of mammals, perhaps allowing the predators to increase before the medium sized mammals were able to recover. It is during this time that predators could have had a serious impact on medium sized mammal species. While cats, foxes and dingoes continue to roam the Tanami Desert, the future of the remaining threatened mammal species in the area - the bilby, mulgara and marsupial mole - may not be secure.

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CHAPTER 4

THE ABUNDANCE OF FOXES, CATS AND DINGOES IN RELATION TO PREY AVAILABILITY IN TWO AREAS OF THE TANAMI DESERT

Preamble to Chapter 4

In chapter 3, I established the importance of reptilian prey in the diets of cats, foxes and dingoes in the Tanami Desert. Birds were found to increase in importance during the winter months. This chapter presents information on the relative abundance of cats, foxes and dingoes in relation to prey availability, in two areas of the Tanami Desert.

I aimed to investigate the persistence of predator populations during drought, and their rate of recovery after drought. I examine utilisation of the major habitat types by predators, to determine whether prey are likely to have any refugia from predation.

In this chapter I also challenge the concept that fox distribution is linked to that of the rabbit in central Australia, and that extinctions of medium-sized mammals occurred in many desert areas prior to invasion by foxes.

4.1 INTRODUCTION

Ten species of Australian arid zone mammals are now extinct in central Australia, and thirteen persist in mere fragments of their former distribution, many restricted to offshore islands (Morton 1990). A combination of habitat degradation by introduced herbivores, altered fire regimes since Aboriginal People ceased living traditional lifestyles, and predation by cats (*Felis catus*) and foxes (*Vulpes vulpes*) are believed to have caused the declines, but there is disagreement over the significance of each factor in causing the declines (Finlayson 1961, Bolton and Latz 1978, Burbidge and McKenzie 1989, Morton 1990, Smith and Quin 1996, Short *et al*. 2002).

Predation by introduced predators has often been dismissed as a primary cause of mammalian extinctions on the Australian mainland (Kitchener *et al*. 1980, Burbidge and McKenzie 1989, Johnson *et al*. 1989, Morton 1990) for reasons including (i) the cat colonised the arid interior at least 50 years (and possibly many more) before the declines were evident, (ii) extinctions occurred in the northern deserts where foxes apparently never occurred and (iii) if a new eutherian predator was going to have such a devastating impact, why didn't the dingo (*Canis lupus dingo*)? Cats and foxes are considered to be capable of eliminating prey populations only when predator numbers are bolstered by introduced species (such as rabbits, *Orcytolagus cuniculus*, or house-mice *Mus domesticus*; Smith and Quin 1996) or when prey populations have already been reduced by habitat degradation (Burbidge and McKenzie 1989, Morton 1990). However, arid zone mammals are regularly subjected to drought conditions, causing natural contraction of populations (*e.g.* Short *et al*. 1997). If cats and foxes are able to maintain predation pressure on prey populations during such periods, local extinction of populations may be possible.

Further debate on the role of introduced predators in the mammalian declines is hampered by a lack of information on the timing and extent of fox colonisation in the Northern Territory and little understanding of factors affecting the distribution and abundance of predators in central Australia in non-pastoral areas. Whether predators target refuge habitats such as palaeodrainage lines (Morton 1990) during dry periods, and their ability to sustain predation on fragmented populations of prey both during droughts and in the post-drought recovery, are important issues in determining the potential for predators to have caused extinctions of Australian arid zone mammals.

The dingo is the best studied of the large carnivores in the Northern Territory, but research has focused on rabbit-infested (primarily pastoral) areas to the south (Corbett and Newsome 1987) and tropical systems to the north (Corbett 1995a). The predation models developed do not apply to the spinifex grasslands of central Australia. The dingo is assumed to be distributed throughout the Northern Territory (Corbett 1995b), but its requirement for drinking water (except when prey are particularly abundant, Green 1973) probably limits its distribution through the desert areas (Fleming *et al.* 2001).

Cats were present in central Australia before the end of the nineteenth century (Abbott 2002). They are distributed throughout the Australian deserts and are considered to be capable of surviving independently of fresh water (Johnson 1991). Factors affecting their abundance at landscape and local scales are unknown.

There have been no specific studies of foxes in the Northern Territory, or adjacent parts of Western Australia. The colonisation of this area by foxes has not been documented (Jarman 1986) but it has been suggested that the distribution of foxes in the Northern Territory is linked to rabbit populations (Low 1984). After comprehensive fauna surveys of the Great Sandy and Tanami Deserts between 1977 and 1983, it was concluded that foxes were virtually absent from these regions (McKenzie and Youngson 1983, Gibson 1986).

The bilby (*Macrotis lagotis*) is an example of a medium-sized mammal that suffered a massive decline in distribution during the period that many other mammal species disappeared. It is now patchily distributed across one fifth of its former range. In the Northern Territory bilbies are restricted to the Tanami Desert, but appear to be declining at the southern edge of their current range (Southgate 1990a). Historically, foxes were implicated in the demise of the bilby (Wood Jones 1925, Finlayson 1961) and it has been suggested that bilbies are able to persist in northern parts of the Tanami Desert because foxes do not occur there. Effective management of this rare species requires a better understanding of predator distribution and abundance at both landscape and local scales, particularly in relation to rainfall and prey availability.

This chapter presents information on the abundance of cats, foxes and dingoes in two areas of central Australia: (i) an area of the northern Tanami Desert which was believed to be outside the normal range of the fox (Coman 1995) but at the core of bilby distribution (Southgate 1990a) and (ii) 400 km to the south, which corresponds to the southern edge of bilby distribution in the Northern Territory. Rabbits were absent from both study areas and the study was conducted during dry to average seasons when native mammals were scarce. I aimed to determine whether cats, foxes and dingoes were able to persist in the spinifex grasslands during dry conditions when native mammals were scarce, and to document their abundance when seasonal conditions improved. Predator activity was compared between two major habitat types: sandplain and palaeodrainage channels. Enhanced moisture and nutrient levels of the palaeodrainage channels are thought to have provided refuge for many of the extinct medium-sized mammal species during droughts (Morton 1990), and are considered to be important for the bilby and mulgara (Southgate 1990b, Gibson and Cole 1992). It has been suggested that predators would target these refugia during droughts (Morton 1990).

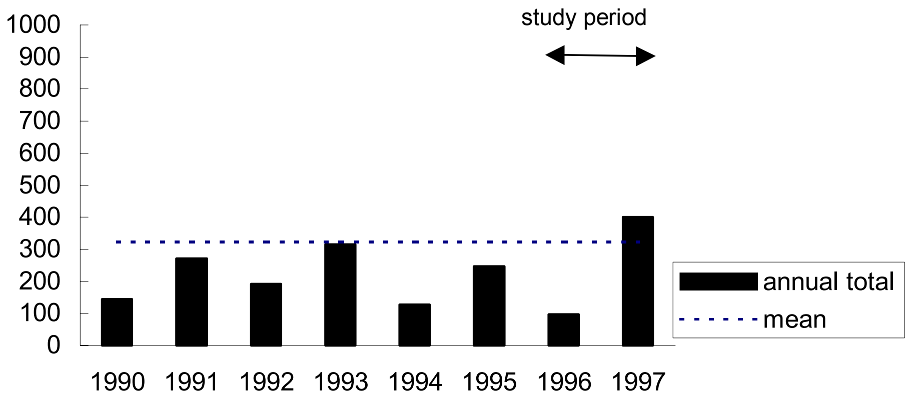
4.2 METHODS

4.2.1 Study Areas

The study was conducted in two locations in the Tanami Desert, at latitudes approximately 400 km apart. The northern study area, 'Tennant' was situated in the northern Tanami Desert (19° 12′ S, 132° 40′ E), 200 km north-west of Tennant Creek. This area was chosen as being in the center of bilby distribution in the Northern Territory (Southgate 1990a), and belongs to the Tanami Bioregion (Thackway and Cresswell 1995). The southern study area 'Kintore' represents the southern limit of current bilby distribution in the Northern Territory (Southgate 1990a), and is located approximately 450 km west-north-west of Alice Springs (22° 51′ S, 129° 57′ E), at the intersection of the Tanami, Great Sandy and Gibson Deserts. This study area is situated between Nyirripi and Kintore Aboriginal Communities and falls within the Great Sandy Desert Bioregion (Thackway and Cresswell 1995). The entire study region is Aboriginal Freehold land, and is sparsely populated and undeveloped.

The climate of the area is semi-arid, with very hot summers and mild winters. Mean annual rainfall is higher at Tennant (422 ± 192(SD) mm) than Kintore (322 ± 186(SD) mm). When the study commenced, in 1996, Kintore was experiencing drought conditions, as five of the previous six years had received below average rainfall (Fig. 4.1). During 1996, Kintore received only one third (97 mm) of its mean annual rainfall.

(a) Kintore



(b) Tennant

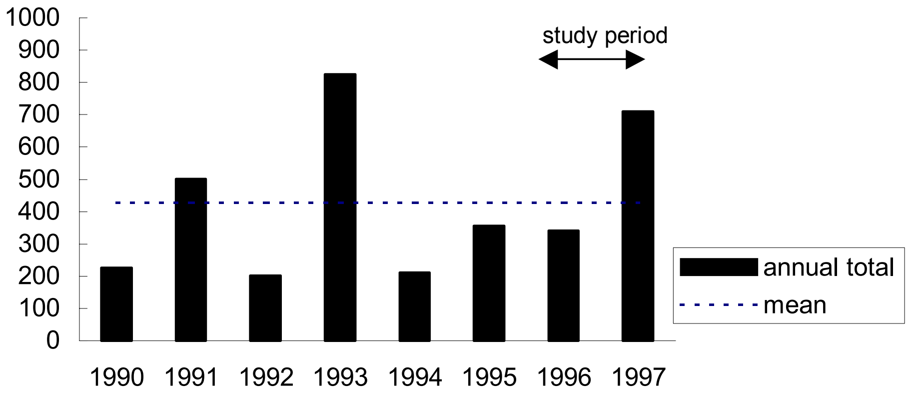


Fig. 4.1 Annual rainfall totals in the two study areas (a) Kintore and (b) Tennant, 1990-1997.

However, good summer rains fell in early 1997, and the annual total for 1997 was 400 mm. Rainfall at Tennant was slightly less than average in 1996 (annual rainfall = 342 mm) and considerably more in 1997 (annual rainfall = 706 mm). This was the first year of above-average rainfall at Tennant since 1993 (Fig. 4.1).

Both study areas comprise predominantly sandplain habitat, dominated by a mixture of spinifex species (*Triodia pungens and T. schinzii* at Tennant and *T. pungens* and *T.*

basedowi at Kintore) with an overstory of scattered shrubs. Palaeodrainage channels, characterised by the presence of *Melaleuca* spp., also occur in both areas. Full descriptions of the study areas are presented in Chapter 2.

Within each study area, I established three monitoring sites, approximately 20 km apart. Nested within each site was a pair of study plots, each 4 km^2 in area. The two plots were positioned approximately 4 km apart, one plot located in sandplain habitat and the other in palaeodrainage habitat. All study plots were situated in mature (unburnt for > 5 years) spinifex communities, which remained unburnt throughout the study.

4.2.2. Data collection

Field surveys were conducted approximately every four months from April 1996 to November 1997 at Tennant, and May 1996 to December 1997 at Kintore. Monitoring was conducted for three consecutive days at each site.

At the beginning of the study, a permanent tracking transect was established around the perimeter of each study plot, to monitor predator abundance using track counts. The study plots were rectangular in shape, 4 km long and 1 km wide, and thus the tracking transect was 10 km in length. A heavy implement (e.g. chain attached to a piece of heavy steel, 1.5 m long) was dragged behind a four-wheel-drive vehicle prior to the first day of tracking at each plot, to loosen the sand and clear animal tracks and vegetation from the transect. Inspection of the transects on subsequent days was done from an all-terrain-vehicle travelling at a constant speed of 10 km/h, and dragging a lighter implement (e.g. light steel bar with chain) to eliminate accumulated tracks and prepare a fresh tracking surface. The sandy substrate of both the palaeodrainage and sandplain habitats enabled footprints of predators to be registered clearly. When tracks were seen, the vehicle was stopped until the tracks were identified. Tracks were distinguished on the basis of size, shape, the presence of claw-marks (which were often visible at fox and dingo tracks but not cat tracks) and gait (Triggs 1996). For each new set of carnivore tracks seen, the following data were recorded: predator species, distance of tracks from start of transect, distance tracks followed transect, approximate size of tracks, and whether the tracks belonged to one or more individuals.

Prey availability was monitored at each study plot during the same 3-day period as the predator surveys were conducted. A detailed description of the prey monitoring procedures is described in Chapter 2. Briefly, small mammals and reptiles were monitored using pitfall and Elliott traps (180 trap-nights per study plot per survey). Invertebrates were collected from pitfall traps to obtain dry biomass measurements. The relative abundance of birds was assessed along 1 km walked transects (1 transect per study plot), and activity of macropods, goannas and bilbies was monitored by track counts along the tracking transects, with data expressed as the proportion of 500 m cells per plot with sign recorded.

4.2.3 Data analysis

Predator track counts were converted to an index of abundance for each species, based on a technique that took into account the daily home range size of the predators, the position of tracks along the transect, the number of tracks observed travelling together and the relative size of the tracks. Dingoes were assumed to have daily home ranges large enough to encompass entire study sites (including both study plots) based on data from north-western Australia (Thomson 1992) and Kosciuzsko National Park in New South Wales (McIlroy *et al*. 1986) where the mean minimum distance travelled by dingoes in a 24 h period ranged between 3.3 and 5.8 km. Consequently, if tracks were present, only one dingo was recorded per site unless multiple tracks travelling in parallel indicated that dingoes were travelling in groups. Where dingo tracks were recorded on both study plots within a site on the same night, a value of 0.5 animals was assigned to each study plot. (Although this may not be technically correct procedure, as the 0.5 values are being treated as independent data in the analysis when they are clearly not independent, it was extremely rare for dingoes to be recorded on both transects within a site on the same day: it occurred on 2 out of 54 days at Kintore and 3 out of 54 days at Tennant.)

There are no data available on daily movement patterns of foxes in Australia but, in this study, foxes were recorded travelling continuously along the transects for at least 2 km on four occasions, and in two instances I tried following the tracks of individual foxes from their dens (with experienced Aboriginal trackers) and eventually lost the tracks after 4 km or more. For the purpose of data analysis in this study, it was assumed that the home range of a fox would encompass an entire study plot, but simultaneous tracks on both study plots during a 24 h period were likely to be made by different animals.

Consequently, if fox tracks were present, one fox was recorded per plot, unless tracks of markedly different size were evident.

Daily home ranges of cats are smaller than those of foxes and dingoes: the mean maximum distance between the outer-most points of the daily home ranges of five cats in the Kintore study area was 2.2 km (Appendix A) and the shape of the daily home ranges was approximately linear. This was based on fifteen 24 h tracking periods conducted over a 9 month period. Using this information, the precise locations of cat tracks on the study plot were mapped each day and cat tracks located more than 2.2 km apart were assumed to be different individuals. However, the gait and relative size of the tracks were used to classify cat tracks into three different size classes, called males, females and "young ones", by Aboriginal trackers employed on the surveys. Where markedly different sized tracks were recorded within 2.2 km of each other, these were also counted as different animals.

Using the above criteria, the numbers of cats, foxes and dingoes recorded at each study plot were evaluated for three consecutive nights; the counts were then summed over the 3-day period. The abundances of each predator were compared between habitats and study areas and between the 6 survey periods using 3-factor analysis of variance, where time of survey was a repeated measures factor, study area and habitat were fixed factors, and the three sites in each study area were spatial replicates. Similar analyses were conducted on the various prey categories, except that the activity data from the tracking transects (for varanids, bilbies and macropods) were first normalised by the arcsine transformation, as proportion data form a binomial distribution (Zar 1996).

The relationships between the abundance of each predator species and the abundances of individual prey categories were determined using Pearson correlation analysis (in the Basic Statistics module of Statistica Release 5, Statsoft 1995). Relationships between the abundances of the three predator species were also investigated, as were the correlations between predator abundance and cumulative rainfall in the previous 3, 6, 12 and 18 months. Rainfall data for each study area were obtained from a gridded data set provided by the Bureau of Meteorology, which extrapolates monthly rainfall totals for 0.25 degree blocks from the nearest meteorological stations using the Barnes successive correction technique (Jones and Weymouth 1997).

4.3 RESULTS

Results of the Analyses of Variance of the effects of study area, habitat and time on the abundances of cats, foxes and dingoes are presented in Table 4.1. Correlations between predator abundances and variables relating to prey availability and rainfall are presented in Table 4.2.

4.3.1. Foxes

Track surveys revealed that foxes are not, in fact, absent from the northern Tanami Desert, despite previous suggestions by Low (1984) and Gibson (1986). They were recorded at all sites in both study areas. Furthermore, Traditional Owners of the Tennant study area revealed that they had first hunted foxes in this area during the time of the second World War (Irene Driver, Engineer Jack, personal communications).

Overall, foxes were equally prevalent at Tennant and Kintore. Although the effect of study area was not significant, there was a significant interaction between time and study-area, because foxes were more abundant at Kintore than Tennant during some survey periods but not others (Fig.4.2a).

Fox abundance declined to very low levels at Kintore during the dry conditions of 1996, and by December 1996, they were present at only one of the three Kintore sites. However, seven months later they were present at all sites. By December 1997, abundance had again decreased, but an active den with juvenile fox tracks present was found at one site during this survey. Fox abundance peaked at Tennant in autumn 1997. There was a significant decrease in fox numbers in the following six months, and they were at their lowest point for the study period in November 1997.

There was a significant interaction between latitude and habitat because at Kintore foxes tended to utilise the palaeodrainage habitat more than the sandplain, whereas at Tennant the majority of fox tracks were detected in the sandplain habitat.

Fox abundance was positively correlated with the availability of small reptiles, and negatively correlated with dingo abundance.

Table 4.1 Results of the Analyses of Variance comparing the abundances of cats, foxes and dingoes between two study areas, two habitats (fixed factors) and 6 times (repeated measures) fixed factor). The *P* values of significant results are highlighted in bold and the study area or habitat (T=Tennant, K=Kintore, P=palaeodrainage) with significantly higher abundances are shown in parentheses.

Source of variation		**CAT**		**FOX**		**DINGO**	
	d.f.	**F**	***P***	**F**	***P***	**F**	***P***
study-area	(1,8)	9.30	**0.015 (T)**	0.24	0.638	5.65	**0.045 (T)**
habitat	(1,8)	0.63	0.451	1.15	0.314	18.98	**0.002 (P)**
time	(5,40)	8.84	**0.0001**	3.15	**0.017**	2.22	0.071
study-area*habitat	(1,8)	0.32	0.587	6.94	**0.030**	2.51	0.152
study-area*time	(5,40)	5.13	**0.001**	4.02	**0.005**	0.52	0.758
habitat*time	(5,40)	2.10	0.085	1.06	0.395	1.41	0.241
study-area*habitat*time	(5,40)	0.71	0.619	0.59	0.708	0.25	0.937

Table 4.2 Correlations (r^2 values) between the abundances of cats, foxes and dingoes and variables relating to prey availability and cumulative rainfall. Marked correlations are significant at $p < 0.05$.

Variable	**CAT**	**FOX**	**DINGO**
cat	-	-0.12	0.08
fox	-0.12	-	-0.39 *
dingo	0.08	-0.39 *	-
small mammal	-0.04	-0.13	-0.02
bird	0.35 *	0.01	-0.14
small reptile	-0.19	0.29 *	-0.14
goanna	-0.22	-0.03	0.07
macropod	0.37 *	0.18	0.03
invertebrate	-0.27 *	-0.15	0.05
3 month rainfall	0.11	0.26	0.00
6 month rainfall	0.29 *	0.27	-0.04
12 month rainfall	0.43 *	0.16	0.19
18 month rainfall	0.41 *	0.21	0.17

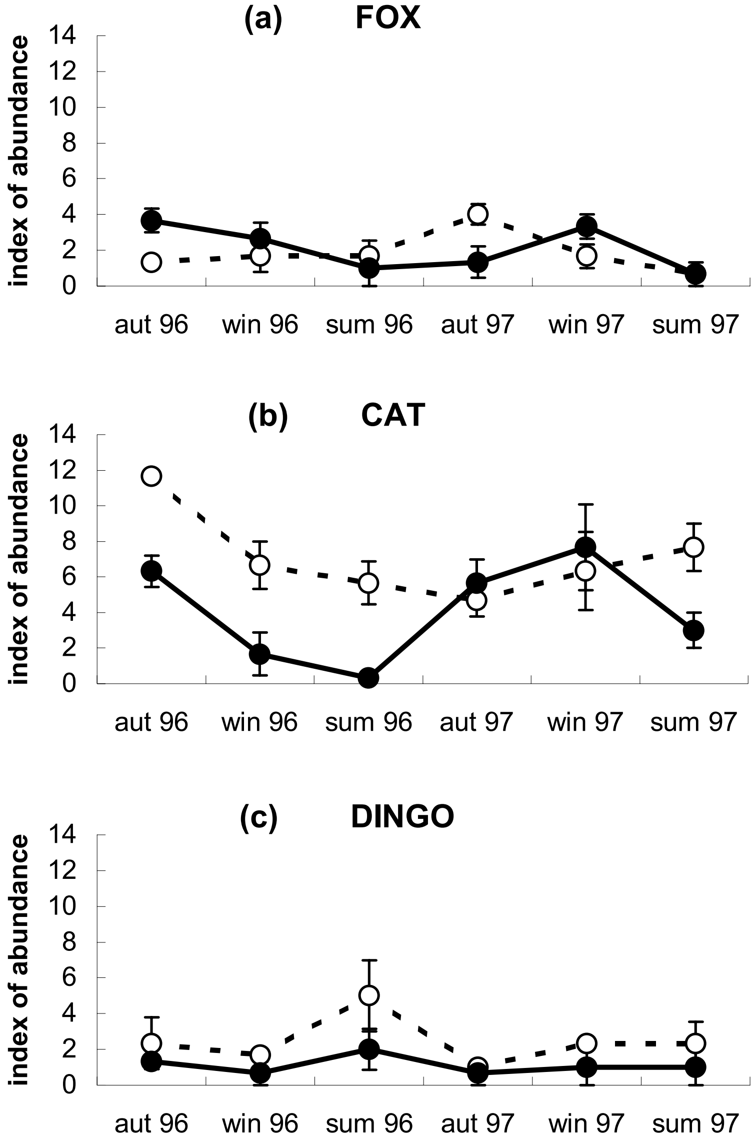


Fig. 4.2. Relative abundance of (a) foxes, (b) cats and (c) dingoes at Tennant (dashed line) and Kintore (solid line), 1996-1997. Data are means of 2 habitats at 3 sites ± standard error.

4.3.2 Cats

Overall, the abundance of cats was significantly higher at Tennant than Kintore (Fig. 4.2b). Cat populations at Kintore declined to very low levels in the first year of the study, and in December 1996 only one cat was recorded during the 9 days of track counts. However, by the following April cats were present on five of the six transects after significant rainfall (260 mm) in the summer months.

Three female cats were captured in the vicinity of one of the Kintore sites in October 1996, for a radio-tracking study. The mean body mass of the three animals was 2.3 kg and none showed any sign of breeding. No sign of kittens was seen at any of the Kintore sites during the 1996 surveys. In August 1997 two different females captured at the same site had a mean body mass of 3.3 kg and both were found to be nursing kittens. Evidence of young kittens was also found within the Kintore study area in February, April and December 1997. Tracks judged to be sub-adult cats were recorded on two transects in July 1997.

At Tennant, cat numbers also showed an initial decline in 1996 but did not fall to levels as low as Kintore. As radio-tracking was not attempted at Tennant, there was less opportunity to detect breeding activity.

Cat abundance was significantly correlated with the abundance of birds. Cats were equally abundant in both habitat types, at both Kintore and Tennant. There was no evidence that cats targeted the palaeodrainage habitat during droughts.

4.3.3 Dingoes

Overall, the abundance of dingoes was significantly greater at Tennant than Kintore during the study period (Fig. 4.2c). At Tennant, dingoes were recorded at all three sites during four surveys and two out of three sites on the other two surveys. Only the first of the Kintore surveys recorded dingoes at all three sites and during four surveys they were present at only one site. Further evidence supporting the disparity in dingo abundance between the two study areas lies in the number of scats collected for dietary analyses. Similar search effort in both study areas yielded a total of 71 dingo scats being collected during the six surveys at Tennant, but none could be found at the Kintore sites.

Apart from a peak in dingo abundance at Tennant in November 1996, dingo densities were quite stable throughout the study period, and within study areas there were no significant fluctuations in abundance between surveys (Fig. 4.2c).

Dingo tracks were rarely recorded outside the palaeodrainage habitat in either study area. There were no significant correlations between dingo abundance and abundance of any of the major prey categories.

4.4 DISCUSSION

4.4.1 Foxes

This study has revealed that the distribution of foxes extends further north into the Tanami Desert than previously reported (Low 1984). During the study period, foxes were present in the Tennant study area during every survey, often occurring at all three sites. In contrast, rabbits were virtually absent from the Tennant study area, dispelling the notion (of Low 1984) that fox and rabbit distributions are linked in the Northern Territory. Rabbit remains did not occur in any of the 53 fox scats analysed from Tennant (Chapter 3).

It has been suggested that the distribution of foxes may temporarily expand during good seasons (Coman 1995). This study commenced after two years of below-average rainfall in the Tennant study area, and the drier-than-average conditions continued during the first year of surveys. Occurrence of foxes at these sites in 1996 indicates that they can persist in the northern Tanami Desert during poor to average seasons, despite a paucity of mammalian prey. Unlike most studies of fox diet in Australia (Green and Osborne 1981, Triggs *et al*. 1984, Jarman 1986, Marlow 1992) mammals were not the staple prey for foxes in the Tanami Desert. In this study, the most important prey were sand goannas (*Varanus gouldi*) and invertebrates (Chapter 3). However birds, small mammals and skinks were also regularly consumed.

Although low densities of foxes were able to persist in both study areas during dry periods, they were not always present at all study sites. At the height of the drought, in December 1996, foxes were only recorded at one of the Kintore sites. However, their mobility allows them to rapidly reinvade vacant territories when conditions improve (Kinnear *et al*. 2002) and by the following winter they were again present at all Kintore sites. This coincided with a significant increase in the abundance of birds at Kintore (Chapter 2), which became the most important prey item for foxes in the area (Chapter 3).

Where is the northern extent of fox distribution in the Northern Territory? In 2001, a fox survey was conducted along a north-south transect, approximately 100 km east of the Tennant study area (Paltridge and Driver, unpublished data). Intensive track searches were conducted in sixty three plots (3 ha in area) along the 250 km transect between locations 19°10'S 135°59'E and 17°22'S 133°04'E. The most northerly fox sign was found at 18°49'S 133°38'E. The only record known further north than this is that of a dead fox found at 18°10'S, 132°48'E in 1993 (David Nash personal communication). There was no sign of foxes at Newcastle Waters (17°20'S, 132°51'E), which was regularly surveyed between during 1996 and 1997, using the same tracking transect method used in the current study (Southgate, unpublished data).

According to Aboriginal People who were still living a traditional lifestyle in the Tennant study area at the time, foxes have been present in the Tanami Desert since the 1940s. This is consistent with the observation that the colonisation of the fox tended to follow that of the rabbit with a lag of about 10-20 years (Jarman 1986). Rabbits were first recorded in the Northern Territory in 1895 and advanced north at a rate in the order of 325 km per year (Strong 1983). They had reached the Tanami Desert by 1910 and were believed to be north of the 20th parallel by 1925 (Terry 1927). Subsequently, fox populations were established in the north-western corner of South Australia by 1932 (Finlayson 1961), and presumably crossed the border into the Northern Territory about this time. Finlayson reported foxes as far north as the 21st parallel in 1956 (Finlayson 1961) and Aboriginal people of the Yuendumu area of the Tanami Desert were familiar with foxes when interviewed by linguists in 1959 (David Nash, personal communication). Since 1965 tracks have been regularly recorded near Rabbit Flat in the western Tanami Desert (Gibson 1986, Parks and Wildlife Commission of the N.T. Biological Records Scheme). A revised map of the distribution of foxes in the Northern Territory based on data from our study sites, and from the Parks and Wildlife Commission of the Northern Territory "Biological Records Scheme" database is presented in Figure 4.3.

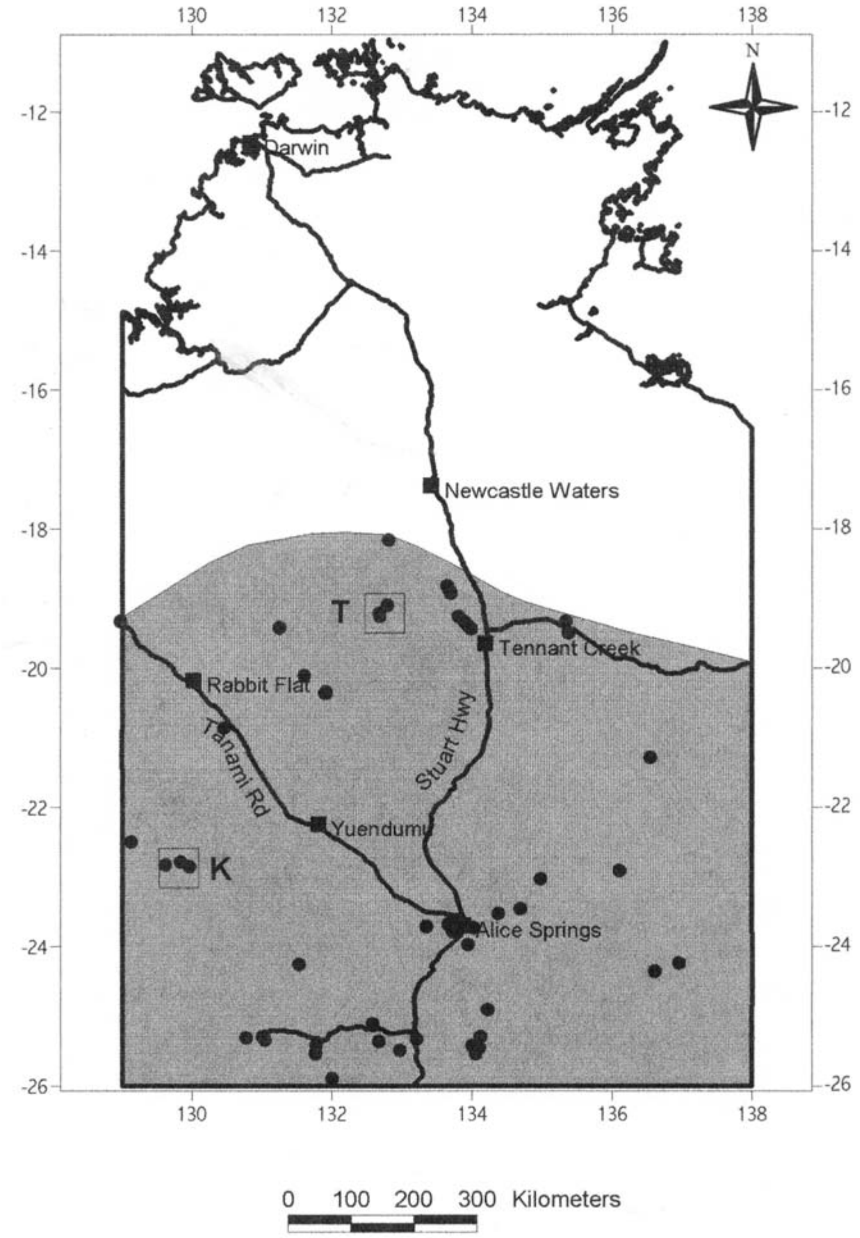


Fig. 4.3 The extent of fox distribution in the Northern Territory (stippled). Data are from the NT Parks and Wildlife Service Fauna Atlas database, as well as records collected during this study. Study sites Tennant (T) and Kintore (K) are shown.

4.4.2 Cats

Overall, cats were the most abundant carnivores in the two study areas. Surveys revealed that they can persist to a certain extent when mammalian prey are scarce, by preying on reptiles (in summer) and birds (in winter; Chapter 3). At the beginning of the study cats were recorded on 5 out of 6 transects at Kintore, despite 6 consecutive years of below-average rainfall (Fig 1.) and very low densities of both birds (< 2 per km of transect) and small mammals (< 2 % trap success). Sand goannas were the most important prey item at this time (Chapter 3). However, when the goanna hibernation period (May-September) coincides with low densities of both mammalian and avian prey, cat populations may eventually experience local extinctions. This occurred at Kintore during 1996. The total number of cats using the six Kintore transects (averaged over a three day period) declined from 6.3 in May to 1.7 in August, and had decreased further to 0.3 by December, when cat sign was only recorded at one of the six transects.

Disappearance of cats from the transects was probably due to a combination of starvation-induced mortality and dispersal out of the study area. In southern Australia, there was substantial mortality caused by nutritional stress each winter, when the staple prey for cats (juvenile rabbits) was not available (Jones and Coman 1982). As felids tend to have low amounts of subcutaneous fat, they have little energy reserved for times of food shortage (Konecny 1987). Cats have also been recorded dispersing large distances (8-48 km) during drought-induced food shortages (Newsome 1991).

However, after 260 mm of rainfall in January and February 1997, cats rapidly recolonised the Kintore study sites, resulting in a significant increase in abundance by April 1997. Although kittens appeared within two months of the first rains, the increase in cat abundance was too rapid to be due to *in situ* breeding alone. The increase must have been caused by cats immigrating into the area, perhaps from more fertile run-on patches outside the study area. Kittens born in February would have only been a maximum of 8 weeks old by the April survey. The average body mass of an 8 week old kitten is 700-800 g (Martin and Bateson 1988), less than one third of adult size. Sub-adult tracks were not recorded on the transects until the July 1997 survey.

This study highlights the importance of nomadic birds to cat populations in the Tanami Desert. Cats showed a numerical response to bird populations in the two study areas and there was a significant positive relationship between cat and bird abundance. When the cat population increased at Kintore in autumn and winter 1997, birds were the most important prey items (Chapter 3). The budgerigar (a nomadic species) was the dominant bird species consumed during this period (60 % of avian prey items), whereas (the resident) fairy-wrens (*Malurus* spp.) were the most frequently recorded birds in cat scats collected from Kintore during the dry conditions of 1996 (65 % of avian prey items). Although our data did not show an increase in bird abundance until winter 1997, bird lists compiled during the April survey recorded the presence of nomadic species including budgerigars, crimson chats, masked woodswallows and pied honeyeaters in the general study area, all of which were absent during 1996. Although these species began moving into the study area in autumn 1997, they were not registered on the fixed bird transects until the winter survey, perhaps indicating that the sampling method was inadequate for flocking species with clumped distributions.

In the Tennant study area, nomadic bird species (including budgerigars, crimson chats, black honeyeaters and masked woodswallows) were present during the winter surveys of both 1996 and 1997. This may explain why cats persisted at all 6 transects throughout the study period, despite similar reptile densities, and lower mammal capture rates than occurred at Kintore (Chapter 2).

4.4.3 Dingoes

Dingoes were consistently more abundant at Tennant than Kintore. They occurred at all three sites on four of the six Tennant surveys, but were present at only one of the Kintore sites on all but two surveys. Abundance of dingoes did not increase in response to the improved seasonal conditions at Kintore in 1997.

The scarcity of dingoes in the Kintore study area was probably due to a lack of drinking water, which is believed to be essential for dingoes, at least during the summer months (Corbett 1995b). They can survive without water in the cooler months if prey are abundant (Green 1973). Despite extensive searches of the area, no standing water was ever observed at Kintore. However, in the Tennant study area, water remained in palaeodrainage channels for up to 6 months after significant rainfall events in both March 1996 and January-February 1997. During three surveys there was water present at all three Tennant sites, and one of these sites was within 5 km of a water source that persisted throughout the entire study period. Packs of dingoes usually establish territories based around a water source (Corbett 1995b), and in this study dingo tracks were rarely recorded outside the palaeodrainage habitat.

Prey resources were also more abundant for dingoes at Tennant than Kintore. Although sand goannas (their most important prey item; Chapter 3) were equally abundant in both study areas, macropods were only recorded in the Kintore study area during two surveys and were significantly more abundant at Tennant (Chapter 2). Macropods were the most important supplementary prey for dingoes when varanids were unavailable (Chapter 3).

4.4.4 Conservation Implications

Previous perceptions that the Tanami Desert was largely fox-free (Gibson 1986) have been dispelled by this study. If the fox is a major threatening process for the bilby, only the northernmost extent of the Tanami Desert can be considered a refuge from foxes.

The suggestion that foxes had colonised the Tanami Desert beyond the 20th parallel by 1950 sheds new light on theories proposed to explain the extinctions of arid zone medium-sized mammals. Previously, the absence of foxes from the northern deserts was one of the main arguments against the fox predation hypothesis. However, Aboriginal People from both the Tennant and Kintore study areas, and others from the Gibson Desert in Western Australia (Charlie Walabi, Mitjili Gibson, personal communication), have revealed that foxes were present at the time when all the other missing mammals were also regularly hunted for food. Similarly, Aboriginal People who moved out of the Great Sandy Desert (WA) in the 1950s (into the non-fox country of the Kimberly region) were familiar with foxes and believed they had always been there (Lowe and Morse 1999, Paltridge unpublished data). Although there is no evidence that foxes ever extended to the northern extent of either the Tanami or Great Sandy Deserts, the majority of arid zone medium-sized mammals did not occur at latitudes north of 20 degrees (Burbidge *et al.* 1988). Of the 12 species that are now extinct in central Australia, only the western quoll (*Dasyurus geoffroii*), golden bandicoot (*Isoodon auratus*) and burrowing bettong (*Bettongia lesueur*) had distributions that extended beyond the range of the fox, as we now know it.

This study has revealed that cats and foxes can persist in the Tanami Desert in dry conditions when water is absent and mammalian prey are very scarce. This is largely due to the presence of reptilian prey, which are an abundant food source (at least in the summer months), even during droughts (Chapter 2). However, populations of cats and foxes will eventually decline in the winter months (when the majority of reptile species are hibernating), if both bird and mammal densities are low. Immigration of nomadic birds within 3 months of significant rainfall provides an abundant food source for cats and foxes however (Chapter 3), and there was a rapid recolonisation of the sites by these predators. Cats commenced breeding immediately after the onset of drought breaking rains. Despite the fact that foxes are seasonal breeders and females do not come into oestrous until winter, within six months of the summer rainfall, foxes had recolonised the two sites that had been vacated during the drought.

Dingoes also persisted during the drought at Kintore, but at very low densities, which I have attributed to a lack of drinking water. They did not increase in abundance in response to increased bird densities. Medium-sized mammals in the spinifex grasslands that were able to survive dry periods without relying on palaeodrainage habitat are likely to have suffered little predation from dingoes when populations were low, as dingo sign was rarely recorded outside palaeodrainage habitat in this study. Therefore dry, waterless areas would have originally provided some degree of refuge from predators. However, after the colonisation of the deserts by the ubiquitous cat and fox, it is unlikely that prey could have relied on any particular habitat serving as predation refugia. Patches of vegetation containing 1080 (sodium monofluoroacetate) poison plants (*Gastrolobium* spp.) that serve as predation refugia for marsupials in parts of Western Australia (Kinnear *et al.* 2002), are rare in the spinifex grasslands and where they do occur, cats and foxes can still be found (P. Latz personal communication). However, within my study sites, where dingoes were common, fox sign was rarely recorded in the palaeodrainage habitat, a result which may have implications for (non-specific) predator baiting programmes. It is possible that palaeodrainage habitat that is inhabited by dingoes may offer some species a refuge not only from drought, but also from fox predation.

My results suggest that cats and foxes could have had a significant impact on mammalian prey both during drought-induced declines, and in the post-drought recovery, due to the presence of alternative prey that can persist longer than mammals in dry times (reptiles) or increase in abundance more quickly than mammals (nomadic birds). If foxes and cats continue to opportunistically prey upon rare species in the presence of abundant alternative prey, rather than exhibiting switching behaviour (ignoring rare species until they reach a certain threshold density, Murdoch and Oaten 1975) predator-prey theory indicates that they are capable of sending species (without predation refugia) to extinction (Pech *et al.* 1995). Foxes have been reported to preferentially kill small populations of burrowing bettongs in the presence of high densities of rabbits, suggesting a Type II functional response, without switching (Short *et al*. 2002).

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CHAPTER 5

GENERAL DISCUSSION

5.1 INTRODUCTION

The main objective of the studies presented in this thesis was to increase our understanding of predator-prey interactions in spinifex grasslands in order to assess whether introduced predators might be capable of extinguishing populations of medium-sized mammalian prey. In Chapter 1, I argued that, if predation by cats (*Felis catus*) and foxes (*Vulpes vulpes*) was a primary agent of arid zone mammalian extinctions (i.e. capable of causing extinctions in the absence of introduced herbivores and changed fire regimes), then the following would be expected:

1. cats and foxes would eat medium-sized mammals when they are available, but be able to survive on alternative prey when mammals are scarce;
2. populations of cats and foxes would be buffered against the declines of mammals during droughts, or would be able to recover more quickly than medium-sized mammals after droughts;
3. medium-sized mammals would be more vulnerable to predation by cats and foxes than by dingoes (*Canis lupus dingo*) and other native predators (due to differences in feeding behaviour, numerical responses to fluctuating prey densities and habitat usage by the predators);
4. there would be a correlation between the timings of the extinctions and the colonisation (or sudden increase) of cats and foxes.

In this final chapter I summarise my findings in relation to these predictions, and use this assessment to construct a new model of mammalian extinctions in central Australia. I conclude with some recommendations for future directions in predator research and management in the Australian spinifex grasslands.

5.2 FINDINGS OF THE STUDY IN RELATION TO PREDICTIONS OF PREDATION MODEL OF MAMMALIAN EXTINCTIONS

5.2.1. Prediction 1. Cats and foxes eat medium-sized mammals when they are available, but can persist on alternative prey when mammals are scarce.

Central to the argument that predation by cats and foxes was a significant factor in the demise of medium sized mammals is evidence that cats and foxes are actually capable of killing medium-sized mammals. In this study, the scarcity of medium-sized mammals at the study sites provided little opportunity to find evidence of predation events on such prey. However, bilby (*Macrotis lagotis*) remains were found in two cat scats and one dingo scat in the Tennant study area (Chapter 3) and fresh fox tracks and scats were found with the remains of a freshly killed adult bilby at Jupiter Well in Western Australia, (Paltridge unpublished data). Mulgara (*Dasycercus cristicauda*) remains were found in several cat and fox scats from the Kintore study area (Chapter 3) and there were fourteen occurrences of marsupial mole (*Notorcytes typhlops*) in predator scats during the study, predominantly in fox scats (Chapter 3).

In other semi-arid and arid regions of Australia, rabbits (*Oryctolagus cuniculus*) are staple prey for cats, including both juvenile (Catling 1988) and adult rabbits (800-1500g; Molsher 1999, Risbey *et al*. 1999). Common ringtail possums (*Pseudocheirus peregrinus*; 700-1,100 g) are also frequently consumed by cats in eastern Victoria (Triggs *et al*. 1984).

Other evidence of cats preying on larger mammal species comes from studies of endangered macropods. Cats are believed to be a significant predator of juvenile bridled nailtail wallabies (*Onychogalea fraenata*) that are left to fend for themselves while their mothers are feeding elsewhere (Fisher 1998). A reintroduction program for mala (rufous hare-wallabies, *Lagorchestes hirsutus*) in the Tanami Desert failed primarily due to predation by feral cats, with 26 out of 55 animals released confirmed to have been killed by cats (Gibson *et al*. 1994). Mala weigh approximately 1,500 g. All life-history stages of mala were taken, but females with pouch-young were particularly susceptible to predation. The fate of reintroduced individuals does not necessarily reflect what might have happened in the wild, but I consider that there is ample evidence that cats are capable of consuming mammalian prey up to at least 1 kg in size which would encompass the rodent, bandicoot, numbat, bettong and quoll fauna of central Australia and other juvenile macropods.

Foxes are well known predators of medium sized mammals, with rabbits forming their staple prey in most areas of Australia (Jarman 1986). In mesic areas where rabbits are rare, ringtail possums are frequently eaten (Triggs *et al.* 1984). Foxes are also significant predators of black-flanked rock-wallabies (*Petrogale lateralis*; Kinnear *et al.* 1988) and they have also been recorded killing mala (Lundie-Jenkins *et al.* 1993), eastern barred bandicoots (*Perameles gunnii*; Short *et al.* 2002) and juvenile eastern grey kangaroos (*Macropus giganteus*; Banks 1997).

Given the information we have on predator diets elsewhere in Australia, it seems likely that, when medium-sized mammalian prey were abundant in the central Australian deserts, they would have been the preferred prey of cats, foxes and dingoes. However, my study indicates that reptilian prey are a “seasonal staple” in the diets of these predators (Chapter 3). Invertebrates and small mammals were important alternative prey for foxes, and cats supplemented their diets with small mammals and birds (Chapter 3).

5.2.2 Prediction 2: Populations of cats and foxes will either be buffered against the declines of mammals during droughts, or be able to recover more quickly than medium-sized mammals after droughts.

In Chapter 2, I showed that reptilian prey are an abundant resource in the spinifex grasslands, regardless of rainfall. At 300-400g, the sand goanna (*Varanus gouldii*) is a particularly useful food source that persists through drought periods, and there are also a plethora of smaller lizard species available (Chapter 2). Although many species of reptile are inactive during the winter months, dietary analyses revealed that, even during winter, at least 60 % of cat scats and 40 % of fox scats contained the remains of reptiles (Chapter 3). I suggest that the abundance of reptilian fauna in the Australian deserts allows populations of cats and foxes to persist into droughts even after the decline in mammal populations. Foxes also utilise invertebrate prey to meet their nutritional needs during unfavourable conditions.

Of course cat and fox populations will eventually decline during droughts, but my results showed that cats are capable of rapidly colonising an area when conditions improve (Chapter 4). One of the first prey types to increase after significant rainfall is the nomadic birds, which provide an abundant food source for cats and foxes before the mammals have had a chance to breed up (chapter 2). Birds dominated the diets of cats and foxes in the autumn and winter samples at Kintore after considerable rainfall occurred in the previous February (chapter 3). This allowed a rapid increase of cats in the study area, that must have initially been due to immigration (chapter 4). However, there was also evidence of breeding activity as soon as the rainfall occurred. Unlike foxes, dingoes and the marsupial predators, cats are capable of breeding at any time of the year and breed continuously. This allows them to rapidly increase their population in response to improved seasonal conditions.

5.2.3 Prediction 3: Medium-sized mammals are more vulnerable to predation by cats and foxes than by dingoes and other native predators.

When a predator invades a new ecosystem, the vulnerability of a prey population depends on the anti-predator behavioural repertoire of the prey species, aspects of its life history and morphology that counter the efficiency of capture by the predator and the availability of refugia from the predator (Short *et al.* 2002). Such attributes of the prey species are a function of the predator environment in which they evolved. What was the predator situation in Australia during the evolution of its mammal fauna?

Compared to the diversity of mammalian predators elsewhere in the world, there was a paucity of large predatory species in Australia (Flannery 1994). For example, whereas North America had at least 30 carnivorous species greater than 5 kg in body mass and South America, Europe, Asia and Africa all either had or still have similarly diverse carnivore guilds, only four species of mammalian predators of this size evolved in Australia: the marsupial lion (*Thylacoleo carnifex*), thylacine (*Thylacinus cynocephalus*), Tasmanian devil (*Sarcophilus harrisii*) and spotted-tail quoll (*Dasyurus maculatus*; Flannery 1994).

Marsupial lions were widespread throughout Australia during the Pleistocene but disappeared 17,000 years ago. They are thought to have fed mainly on the megafauna. However, smaller individuals may have eaten a range of macropod species (Robertshaw and Harden 1989).

Thlyacines are believed to have mainly fed on macropods between 1 and 5 kg (Jones and Stoddart 1998) but probably also consumed echidnas (*Tachyglossus aculeatus*), rats, birds and lizards (Robson and Young 1990). As they were relatively slow runners (Rounsevell and Mooney 1995), they would probably have had little impact on populations of species that could escape down burrows (bilbies, bandicoots and bettongs) or up trees (possums and quolls) but their stamina in pursuit (Rounsevell and Mooney 1995) may have made them a significant predator of some macropods.

Tasmanian devils were originally distributed throughout most of Australia, including central Australia (Megirian *et al*. 2002). They weigh between 5 and 10 kg. Now restricted to Tasmania, they are capable of killing medium-sized mammals such as small wallabies and possums but subsist mainly on carrion (Pemberton and Renouf 1993).

Spotted tail quolls occur on the east coast of Australia and in Tasmania. They weigh up to 7 kg and feed on a wide variety of prey ranging from small wallabies to insects. Their arid zone equivalent was the western quoll (*Dasyurus geoffroii*), which is a much smaller species, reaching a maximum of 1.3 kg. Western quolls are primarily predators of invertebrate prey, but they also feed on birds, reptiles and mammals up to the size of rabbits (Serena and Soderquist 1995).

In addition to the mammalian carnivores, Australia has a high diversity of predatory birds and reptiles, but few species are large enough to prey on medium-sized mammals. Of the 24 species of raptors in Australia, only three are mammal specialists: the black-shouldered kite (*Elanus axillaris*) and letter-winged kite (*Elanus scriptus*), both of which are rodent specialists, and the wedge-tailed eagle (*Aquila audax*), which is primarily a predator of medium-large mammals (Olsen 1995). Some of the other larger raptors are also capable of killing medium-sized mammals. For example, the black-breasted buzzard (*Hamirostra melanosternon*) includes rabbits and young macropods in its diet (Aumann 1999). Apart from the elanid kites, raptors generally occur at low densities in arid Australia with suitable nesting sites a limiting factor (Aumann 1999). Typical densities of wedge-tailed eagles in central Australia are one pair per 30-100 km^2 (Olsen 1995). Eagles are territorial and defend the boundaries of their territories. They have a low reproductive potential with each pair producing a maximum of one brood, comprising 1-3 young, per year. Wedge-tailed eagles do not breed at all in years of less-than-average rainfall (Olsen 1995). They are less able to switch to other prey types than other raptors and may migrate from an area when their mammalian prey declines (Aumann 1999). In the current study, wedge-tailed eagles were recorded only once in the Tennant study area, and not at all at Kintore. The most commonly sighted raptors at the study sites were the brown falcon (*Falco berigora*), nankeen kestrel (*F. cenchroides*) and Australian hobby (*F. longipennis*). In a concurrent study of raptor ecology, conducted near the Kintore study area, brown falcons and nankeen kestrels were found to be generalist predators that fed mainly on reptiles and invertebrates during the study period, whilst the Australian hobby consumed mainly budgerigars and is considered a bird specialist (Aumann 1999).

Of the plethora of reptile species that have evolved in Australia, in the desert areas only the perentie (*Varanus giganteus*) and the carpet snake (*Morelia bredli*) would be capable of taking medium-sized mammals. These two species are more commonly associated with rocky habitats and rarely encountered in the spinifex grasslands habitat (Cogger 1996).

As a result of low risk of predation, there was little evolution of anti-predator behaviours or morphologies amongst the Australian medium-sized mammal fauna that would have served to protect them against cats and foxes. Whilst the echidna's spines have obviously been a successful means of protection against predation (with echidnas being one of the few medium-sized mammal in central Australia not to have suffered any decline (Strahan 1995)), few other examples of anti-predator defense can be found. Common brushtail possums (*Trichosurus vulpecula*) are the only mammal species that central Australian Aborigines reported as behaving aggressively when pursued (Burbidge *et al*. 1988), although presumably the western quoll may have also offered some resistance and Finlayson (1935) considered the lesser bilby (*Macrotis leucura*) to be fierce when handled. Bipedal gait is considered an evolutionary adaptation to improve sprint speed and ability to dodge predators (Kotler *et al*. 1994) and can be seen amongst the Australian macropod and hopping mouse fauna. Several bandicoot species were also reported to be fast runners. However, most of the bandicoot and smaller macropod species sheltered only in shallow nests under spinifex clumps or grass tussocks, and were easy to sneak up on whilst they were sleeping during the day (Burbidge *et al*. 1988). Such shelters would have afforded little protection from predators, particularly those with any inclination for digging, such as the fox.

Despite the apparent vulnerability of medium-sized mammals to predation by introduced species, there is little evidence of extinctions when the dingo arrived in Australia, approximately 3500 years ago (Flannery 1994). Both the thylacine and the Tasmanian devil are believed to have been displaced from the Australian mainland by the dingo, due to its superior hunting efficiency (Jones and Stoddart 1998, Corbett 1995). However, the only extinction attributed to predation by dingoes is a flightless native hen (*Gallinula mortierii*) that used to inhabit the alpine areas of the Australian mainland and is now confined to Tasmania (Baird 1991). Why would the arid-zone mammal fauna be more vulnerable to predation by cats and foxes than dingoes?

In Chapter 1, I presented a table of attributes of a predator-prey system that may influence the likelihood of a predator sending a prey species to extinction (Table 1.1). These attributes can be compared between dingoes, cats and foxes, to investigate differences in the vulnerability of prey populations to predation by these species (Table 5.1).

In the current study, predator diets were investigated in two areas of the spinifex grasslands, in relation to prey population dynamics. Dingoes, foxes and cats were all generalist predators (**Attribute 2**), feeding on a broad range of mammalian, avian, reptilian and invertebrate prey species (Chapter 3). When mammal and bird densities declined during droughts, reptilian prey provided an alternative food source for predators (**Attribute 1**). There was considerable overlap in the diets of the three predator species (due mainly to the dominance of reptilian prey), although dingoes ate more large prey (including macropods, cats and echidnas) than did foxes or cats (Chapter 3). It has been suggested that before the arrival of rabbits to central Australia, dingoes would have fed primarily on medium-sized macropods and bandicoots during flush periods and large kangaroos in droughts (Corbett 1995).

Attribute 3 concerns the feeding behaviour of predators in relation to declining prey populations, essentially whether predators display a Type II functional response and continue to feed on rare species either opportunistically or preferentially when prey densities are low (non-switcher) or exhibit switching behaviour, ignoring prey at low densities to feed disproportionately on more abundant prey species. Switching was not directly investigated in the current study, but other studies have found little evidence of switching by dingoes, foxes or cats. Thus, in central Australia dingoes supplemented

Table 5.1 Attributes of a predator-prey system that may influence whether the predator can send prey to extinction

	Attribute	Prey populations may be extinguished	Predator unlikely to extinguish prey populations	DINGO	FOX	CAT
Prey dynamics	**1. Prey population dynamics**	***Independently fluctuating prey:*** *some prey types remain or increase in abundance when most species are declining (e.g. during droughts)*	***Synchronised fluctuations in prey:*** *prey show similar responses to environmental events (e.g. droughts and bushfires) leading to a food shortage for the predator*	**Independently fluctuating prey:** Reptiles provide an alternative food source when mammalian and avian prey densities decline during droughts.	**Independently fluctuating prey:** Reptiles provide an alternative food source when mammalian and avian prey densities decline during droughts.	**Independently fluctuating prey:** Reptiles provide an alternative food source when mammalian and avian prey densities decline during droughts.
Predator diets and feeding behaviour	**2. Predator dietary requirements**	***Generalist:*** *can increase in response to one of many alternative prey species, meanwhile suppressing low populations of other species*	***Specialist:*** *numerical response will tend to lag behind prey, therefore may regulate prey but won't extinguish it, or predator will starve*	**Generalist:** Very broad diets including reptiles, mammals, birds and invertebrates	**Generalist:** Very broad diets including reptiles, mammals, birds and invertebrates	**Generalist:** Very broad diets including reptiles, mammals, birds and invertebrates
	3. Feeding behaviour of predator	***Non-switcher****: takes prey in proportion to encounter rate, therefore will occasionally prey on rare species even when populations are low*	***Switcher:*** *tends to feed disproportionately on the most abundant prey type, therefore ignores prey at very low densities*	**Non-switcher:** May continue to prey upon preferred species, even after dramatic declines in prey populations	**Non-switcher:** May continue to prey upon preferred species, even after dramatic declines in prey populations	**Non-switcher:** May continue to prey upon preferred species, even after dramatic declines in prey populations
	4. Predator's propensity for surplus killing	***High****: kills in excess of requirements; prey density at which functional response reaches asymptote may never be achieved in the field*	***Low:*** *unlikely to have as much impact on prey populations as functional response will reach asymptote at lower prey densities*	**Medium:** Although capable of surplus killing, no evidence that dingoes kill excessive numbers of medium-sized native prey.	**High:** Many examples of surplus killing of medium-sized mammalian prey by foxes	**Low:** No evidence that cats engage in surplus killing

Numerical response of predator population	**5. Predator's reproductive potential**	***High:*** *can initiate breeding immediately, breed continuously and produce large litters, therefore can rapidly increase in response to increasing prey populations*	***Low:*** *monoestrous, small litter size, social repression of breeding, resulting in a slower numerical response to increasing prey densities*	**Low:** Annual breeders, do not commence breeding until two years of age, only one litter of 1-10 pups is raised per pack	**Moderate:** Annual breeders, producing only one litter per year of 2-10 cubs. Can breed in their first year, but in group situations breeding by subordinates may be suppressed by the dominant female	**High:** Can breed at any time of the year, from 10 months of age, and produce two (even three) litters per year of up to 8 kittens.
	6. Predator's capacity for immigration	***High:*** *highly mobile predators can show a rapid numerical response to increasing prey populations*	***Low:*** *numerical response to increasing prey is slower, as predator population can only increase by breeding.*	**Low:** Dingoes are territorial and show strong site fidelity, however they can travel over large distances.	**Moderate:** Foxes colonise vacated territories relatively quickly	**Moderate:** Cats are capable of travelling large distances in search of food
	7. Territoriality of predator	***Non territorial or flexible territoriality:*** *predators can tolerate high densities of conspecifics when resources are plentiful*	***Territorial:*** *interference from conspecifics will impose an upper limit to the numerical response which may prevent high enough densities accumulating to extinguish a prey population*	**Territorial:** Dingo packs live in large territories at relatively low densities, and defend their boundaries from non-pack members	**Flexible territoriality:** Foxes are normally territorial, but when resources are abundant high densities of foxes may coexist in loose-knit social groupings	**Flexible territoriality:** Cat may exist as individuals actively defending territorial boundaries, in small kin groups of females or in colonies of extremely high densities
	8. Natural Enemies of predator	***Few:*** *relatively free of predators, parasites and pathogens*	***Many:*** *populations are kept in check by predators, parasites and pathogens*	**Moderate:** Dingoes have few predators but have a large range of parasites and pathogens, several of which periodically result in significant mortality to populations	**Few:** Dingoes and humans are the only predators of adult foxes; disease and parasites are not known to cause significant problems in Australia	**Moderate:** Dingo predation may have some impact on cat populations in certain regions.
Refugia for prey	**9. Habitat requirements of predator**	***Ubiquitous*** *(with respect to prey): prey have no refuge from the predators therefore predators can extinguish local populations*	***Specific*** *(with respect to prey): prey may have refugia where the predators do not occur, from which they can recolonise patches*	**Specific:** Dingo territories are based around water points; waterless areas therefore provided some degree of refuge from dingo predation	**Ubiquitous:** Foxes occur in all desert habitat types and are not restricted to areas with accessible water	**Ubiquitous:** Cats occur in all desert habitat types and are not restricted to areas with accessible water

their diet during droughts with cattle carrion, but rabbits continued to comprise at least 40 % of their diet after densities had declined by 40 fold (Corbett and Newsome 1987), and in the Barkly Tableland of the Northern Territory plague rats were still being consumed by 50 % of dingoes, even when researchers could no longer detect the rats in trapping surveys (Corbett 1995). Similarly for foxes, when vole densities in Poland declined by 95 %, their occurrence in fox diet only halved (Jedrzejewski and Jedrzejewska 1992), a 90 % reduction in Canadian snowshoe hares resulted in a decline of only 10 % in its occurrence in fox diet (Theberge and Wedelles 1989) and when Australian rabbit densities fell to 10 % of previous levels, the proportion of rabbit in fox diet halved (Catling 1988). In another case, after foxes had reduced a population of burrowing bettongs (*Bettongia lesueur*) to a low density, they continued to depredate the bettongs in the presence of a very high density rabbit population (Short *et al.* 2002). Cat diets tend to reflect the abundance of available prey, occasionally consuming rare species when the opportunity arises (Newsome *et al.* 1997). Predator-prey theory suggests that when predators continue to take a constant number of prey, or a constant proportion of the prey population at low densities, predation can potentially drive the species to extinction if densities fall below a certain threshold level (Pech *et al.* 1995).

Another aspect of feeding behaviour that may influence the potential for a predator to extinguish a population of prey is a predator’s propensity for surplus killing (**Attribute 4**). No evidence of surplus killing was witnessed in the current study, but a comprehensive review of surplus killing by cats, foxes and dingoes in Australia found numerous examples of foxes killing excessive numbers of native prey species including burrowing bettongs, black-footed rock-wallabies (*Petrogale lateralis*), tammar wallabies (*Macropus eugenii*), eastern barred bandicoots (*Perameles gunnii*), quokkas (*Setonix brachyurus*) and rufous bettongs (*Aepyprymnus rufescens*; Short *et al.* 2002). Individual foxes have been recorded killing more than 10 medium-sized mammals within three days, leaving the majority of prey carcasses uneaten (Short *et al.* 2002). Surplus killing of domestic stock and kangaroos by dingoes is also well documented but no examples relating to medium-sized native mammals could be found (Short *et al.* 2002). There was no evidence that feral cats engage in surplus killing (Short *et al.* 2002).A predator’s capacity to increase in relation to that of its prey will influence the ability of the prey species to escape from the predator pit following contraction of populations during droughts. Of the three predator species in question, cats have the highest reproductive potential (**Attribute 5**) as they can initiate breeding at any time of the year and produce up to three litters per year when conditions are favourable (Jones and Coman 1982). In the current study, kittens were recorded in the southern study area in February 1997, within two months of significant rain falling; they were also observed during the April and December surveys of the same year (Chapter 4). Cat litters may contain as many as eight kittens. Cats become sexually mature at 10 months of age (Jones and Coman 1982). In contrast, dingoes are annual breeders and each pack (comprising 3-12 individuals; Thomson 1992) usually raises only one litter per year, with a mean litter size of five (Corbett 1995). Female dingoes do not breed until two years of age (Corbett 1995). Foxes are also monoestrous, producing only one litter per year of 2-10 cubs (with a mean litter size of 4) but foxes can breed in their first year (Saunders *et al*. 1995). Where foxes cohabit in groups, reproduction in subordinate females may be suppressed by dominant females, but abundant food supplies allow some subordinates to breed (Newsome *et al*. 1997).

Predator populations may also increase in response to increasing food supplies by immigrating into an area (**Attribute 6**). In the current study, sites that were apparently abandoned during the drought were recolonised by cats and foxes within several months of significant rainfall (chapter 4). Although they are obviously not as mobile as avian predators which can travel hundreds of kilometers in search of food (Olsen 1995), foxes are capable of rapidly re-invading territories that have been vacated (Kinnear *et al*. 2002). However, when large areas (>3000 km^2) become devoid of foxes, recolonisation may negligible until the main dispersal period, which occurs in the autumn (Thomson *et al*. 2000). While cats have sometimes been described as slow to recolonise areas where populations have been controlled (Newsome *et al*. 1989, Coman 1991), a dramatic increase in cat abundance (too rapid to have been due solely to reproduction) was also observed in response to an irruption of long-haired rats (*Rattus villosissimus*) in south-western Queensland (Pettigrew 1993). Dispersal movement rates of 20-110 km in just 10 days have been reported (Pettigrew 1993). Abundance of dingoes did not increase in response to improved seasonal conditions in the current study (chapter 4). Dingoes are generally territorial and show strong site fidelity, however, males in the Simpson Desert have been recorded moving up to 250 km following eruptions of small mammals (Corbett 1995).

One of the key differences between dingoes, cats and foxes is the extent of territoriality displayed within populations (**Attribute 7**), which influences the numerical response of predator populations to increasing prey densities. The social structure and territoriality of dingoes prevents high densities accumulating; typical densities are in the order of 1 animal per 8 km^2 (Fleming *et al*. 2001). Dingoes tend to live in stable packs that maintain large territories (approximately 70 km^2) in the arid zone to ensure reliable access to food resources (Corbett 1995). Home-range size remains constant from year to year, despite fluctuations in prey densities (Thomson 1992). Although pack size may increase when food is abundant, maximum dingo densities attained in South Australia during the height of a rabbit plague were one animal per 3 km^2 (Fleming *et al*. 2001). Fox pairs or groups also tend to occupy well defined territories, with non-overlapping adjoining, stable boundaries (Saunders *et al*. 1995). However, when resources are locally plentiful, territoriality may be abandoned in favour of loose-knit social groupings (Macdonald *et al*. 1999), and high densities of conspecifics may be tolerated. The highest densities of foxes reported are 15 per km^2 in urban areas of Britain; in Australia densities of up to 12 per km^2 have been recorded in Melbourne and 7 per km^2 in northern New South Wales (Saunders *et al*. 1995). Cats are similarly flexible in their territoriality. In some environments cats (particularly males) maintain exclusive territories by actively patrolling their boundaries and aggressively chasing away intruders (Langham and Porter 1991) or advertising their boundaries with prominently deposited scats (Corbett 1979, Molsher 1999). Other studies have found female cats to live in colonies (usually of closely related animals), with males moving between the groups (Macdonald and Apps 1978). In situations where resources are rich and clumped, extremely high densities of cats may accumulate. For example 182 cats were removed from 25 km of river channel in south-west Queensland within a three day period (Pettigrew 1993). The majority of cats were adult males and as many as nine cats were observed cohabiting in individual trees.

Exotic species that successfully colonise a new continent may lack many of the natural enemies (predators, parasites and pathogens, **Attribute 8**) that keep population numbers in check within their native range. It has been suggested that cat and fox populations may be limited by dingo predation and/or competition, in some regions (Pettigrew 1993, Lundie-Jenkins *et al*. 1993, Corbett 1995). Although a number of diseases and parasites have been recorded in cats and foxes in Australia, there is little evidence of significant impacts on population abundance (Coman *et al*. 1981, Saunders *et al*. 1995). In contrast, 38 species of parasites and pathogens have been recorded in dingoes, 11 of which are known to be fatal (Corbett 1995). Canine distemper is capable of eliminating entire local populations of dingoes and mortality rates of up to 50 % have been recorded during Heartworm epizootics (Corbett 1995). Humans are the only significant predator of dingoes (Corbett 1995).

The ability of low density prey populations to avoid being extinguished by predators is partly dependent on whether prey have access to predator-free refugia (Rosenzweig and MacArthur 1963) which is a function of the predator's distribution and habitat utilisation in relation to the distribution of prey (**Attribute 9**). In the current study, cats and foxes were nearly always present at all three sites in both study areas, and are clearly capable of surviving without drinking water (Chapter 4). Cats were equally prevalent in both sandplain and palaeodrainage habitats. Foxes occurred in both habitats in the southern study area, but tended to avoid the palaeodrainage habitat in the northern study area, perhaps because of abundance of dingoes there (Chapter 4). Dingoes were rarely detected outside of the palaeodrainage habitat in either study area, and were often absent from at least two of the Kintore sites (Chapter 4). I have attributed this to their dependence on drinking water. Dingoes normally drink every day (Green 1973), and territories are usually based around water points (Corbett 1995). As a result, dingoes are considered naturally sparse in the spinifex grasslands of the Tanami Desert, the eastern arid half of Western Australia and adjoining parts of South Australia (Fleming *et al*. 2001). Therefore, before the colonisation of the deserts by cats and foxes, waterless areas of the spinifex grasslands may have provided medium-sized mammals with refugia from predation. When cats and foxes invaded these refuge areas, it was potentially possible for them to cause local extinctions of prey populations.

In summary, although all three predator species are capable of killing medium-sized mammals, and can be sustained by alternative prey when mammal populations are low, such prey may have been more vulnerable to predation by cats and foxes than dingoes because the distribution and abundance of cats and foxes are not restricted by drinking water, they can exist at much greater densities than dingoes, and show a higher rate of increase. Populations of medium-sized mammals would have been particularly vulnerable to foxes, which have the capacity to kill excessive numbers of prey in a short space of time.

5.2.4 Prediction 4: There is a correlation between the timings of the mammal extinctions and the colonisation (or sudden increase) of foxes and cats.

It has been postulated that mammalian extinctions occurred in many areas of the northern deserts prior to their invasion by the fox, or where foxes have never occurred (Burbidge and McKenzie 1989, Johnson and Southgate 1990). Prior to this study, foxes were believed to be absent from large areas of both the Tanami and Great Sandy Deserts (McKenzie and Youngson 1983, Gibson 1986), but restricted to areas further south, where rabbits occurred (Low 1984). However, we now know that they are distributed much further north than previously thought. Furthermore, Aboriginal informants have revealed that they have occurred in these deserts since the 1940s.

Most of the medium-sized mammals persisted in the northern and western deserts until about 1960 (Burbidge *et al*. 1988). Traditional Owners of the area west of Tennant Creek recall eating foxes around the period of the second World War (Irene Driver and Engineer Jack personal communication). Aboriginal People at both of my study sites as well as from the Gibson Desert in Western Australia (Paltridge, unpublished data) list foxes as being present at the time when all the other missing mammals were also regularly hunted for food. Similarly, Aboriginal People who moved out of the Great Sandy Desert in the 1950s (into the non-fox country of the Kimberley region) were very familiar with foxes and believed that they had always been there (Lowe and Morse 1999, Paltridge unpublished data). The spearing of foxes for meat and medicine was also described by Martu Traditional Owners from the southern Great Sandy Desert, when interviewed about hunting during contact time in the 1950s (Walsh unpublished data). The extinction of most of the medium-sized mammals in the northern and western deserts in the 1950s-1960s is thus entirely consistent with the colonisation of the fox.

Similarly, in north-western South Australia, foxes were present by 1932, prior to the major period of decline and extinction of medium-sized mammals in the area, which occurred between 1935 and 1950 (Finlayson 1961). In New South Wales, the extinctions of three species of rat kangaroos closely followed the colonisation pattern of the fox between 1895 and 1915 (Short 1998). Around Tamworth (New South Wales) and near Port Lincoln in South Australia, the American collector Charles Hoy noted a decline in medium-sized mammals between 1915-1918, following the arrival of the fox (Short and Calaby 2001). And the disappearance of native mammal species from the

Nullabor Plain in Western Australia has also been linked to the appearance of foxes in the area (Richards and Short 1996).

It is unclear when cats first arrived in the Australian deserts, but several authors have suggested that they may have colonised Australia even before the arrival of European settlers (Macknight 1976, Burbidge *et al.* 1988, Newsome 1995, McKay 1996). This is now considered unlikely, as a comprehensive search of historical sources found no evidence that the cat was present on the mainland of Australia prior to settlement by Europeans (Abbott 2002). It is now believed that feral cats did not colonise the arid interior of Australia until the 1880s (Abbott 2002).

Although early extinctions of a number of smaller mammals (<220 g) can be reasonably attributed to predation by feral cats (Dickman *et al.* 1993), clearly cats initially coexisted with many species of medium-sized mammals in Australia for at least several decades, causing few declines. Does this imply that the cat could not have been a primary factor in the extinction process? Or was there a subsequent increase in cat abundance that coincided with the mammalian declines?

The introduction of the rabbit would have been one factor that caused elevated cat densities (Smith and Quin 1996), but even in areas of the spinifex grasslands that were not infested with rabbits, I believe there may have been an increase in the cat population from about 1930. Historical accounts reveal that cats remained at low densities for several decades after their introduction (Abbott 2002). I propose that until the 1930s, cat populations in the spinifex grasslands were kept in check by predation by both Aboriginal people and dingoes.

In Appendix A, I describe the extraordinary skills of contemporary Aboriginal People in capturing cats in the central Australian deserts. Aboriginal people have been hunting cats for meat and medicine since cats were first recorded in inland Australia (Abbott 2002) and there are numerous references to Aboriginal people’s enthusiasm for cat hunting across Western Australia, South Australia and the Northern Territory (Abbott 2002). As Aboriginal people gradually left the deserts to live in settlements, there may have been a relaxation in predation pressure on populations of feral cats in desert areas, allowing their numbers to increase. The idea that Aboriginal hunting may have had a significant impact on cat populations was also considered by Finlayson: “as the natives hold it in such high esteem gastronomically, it may possibly be checked somewhat, wherever there are active hunting populations" (Finlayson 1961 p. 185).

The Gibson Desert of Western Australia supported one of the last tribes of Aboriginal people living a traditional lifestyle. This is also the area where many species of medium-sized mammals are believed to have persisted the longest (Burbidge *et al.* 1988). In 1955, there were still several hundred Pintubi people living in the Gibson Desert but most of them had moved into settlements by 1964 (Long 1989). Cats and hopping mice were the mammals that were most commonly eaten by Aboriginal People in this area in 1957 (Thomson 1975). Whenever cat tracks were detected they would be pursued until the animal was procured. All deserted campsites showed the remains of cat bones and cat was regarded as a greater prize than any other small game (Thomson 1975). Similarly, in 22 stories recorded from people living in the Great Sandy Desert between 1950 and 1960, cats were cited as food more often than any other animal (F.Walsh, personal communication). A steady stream of people left the Great Sandy Desert between 1930 and 1950, coinciding with the period when the medium-sized mammals disappeared (Burbidge *et al.* 1988).

The other major predator the cat would have encountered as it colonised Australia, is the dingo. In the current study, cat remains were found in 9 % of dingo scats, suggesting that dingoes may be an important predator of cats. Low levels of consumption of cats by dingoes have been found elsewhere in Australia (Corbett 1995). Although dingoes have probably always been sparse through the spinifex grasslands (Fleming *et al.* 2001), when the dingo bounty scheme was introduced to central Australia in the 1920s (Stephens 1969), populations of dingoes were probably reduced further, and this may have allowed an increase in cat densities.

Dingo control in the western deserts commenced in 1920 (Corbett 1995), with Afghan camel teams travelling through trading for dingo scalps (Long 1989). When the Haasts Bluff settlement was established for Pintubi people in 1941, only women and the old and infirm received rations. However, men could trade dingo scalps, kangaroo skins and other 'curios' in exchange for rations (Long 1989). As a result, there were many teams of doggers collecting dingo scalps in the area west of Haasts Bluff and beyond the WA border in the 1950s and 1960s (Long 1989). As dingoes usually den within 5 km of water it would have been relatively easy for Aboriginal people to target these areas and remove a significant proportion of the dingoes from an area, potentially reducing the predation pressure on feral cats.

5.3 A NEW MODEL OF MAMMALIAN EXTINCTIONS IN THE SPINIFEX GRASSLANDS

None of the hypotheses of mammalian extinctions adequately explains the population declines over their full distributions. This study focused on the spinifex grasslands habitat, where there were few confounding factors: grazing stock were never present, there is no evidence that rabbits were ever more than patchily distributed, and traditional burning was still occurring in remote areas during the period that species were declining. However, the declines and extinctions still occurred and it is the introduced predators (cats and foxes) that I propose to be the common link between the spinifex grasslands and the rest of arid Australia.

I have used the information collected during this study of predator-prey interactions in the Tanami Desert, to construct an alternative model of mammalian extinctions in the spinifex grasslands of Australia, that promotes predation by introduced predators as the primary agent of extinction. I believe that foxes and cats are capable of causing extinctions of medium-sized mammals, even in the absence of introduced herbivores and altered fire regimes. The model is depicted in Figure 5.1.

When cats first colonised the arid zone, they may have had early impacts on some of the smaller mammalian species (< 220 g) that inhabited open habitats. For example, in western New South Wales, where cats are believed to have occurred since the 1840s (Abbott 2002) ten species of native mammals in this size range had disappeared by 1857, before the arrival of the fox to the area, or commencement of any major pastoral activity (Dickman *et al.*1993). Similarly, in Western Australia, four of the six mainland extinctions of rodents occurred prior to the arrival of the fox and rabbit, but subsequent to the arrival of the cat. All weighed less than 220 g and most sheltered in above-ground nests or shallow burrows (Morris 2000), attributes that would render them vulnerable to cat predation.

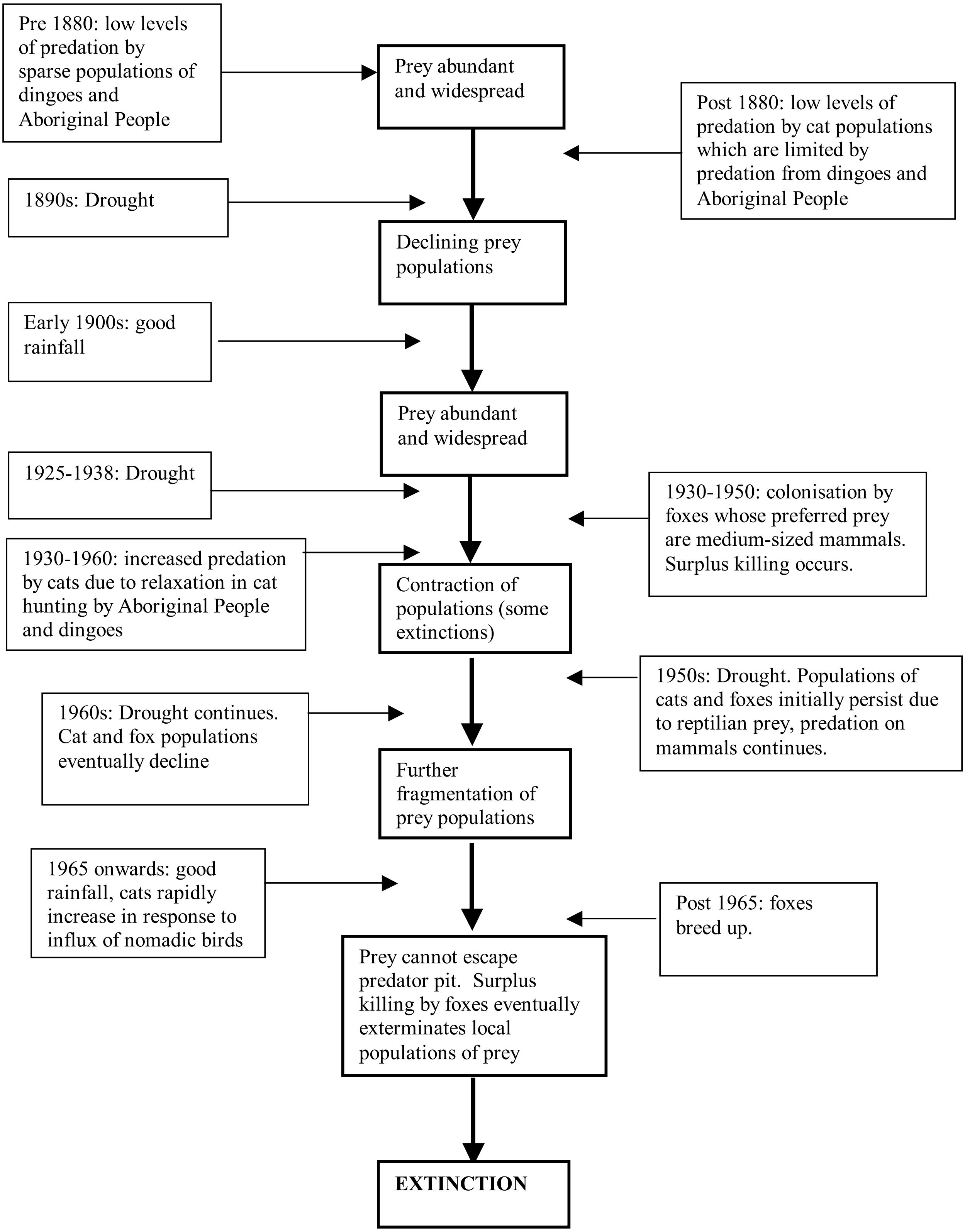

Figure 5.1 Model of mammalian extinctions in the spinifex grasslands of Australia, promoting foxes and cats as the primary agents of extinction.

Most of the larger mammals survived the early years of cat invasion, and the evidence suggests that cat densities remained low for several decades after their arrival (Abbott 2002). In the previous section (5.2.4) I suggested that cat abundance was initially limited by predation by both Aboriginal people and dingoes. As these pressures were released with the relocation of Aboriginal people into settlements and the advent of dingo control, cat numbers increased.

Results from this study have suggested that cats are able to persist longer than herbivorous species during droughts, due to the availability of reptilian prey, at least during the warmer months. Nevertheless, a series of dry winters would have eventually resulted in a decline in cat densities. The rapid response of nomadic birds to a break in the drought provides a ready food source for feral cats, which can rapidly recolonise areas and start breeding. Whereas native marsupial predators are seasonal breeders and wouldn't have started to increase until their mammalian prey had increased their densities, cats can breed at any time. With large litter sizes and the ability to breed at least twice a year, cats have the potential for rapid population growth and populations can increase more quickly than some of the native species. Vulnerable prey species then become trapped in a "predator pit", where their reproductive rate is insufficient for the population growth rate to exceed the predation rate. Small mammals, with their rapid breeding cycles, may be able to keep up with the cats but most of the medium-sized mammals have lower reproductive potentials. For example, the spinifex hopping mouse (*Notomys alexis*) and sandy inland mouse (*Pseudomys hermannsburgensis*), two species of small mammals that remain common and widespread throughout arid Australia, can produce up to 6 young every two-three months (Breed 1995a, Breed 1995b). In contrast, species of bettong and hare-wallaby only produce a single young at a time, and their maximum output is three per year in good conditions (Burbidge 1995, Christensen 1995, Johnson and Burbidge 1995). Bandicoot and bilby species can produce one or two young, every three to four months, therefore an annual production of eight young may be possible under favourable conditions (Johnson 1995, McKenzie *et al*. 1995, Southgate *et al*. 2000).

Thus, cat predation may have exacerbated the declines of native prey populations during droughts and delayed their recovery when seasonal conditions improved. Even more devastating was the arrival of the fox to the Tanami Desert, possibly as early as the 1930s. Increased hunting of dingoes (for bounty payments) at this time would have aided its colonisation. Foxes are particularly destructive hunters, due to their predisposition for surplus killing, where more animals are killed than can be eaten. A local population of naïve prey could therefore be rapidly decimated by a single pair of foxes. Unlike most predators, in which the functional response curve plateaus due to satiation, foxes can keep on killing. When medium-sized mammals are available, foxes will certainly target these species but they can persist in unproductive environments by feeding on invertebrates when other prey are scarce. They are accomplished diggers and can probably dig up lizards even when they are hibernating.

Droughts are a regular feature of the central Australian climate. A drought may be defined as a period of at least 10 months with little or no rainfall (Corbett 1995). Between 1874 and 1992, 17 droughts were recorded in central Australia, with an average duration of 22 months (Corbett 1995). The most severe droughts occurred in 1925-30 and 1958-65 (Corbett 1995). Medium-sized mammal populations show natural contractions in abundance during droughts (Short *et al*. 1997); for example populations of mala, burrowing bettongs and eastern barred bandicoots were reduced by 60-75% during a drought on two Western Australian islands (Short *et al*. 1997). Such species would have been reliant on the good seasons to expand their populations and recolonise patches where local extinctions had occurred. Predation by cats and foxes would have increased the rate of local populations disappearing, causing the overall size of the prey population to shrink further during each dry spell.

Patrols to the Gibson Desert in 1957 found that Aboriginal people were generally healthy with adequate food supplies (Long 1989). Soon after this, the area suffered from serious drought and, by 1960, most of the smaller game were found to have "virtually died out or have been so depleted in numbers as to no longer maintain the people in their meat needs" (Long 1989, p. 29). When the drought broke in 1966, cats and foxes would have been able to breed up in response to nomadic bird populations and unlimited by the very low populations of dingoes or the virtually absent Aborigines they may have prevented any recovery of medium-sized mammals that should have occurred post-drought.

Further south, in the Petermann Ranges, a similar situation had occurred several decades previously. There was a fairly rapid depopulation of Aboriginal people into Docker River in the 1930s, which was also a period when much dingo scalp collecting occurred (Thompson 1975). By 1939, few people remained in the bush and this was attributed to "a series of dry years which had depleted the area of game". Again the post-drought recovery would have been hampered by the high populations of cats and foxes which had been allowed to increase due to reduced populations of dingoes and the disappearance from the area of most Aboriginal People, who would have hunted the cats. Dingo scalps were still a regular source of income for people in this area in 1963 (Thomson 1975). In adjacent areas of northern South Australia, the annual totals of dingo scalps traded at Ernabella between 1949 and 1956 ranged from 500 to 3,000, with an average of 1,300 (Finlayson 1961).

After Aboriginal People had moved into settlements and patch burning was no longer being practiced across much of the landscape, a run of good seasons following a drought often culminated in a period of severe bushfires. Vast tracts of the arid zone were burnt by wildfires in the 1930s, 1950s and 1980s (Kerle and Fleming 1996). Lack of cover in the freshly burnt areas would have increased the vulnerability of many species to predation, particularly those that did not live in burrows.

5.4 THE PREDATION MODEL IN COMPARISON WITH OTHER THEORIES ON THE EXTINCTION OF MEDIUM-SIZED MAMMALS IN THE AUSTRALIAN ARID ZONE

The predation model presented is an extension of the "Environmentally Modulated Predation" theory (Newsome *et al.* 1989) which suggests that predators can regulate populations of medium-sized mammals after their densities have been reduced by drought or wildfire, because predator populations are sustained by the carrion that results from the drought or wildfire, and prey become trapped in a "predator pit". My Predation Model suggests that predators can not only regulate, but can actually extinguish local populations of mammalian prey, because of their ability to survive on naturally occurring alternative prey (reptiles and nomadic birds) that show contrasting patterns of fluctuation to the mammalian species. It therefore differs from the Hyperpredation hypothesis (Smith and Quin 1996), which requires the presence of exotic prey species to sustain predator populations at a level where native prey are trapped in a "predator pit".

The "degradation of refugia" hypothesis (Morton 1990) also focuses on the impacts of exotic species (primarily rabbits and grazing stock) on the arid zone ecosystem. It proposes that introduced herbivores destroyed the refuge areas that native mammal species depended on during drought periods (Morton 1990). But grazing stock have never occurred in most of the spinifex grasslands, and there is little evidence that rabbits were ever common in the northern deserts, especially in the sandplain, sand-dune and mulga habitats where many of the medium-sized mammals occurred (Johnson *et al*. 1989). While the wetter, more fertile areas (believed to have been targeted by rabbits), may have been crucial for the survival of some of the herbivorous species (i.e. the macropod, stick-nest rat and possum fauna), only half of the medium-sized mammals to have disappeared or declined were herbivores (Morton 1990), and such refugia are unlikely to have been as important for the omnivorous and carnivorous species of medium-sized mammals. The five species of bandicoots and bilbies that originally occurred in central Australia included significant quantities of ants and termites in their diets (Strahan 1995), which are not necessarily more abundant in more productive habitats (Stafford Smith and Morton 1990). Similarly the prey (invertebrates, reptiles and small mammals; Strahan 1995) of the western quoll and the dunnarts that are believed to have declined, were not found to be any more abundant in the palaeodrainage habitat than the sandplain habitat in this study.

Although there was significant overlap in the diets of rabbits and mala (Lundie-Jenkins *et al*. 1993), the diets of burrowing bettongs and brush-tail possums showed little overlap with that of the rabbit (Robley *et al* 2002, Foulkes 2001). In some areas, burrowing bettongs and rabbits are believed to have coexisted for up to 60 years (Finlayson 1958). Furthermore, a reintroduced population of burrowing bettongs at Heirisson Prong in Western Australia, was found to thrive in the presence of high densities of rabbits, even after the rabbits had caused widespread defoliation and subsequent death of many shrub species (Robley *et al*. 2002). Thus, while the "degradation of refugia" theory (Morton 1990) may be an accurate depiction of the demise of certain herbivorous species across much of the rangelands of Australia, it does not adequately explain the patterns of decline of the whole suite of taxa, across their entire distributions.

The other major theory to explain the loss of medium-sized mammals is the "altered fire regime" hypothesis. Medium-sized mammals are believed to have become adapted to the mosaic of different aged vegetation that resulted from Aboriginal burning practices, which ensured adequate food supplies (in recently burnt habitat) occurred in close proximity to mature vegetation required for shelter (Bolton and Latz 1978). The vegetation mosaic does not appear to be essential for the survival of all arid-zone medium-sized mammals however, because healthy populations of golden bandicoots (*Isoodon auratus*) brushtail possums and burrowing bettongs occur on Barrow Island, where Aboriginal burning has not occurred for at least 8,000 years (Short and Turner 1994). Major fires, caused by lightning strikes, occur on the island approximately every 50 years, and during such events the whole island burns at once. The impacts of an artificially imposed vegetation mosaic (caused by clearing) on populations of burrowing bettongs, golden bandicoots and brushtail possums were investigated on the island, but there was no evidence that any of these species required a particular spatial pattern of burning to persist (Short and Turner 1994). While altered fire regimes have undoubtedly affected medium-sized mammal populations in central Australia, it is probably more a function of increased vulnerability to predation than changed food availability (Short and Turner 1994) and, in the absence of exotic predators, altered fire regimes are unlikely to have resulted in widespread extinctions of medium-sized mammal fauna (Short and Turner 1994).

5.5 FUTURE DIRECTIONS IN PREDATOR MANAGEMENT IN CENTRAL AUSTRALIA

In the 1980s, bilbies were considered common and widespread in the Tanami Desert, and foxes were virtually absent (Gibson 1986). Today foxes are common and widespread through most of the desert, and bilbies are becoming increasingly rare. Clearly it is impossible to manage an area as vast as the Tanami Desert, but a series of predation refugia, from which bilbies can recolonise areas after droughts, may help their survival. Predation refugia could include a combination of predator-proof enclosures, zones in which foxes are killed through poison baiting and areas where Aboriginal people are employed to utilise traditional hunting methods to control introduced predators.

Predator-proof enclosures are very costly to establish. For example, a one square kilometer mala enclosure in the Northern Territory cost $62,000 to construct (C. Pavey, N.T. Parks and Wildlife Service, personal communication). However, if situated in an accessible area, such as within a national park, a predator-proof enclosure should be relatively inexpensive to maintain. As a single fire or outbreak of disease could eliminate the entire population within a predator-proof enclosure, a series of such populations are required to insure against the loss of a species. Although predator-proof enclosures can provide a safeguard against extinction, and may provide information on whether there are still sufficient food resources in the environment to sustain particular species (Southgate 1994), they tend to only preserve a small fraction of the species within an ecosystem. Used in isolation, this method results in the abandonment of vast areas of surrounding habitat, where threatening processes continue to operate and less charismatic species may be declining, unnoticed.

If labour is available, poison-baiting can be successfully used to control fox abundance (Saunders *et al*. 1995). In Western Australia, this method has resulted in significant population recoveries of 11 species of native mammal populations, (Kinnear *et al*. 2002). The main problems with baiting are that techniques are not yet available to selectively target foxes without killing dingoes, and cats are rarely affected by baiting programmes (Lundie Jenkins *et al*. 1993, Christensen and Burrows 1994). It has been suggested that dingoes offer a form of protection to prey species from cats and foxes, which are repelled by the presence of the larger predator (Pettigrew 1993, O'Neill 2002). Removing resident dingoes by poison-baiting may result in significant increases in fox and cat abundance (Lundie-Jenkins *et al*. 1993, Pettigrew 1993). There is anecdotal information on the interactions between dingoes and the smaller predators, but little empirical data, and this should be a priority for future research. The effects of experimental dingo control on the abundance and habitat utilisation of cats and foxes, and flow-on effects to populations of threatened species would be useful avenues of research. If dingoes are found to play a role in regulating cat and fox populations, research should also be focused on designing a discriminatory baiting system. This may involve fox-specific delivery devices, or take into account differential habitat utilisation by the predators. For example, in the Tanami Desert, baiting at least 10 km from a water source may be a way of targeting foxes rather than dingoes. This could be investigated further with a satellite telemetry study into the movement patterns of foxes and dingoes in and around palaeodrainage lines and other water sources in the Tanami Desert.

The ability of foxes to rapidly recolonise areas is well known (Saunders *et al.* 1995). Thus, to have any long term impact on prey populations, baiting must occur on a regular basis and over large areas. While this is logistically difficult in places as remote as the Tanami Desert, collaborating with Aboriginal community ranger programs would make a regular baiting program more feasible. However, it is important that the impacts of any poison-baiting programs on both the predator community and as many prey species as possible should be carefully monitored, in case there are any unwanted consequences of predator control (Caughley and Gunn 1996). For example, fox control is believed to have caused an increase in the feral cat population at a site in Western Australia, which in turn resulted in a significant decline in the abundance of small native mammals (Risbey *et al*. 2000). In other situations, fox control may result in an outbreak of rabbits (e.g. Banks *et al*. 1998), potentially providing unsustainable competition for a species such as the bilby. The effects of predator control on survival and breeding success of threatened species populations should be monitored at replicated treatment sites to sample the natural range of variability in the system, as well as at scientific control sites, to render the conclusions unambiguous (Caughley and Sinclair 1994). Monitoring predator diets, through scat analysis, during any predator manipulation exercise, would also assist the interpretation of the results of predator control.

With cats proving resistant to baiting programs, traditional hunting by experienced Aboriginal trackers is currently the most effective method of killing cats in the sandy desert country (see Appendix A), and these skills could be capitalised on for conservation purposes. There is already anecdotal evidence that threatened species such as the bilby, mulgara and great desert skink are surviving better in areas close to Aboriginal communities than in more remote areas (McAlpin 2001, Paltridge unpublished data). This may be due to a combination of regular cat hunting, frequent patch-burning, and perhaps even the presence in the communities of high densities of dogs, which may repel foxes. I believe that such hypotheses are worthy of future research: quantifying the impacts of traditional Aboriginal land management practices (cat hunting and patch-burning) on the abundance of threatened species. If it can be demonstrated that Aboriginal hunting does have a positive impact on threatened species populations, Aboriginal people should be given the opportunity of employment to conduct such activities. Currently, the number of communities engaging in regular cat hunting is declining and fewer young people are learning the art of tracking. If financial incentives were provided, perhaps in the form of bounty payments for cats and foxes, this would encourage people to continue the tradition, and stimulate younger people to become involved. Employment opportunities for Aboriginal people in communities are extremely limited – being paid as part-time pest control officers is likely to be regarded favourably.

Bounty systems are not encouraged by federal authorities for reasons including: 1) such systems are subject to fraud, 2) it is not a cost-effective method of control and 3) the system tends to remove the most vulnerable individuals in a population such as the young, inexperienced, sick or very old animals which do not cause the most damage and may not have survived natural competition anyway (Saunders *et al*. 1995, Fleming *et al*. 2001). Where I have used bounty systems in conjunction with remote Aboriginal communities, the scheme has applied to clearly delineated areas, rather than diluting the impact of activity over broad regions. Bounty claimants are expected to indicate on a map where cats were obtained, and present both the tail and stomach of cats to claim their payments. Hair length and colour and stomach contents should indicate whether or not cats are from a feral situation, and reduce the opportunity for fraud. My experience with Aboriginal cat hunters suggests that they do not target the most vulnerable individuals in the population, but all fresh tracks are pursued, and very few cats escape. Used in discrete areas to protect populations of threatened species, bounty payments of $30 per cat are a cost-effective management method, when compared to the low trap success rates obtained in other arid zone areas (see Appendix A).

If cat hunting is regular and ongoing, it should provide some relief for threatened species from predation. Even if the area intensively hunted is only a 10 km radius around an Aboriginal community, this could potentially provide an important refuge zone for species such as the bilby, mulgara and great desert skink of approximately 300 square kilometers (based on area = πr^2), which is an order of magnitude larger than any predator exclosures.

Foxes are more difficult to procure using traditional tracking, as they travel over greater distances. They are also less appealing food than cats. However, if fox dens can be located by tracking, they could either be dug up to remove their inhabitants, or targeted with baits or traps. This would be a good start towards controlling foxes in particular areas without broadscale baiting, which would discourage people from eating cats in the area, and cause concerns for dogs.

If the predation model presented in this thesis is correct in identifying introduced predators as primary agents of the extinctions of medium-sized mammals, self-sustaining biological control of foxes and cats is the only long-term solution to the problem, and this should be a major priority for future research. While there have been some advances into fertility control for foxes by means of bait-delivered immunocontraception (Bradley *et al*. 1997), there has been no research into biological control of cats in Australia, and it remains to be seen whether reduced fertility will cause a significant reduction in the impacts of foxes on wildlife. Clearly, biocontrol methods will not be available for many years. In the meantime, more labour-intensive methods of predator control such as predator-proof fencing, baiting and traditional hunting, may be critical to the survival of threatened species such as the bilby.

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APPENDIX A

A NEW TECHNIQUE FOR MONITORING THE MOVEMENT PATTERNS AND HUNTING BEHAVIOUR OF FERAL CATS IN THE SANDY DESERTS OF CENTRAL AUSTRALIA[#]

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Abstract

Feral cats have been implicated in the demise of many arid zone mammals. As a consequence cats have been the focus of a variety of studies investigating their ecology and methods of control. Track counts are increasingly being used to monitor the relative abundance of cats in Australia's sandy deserts, but information on distances moved by individual cats is required to relate track counts to a measure of abundance. This study describes a novel method of documenting 24 h movement patterns of cats in the spinifex grasslands of central Australia. The method integrates traditional Aboriginal tracking techniques with radio telemetry and satellite navigation. From 19 tracking sessions, including 7 cats, we found the mean distance travelled by a cat in a 24 h period was 3.96 ± 2.56 km. The mean distance reached from the starting point within 24 h (daily home-range width) was 2.20 ± 1.29 km. This did not vary significantly between seasons or between the two sexes, although males occasionally made long-distance excursions. Information on hunting behaviour of feral cats was also collected, enabling maps to be produced depicting the activity of a cat over a 24 h period. The tracking skills of Aboriginal People were integral to the success of this study and we believe this technique could become an important research tool in behavioural studies of a variety of species in the 2 million square km of sandy desert country of inland Australia.

[#] Paper in preparation for submission to *Australian Mammalogy*

INTRODUCTION

Feral cats (*Felis catus*) are distributed throughout Australia, including the arid interior (Dickman 1996). They have been implicated in the demise of many species of arid zone mammals (Morton 1990, Short *et al*. 1992, Gibson *et al*. 1994). Because of this, feral cats have received considerable attention in recent years with various studies attempting to investigate their ecology and methods of control (Jones and Coman 1981, 1982, Paltridge *et al*. 1997, Edwards *et al*. 1997, 2001, Risbey *et al*. 1997, Short *et al*. 1997, Mahon *et al*. 1998, Molsher *et al*. 1999, Read and Bowen 2001). Few studies have collected quantitative data on the impacts of cats on prey species however (Dickman 1996), and we have little information on the behaviour of feral cats in the Australian environment to contribute to development of effective control techniques.

In central Australia, feral cats have proven to be particularly difficult to capture or observe, due to their shy nature, nocturnal habits, relatively low density and aversion to baits (Mahon *et al*. 1998, Edwards *et al*. 2000). Studies of their population dynamics and feeding habits have therefore focussed on indirect methods of observation. For example, population dynamics are monitored by counting frequency of fresh tracks along a prepared tracking surface (Mahon *et al*. 1998, Edwards *et al*. 2000). Daily counts of fresh tracks give an index of abundance, but to be able to relate track counts to the actual number of cats in a given area, it is necessary to know the cats' daily home range, or at least how far individuals move within 24 hour periods (Edwards *et al.* 2000, Wilson and Delahay 2001). It is also important to know the extent of home range overlap that occurs between different individuals. This information can then be used to predict whether subsequent sets of tracks recorded along a transect belong to the same or different cats.

The functional and numerical response of predators to fluctuating prey densities can be used to predict the impact of predation on prey species. Functional response is based on the number of prey killed per predator per unit of time, and is very difficult to measure accurately for vertebrate predators in the field (Boutin 1995). Most studies have estimated functional response by monitoring changes in the proportion of prey types in a predator's diet, but this may not be an accurate representation of the number of prey that have been killed by a predator, particularly if caching or partial consumption of prey occurs during periods of high prey density (Boutin 1995). Also, at low prey densities, the proportion of scats containing certain prey may remain constant, but defecation rates may be reduced if the predator is eating less (Boutin 1995). Dietary studies of feral cats have previously been based on either gut content analysis (e.g. Paltridge *et al*. 1997), or scat analysis where destructive sampling was inappropriate (e.g. Molsher *et al*. 1999). To make scat analysis more quantitative, it would be useful to know the defecation rates of cats, often assumed to be one scat per day (Liberg 1984). However, determining the number of kill sites a predator has operated at per unit time could potentially provide more accurate data on functional response than either gut or scat analysis.

Integral to the success of any control program for feral cats is knowledge of their behaviour, such as information on habitat utilisation, daily activity patterns, identity of refuges and hunting strategies. Where direct observation of animals is not feasible, remote radio-telemetry is a commonly used method of studying the movement patterns of animals (White and Garrott 1990). Radio-telemetry data can provide information on distances travelled by animals, and which habitats are being utilised, but it reveals nothing of what an animal is actually doing in its travels and the precise micro-habitats being traversed.

Aboriginal people in central Australia have been hunting feral cats for meat and medicine for at least 100 years (Johnson 1991). Many of these people are highly skilled trackers, possessing detailed knowledge of the behaviour and ecology of cats and of many other species. The benefits of incorporating traditional ecological knowledge of Aboriginal people into scientific research have been advocated by Baker *et al*. (1992), and utilised in some studies in Australia (Burbidge *et al.* 1988, Walsh 1990, Baker *et al*. 1992). However, we know of no published studies where Aboriginal tracking skills have been an integral part of studies of the behaviour and movement patterns of animals in Australia. This is in contrast to wildlife research in Africa, where tracking and the interpretation of spoor by indigenous people have been accepted as a scientifically sound method in ecology (Stander *et al*. 1997). Radio-telemetry data collected in conjunction with track interpretation provides much more information than either method used in isolation (Libenberg 1990).

In this study, Aboriginal tracking techniques were integrated with radio-telemetry and satellite navigation to study the movement patterns and hunting behaviour of feral cats at one site in the Great Sandy Desert in central Australia. We aimed to determine mean daily distances travelled by cats under different seasonal conditions and to measure daily kill rates and defecation rates. This information contributes to a broader study of the ecology of cats in central Australia .

METHODS

Study Area

The study was conducted at a remote site in the Great Sandy Desert bioregion (Thackway and Cresswell 1995), approximately 450 km west-north-west of Alice Springs in the Northern Territory (22 º 51' S, 129 º 57' E; Fig. 1). The study area falls at the intersection of the Tanami, Great Sandy and Gibson Deserts, and is Aboriginal freehold land. The nearest human habitation is the community of Nyirripi (population 400), 80 km northeast of the study site. There is no infrastructure in the area other than a dirt road which passes within 10 km of the site, The area has never been used for pastoralism or tourism.

The area has a climate of long hot summers, mild winters and an unpredictable summer-dominated rainfall. The mean daily maximum and minimum temperatures in the hottest month (January) are 36.2ºC and 21.3ºC, but temperatures over 40ºC are common. The mean daily minimum temperature in the coldest month (July) is 4.1ºC, rising to a daily maximum of 19.5ºC. The mean annual rainfall at the nearest meteorological station (Newhaven station, 130 km E of the study site) is 322 mm with a coefficient of variation of 79%. Seventy seven percent of rainfall occurs in the summer months.

The topography of the area consists of red earthy sand plains bisected by low sand dunes (average height of 8 m), in an east-west alignment and approximately one kilometre apart. The sandplain supports hummock grassland, dominated by two species of spinifex (*Triodia pungens* and *T. basedowii*), with a sparse overstorey of scattered shrubs including species of *Eucalyptus*, *Hakea*, *Grevillea* and *Acacia*. Desert bloodwood trees (*Corymbia chipendalei*), grow on the dune crests with spinifex and low shrubs such as *Thryptomene maisonneuvei*.

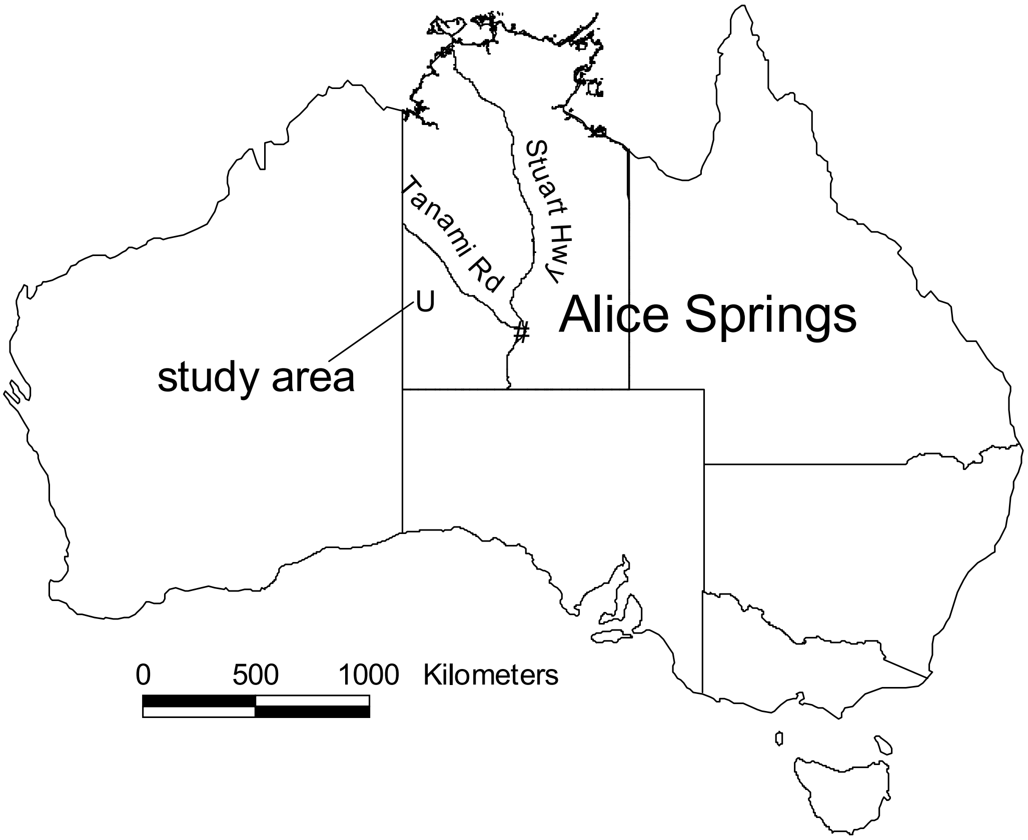

Figure 1. Map of Australia showing location of the study area

Capturing cats

We initially attempted to capture cats using Victor® soft-catch leghold traps (size 1.5). The traps were baited with kangaroo meat plus a lure (either synthetic fermented egg or bobcat anal gland paste) and set in groups of three on the crests of dunes and along roads where fresh tracks were seen. A fresh kangaroo carcass (roadkill) was dragged behind the vehicle between traps to make a scent trail. A total of 77 trap-nights (where a set of three traps is considered as a single trap) failed to capture any cats, and there was no sign of cats visiting any of the sites or being attracted to the scent trail. Dingoes (*Canis lupus dingo*) and foxes (*Vulpes vulpes*) set off some traps but did not get caught, probably because of the small size of the traps.

Cats were captured by following their tracks on foot, with the assistance of Aboriginal trackers. An initial search for fresh cat tracks was conducted from a four-wheel-drive vehicle, travelling at 10 km per hour. When fresh tracks (estimated at < 12 h old) were found, they were followed on foot at a walking pace by two Aboriginal trackers plus the scientific observer. A fourth person trailed the pedestrians with the vehicle, at least 150 m to the rear. When the cat was flushed for the first time, the chase accelerated to a jogging pace, and the driver of the vehicle drove in a wide arc around the cat to direct it back towards the pursuers and encourage it to go to ground. When the cat stopped to rest or attempted to hide in the grass, a hoop net was thrown over it. It was then subdued by being covered with a blanket, and if necessary anaesthetised with an intramuscular injection of one part xylazine (Rompun: Bayer Australia Ltd.) to two parts ketamine hydrochloride (Ketalar: Parke Davis Australia Ltd.) at a dose rate of 0.1 ml per kg of body mass. All cats were weighed, sexed and given a general examination before having radio-collars fitted. They were then left in the shade to recover. Two-stage Sirtrack (Sirtrack Ltd., New Zealand) radio-transmitters were used. The transmitters were powered by AA lithium cells (40 pulses per minute), and attached to leather collars. Each collar had a 22 cm vertical whip aerial.

Monitoring 24 hour movement patterns.

To monitor the behaviour and movement patterns of a cat over a 24 hour period, the following procedures were followed. On the morning of day one, the cat was located to its den using radio-telemetry equipment (a folding three element hand-held directional antenna: Sirtrack, New Zealand, and a portable scanner/receiver, model TX3: Biotelemetry, Australia). Care was taken not to flush the animal from its den. We returned to this location the following morning and searched for tracks leading away from the resting place. The tracks were then followed vigilantly until the cat was sighted. The telemetry receiver was used at regular intervals to assess whether the cat was in close proximity. If the strength of the radio signal and the appearance of the tracks indicated that the cat was running ahead of us, the tracking session was terminated. However, we were usually able to follow the animal's tracks to its resting place, either inside a clump of spinifex or down a bilby (*Macrotis lagotis*) hole. When the radio signal indicated that the cat was very close, it was approached quietly to avoid flushing it. Often the cat would be hiding inside a clump of spinifex and usually did not run away. The area was marked so we could return the following day to recommence tracking.

We carried a Magellan Promark 10 Global Positioning System (GPS) throughout the tracking session, and this automatically evaluated and recorded our position every 30 seconds. Any action that was seen in the tracks was described by the trackers and stored on an attribute file on the GPS. The attribute file contained the following pre-set categories: running, walking, sitting down, lying down, into hole, into spinifex, urinated, defecated, other male cat tracks, other female cat tracks, any interaction, rodent, dasyurid, dragon, skink, *Egernia* skink, bird, pounce and miss, lost tracks, found tracks. Additional words could also be typed onto the attribute file during a tracking session. Thus if the tracks indicated the cat had pounced on a dragon but the dragon had run away “dragon” and then “pounce and miss” would be entered onto the GPS. Alternatively, pouncing tracks beside a scattering of green budgerigar (*Melopsittacus undulatus)* feathers would be entered as “bird” and then the species would be typed in. If the tracks were temporarily lost during pursuit “lost tracks” would be recorded on the GPS, and then “found tracks” when they were rediscovered; the intervening wandering around in search of tracks could then be deleted from the computer-generated map.

By the end of the study (20 months after commencement), no signals could be heard from any of the radio-collared cats, so we attempted aerial tracking from a light aircraft, but still did not find the cats.

Scat Analysis

Any scats deposited by the cats being followed were collected and returned to the laboratory for analysis. Prey remains were initially sorted under a dissecting microscope. A representative sample of each hair type was cross-sectioned and examined under a compound microscope and identified by comparison with a reference collection of photographs of known material. Reptiles were identified to the family level on the basis of scales and jaw-bones. Jaw bones, feet and bird’s beaks were used to determine the number of vertebrate prey items present in scats.

When individual cats were tracked for several consecutive days and scats were collected on the second or third day of the tracking session, the prey remains in the scats were used as a calibration of the accuracy of our interpretation of the cat’s prey consumption from the tracks. Interpretation accuracy was defined as (number of prey items common to tracks from day 1 and scats from day 2 / number of prey items found in the scats from day 2 x 100). This is based on two assumptions: (a) all prey items consumed can be accurately identified from scats and (b) passage rates of the various prey items are approximately equal and not significantly greater than 24 hours.

Prey availability

Potential prey available to cats was monitored using pitfall traps and Elliott traps, and counting birds along a 1 km walked transect. Traps were opened for a three day period during spring 1997, summer 1998 and winter 1998. Two lines of five pitfall traps were located 500 m apart. Pits (25 L white plastic buckets) were situated at 7 m intervals and connected by a flywire drift fence standing 25 cm and partially buried into the sand. The lids of the buckets were propped up above the buckets at fence height to provide shade within the pits. The pitfall traps were checked at least twice per day. Two parallel lines of 25 Elliott traps were set 100 m apart. Traps were positioned at 20 m intervals and baited with balls of peanut butter and oats. Elliott traps were opened in the late afternoon and closed early the next morning. The bird transect was surveyed twice per season approximately half an hour before sunset. All birds seen and heard within a 50 m strip on either side of the transect were counted and identified to species with the aid of 10 x 50 binoculars.

Data analysis

The GPS data files were downloaded into a spreadsheet on a laptop computer, using Magellan software. After editing (e.g. deleting any data points collected when the cat's tracks were temporarily lost), the data files were imported into Arcview version 3.0a. Maps were produced of daily movement patterns, and the distances moved by cats measured using the ruler tool in this program. The mean distances moved by cats were analysed for differences between sexes and between seasons using two-sample, two-tailed t-tests, assuming equal variances between the two samples (Zar 1996).

RESULTS

Capturing cats

Seventeen cats were captured at the site between October 1996 and June 1998. Fifteen individuals were radio-collared. All cats were captured as a result of tracking and chasing by the Aboriginal trackers. The mean distance travelled in pursuit of cats, from the point where the tracks were first found to the point of capture, was 3.9 km. This took an average of 2.1 hours per cat. However this does not include time spent searching for fresh tracks in the vehicle, which varied between 15 minutes and 2 hours. The 17 cats were captured over a period of 23 days and when number of trackers employed is taken into account, 74 tracker-days were utilised.

The predominant coat colour of the cats that were captured was grey tabby (82%) but there were also three ginger cats. The mean body mass (± s.d.) of the ten males captured was 3.8 ± 0.5 kg and of the 7 females captured, 2.9 ± 0.5 kg.

Only two of the fifteen collared cats were tracked for more than three months. Eight cats disappeared between two days and two months after capture, and were never detected again, despite aerial searching from a light aircraft. It is unknown whether these cats dispersed large distances or whether their radio-transmitters failed.

Five cats died during the study. The remains of one cat, whose signal was lost soon after being radio-collared, were found 10 months later, 3.5 km from the point of release. The cat appeared to have been dead a long time and had obviously been eaten by predators, but it is unknown whether predators had killed the cat or scavenged the dead carcass. Another cat that was last seen alive four months after being radio-collared was found dead 2 months later. There was no sign of attack by predators. A third cat was already very weak when captured, and regularly visited our camp during the week between being radio-collared and dying, possibly seeking food, water or shade. Two cats died after being chased to capture them for radio-collaring. They were hyperventilating by the end of the chase and died within several hours. Four of the five deaths occurred in the summer of 1997-1998. Two other recently dead (uncollared) cats were also seen at the end of summer 1997-1998; one had not been disturbed by predators at all, the second had been eaten by birds of prey, judging by the faeces and tracks around, but they may have been scavenging a dead carcass. No post mortems were conducted on any cat carcasses.

Daily movement patterns

The combined tracking technique was a very successful method of monitoring movement patterns of cats in our study area. We successfully completed 19 mapping sessions from 26 tracking attempts. Some examples of the maps produced are displayed in Figures 2-4.

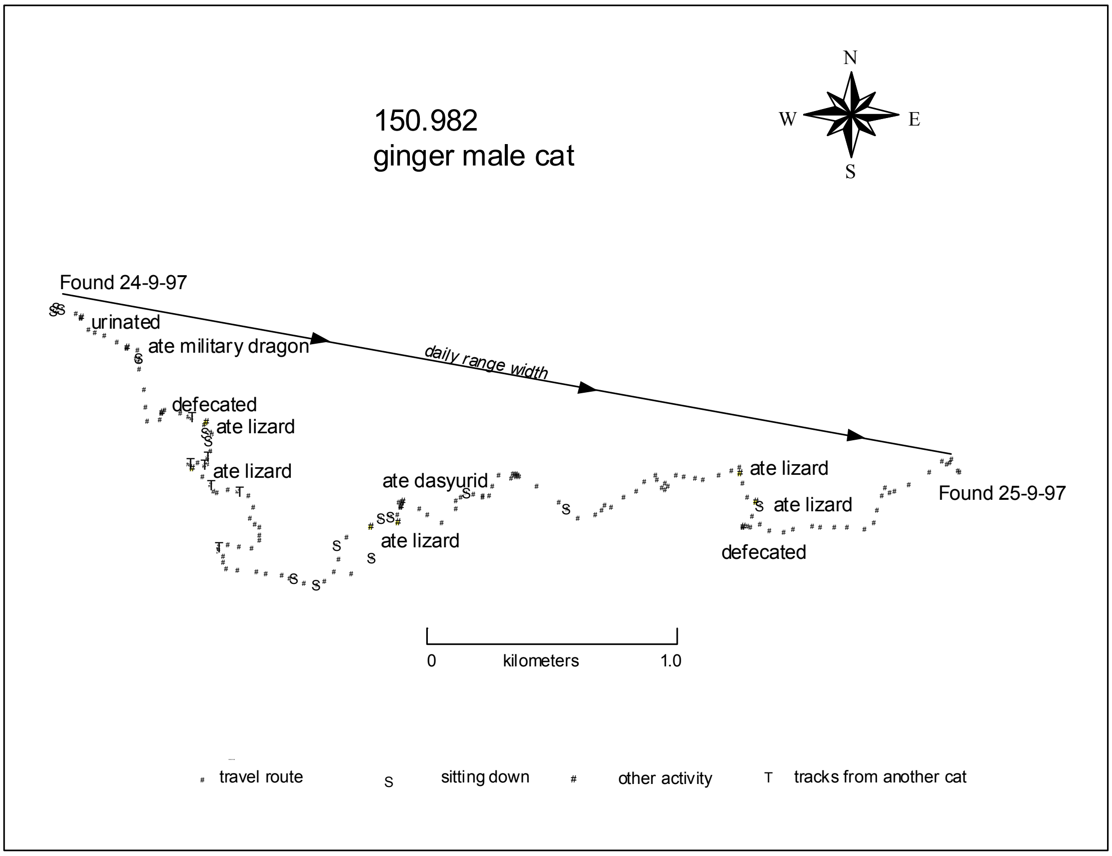

Fig. 2 Activity of a 3.8 kg ginger male cat over a 24 hour period, September 1997. It travelled 6.10 km and the width of the daily range was 3.9 km. During the 24 hour period it ate 6 lizards including at least one military dragon (*Ctenophorus isolepis*) and one small dasyurid (*Sminthopsis* sp.). Evidence of one urination and two defecations were recorded during the tracking period.

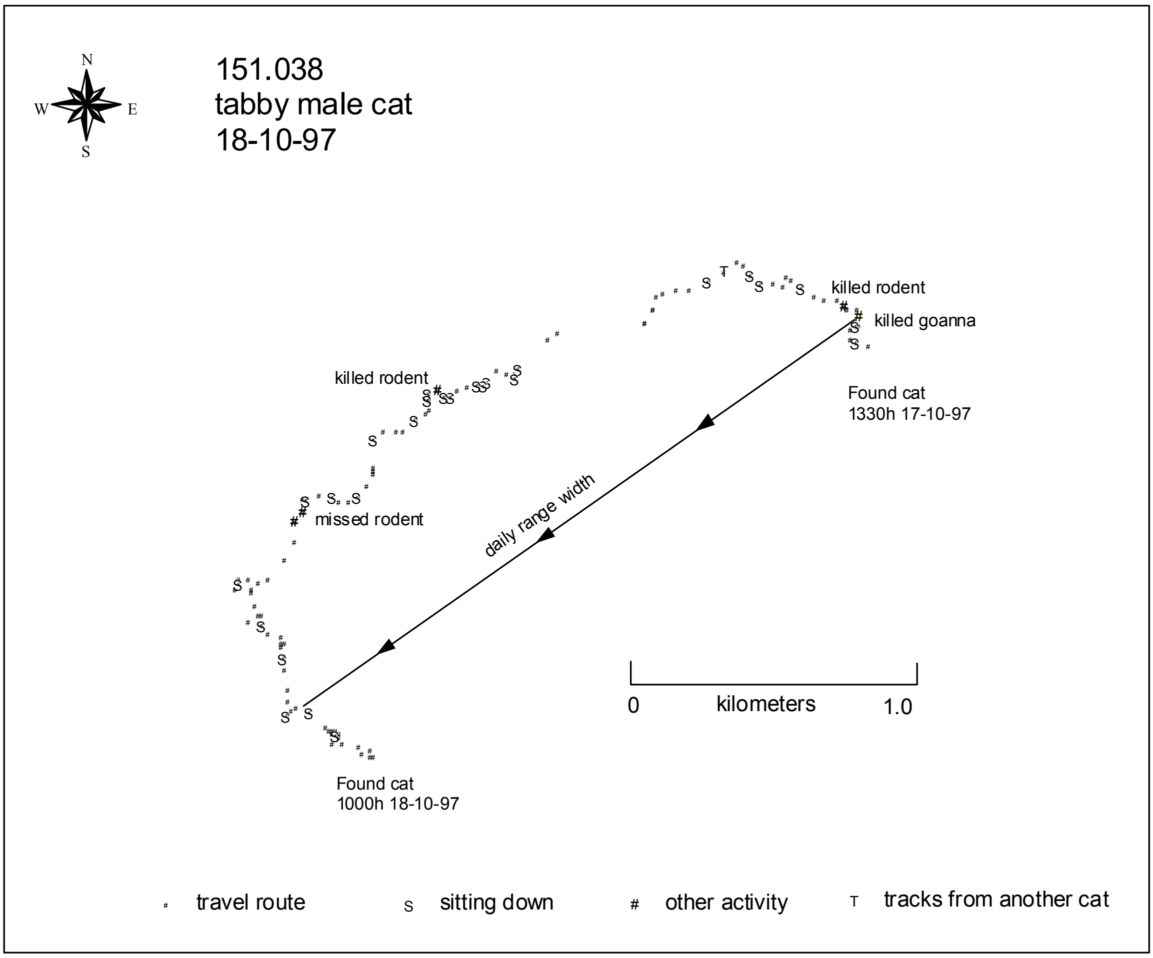

Fig. 3. Activity of a 4.4 kg grey tabby male cat in a 24 hour period, October 1997. It travelled a total distance of 3.93 km. The width of its daily range was 2.16 km. It ate one sand goanna (leaving the head as evidence), and two rodents during the 24 hour period. It pounced on a third rodent which apparently escaped. There was another cat in the area, but there was no evidence in the tracks of any interaction between the cats.

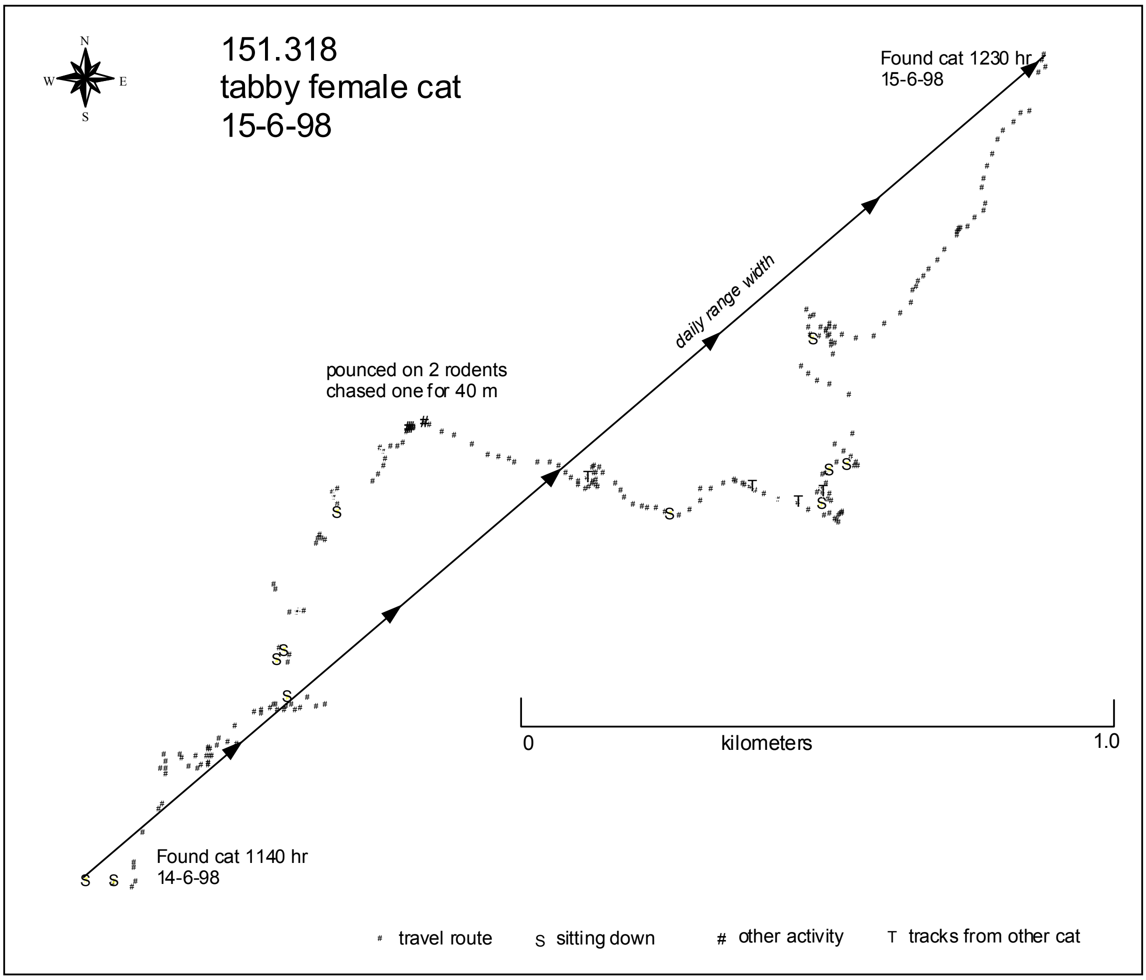

Fig. 4 Activity of a 3.0 kg grey tabby female cat in a 24 hour period, June 1998. The cat travelled a total distance of 3.2 km. The width of its daily range was 2.1 km. It captured two spinifex hopping mice during the 24 period. There was a male cat in the area but there was no evidence of any interaction between the two animals.

Our rate of tracking was approximately one kilometer per hour, but varied according to the clarity of the tracks, which depended on the weather conditions of the previous 24 hours (primarily wind and rain) and surface qualities, such as soil compaction.

Fresh tracks belonging to other cats were regularly encountered during the tracking. Usually the tracks were of sufficiently different size to indicate to the Aboriginal trackers that they either belonged to animals of the opposite sex or were juveniles. Sometimes the cats appeared to have been travelling together. When capturing cats, pairs of cats were flushed from individual holes on three occasions. Only one definite physical interaction was recorded from the tracks. The tracks of a male that was being followed converged with a set of smaller tracks and scuffle marks could be seen in the sand, which the Aboriginal trackers interpreted as copulation. No interactions were interpreted as fighting. Spraying was recorded in 42% of tracking sessions during the current study. One female that was followed for three consecutive days appeared to be in oestrous. On the first day she sprayed three times, but no sign of any other cat was recorded. On the second day she sprayed once and her tracks were followed by one of the radio-collared male cats for at least 500 m. On the third day male cat tracks were regularly encountered throughout her movement path but we saw no evidence of any physical interaction between the two animals.

None of the cats that were tracked returned to their starting point within a 24-hour period. Rather, movement patterns were relatively linear. The overall mean distance travelled by cats (± s.d.) within a 24-hour period was 3.96 ± 2.56 km (Table 1). The overall mean maximum width of the daily range (i.e. the maximum distance from the starting point reached within 24 hours; see Fig. 2) was 2.20 ± 1.29 km (Table 1). Daily range width showed little variation between seasons, ranging from 2.08 ± 0.95 km in spring (n = 8 days based on 4 cats) to 2.35 ± 1.76 km in winter (n = 8 days based on 4 cats; P=0.69). The mean width of male daily ranges was 2.38 ± 1.46 km (n = 14 based on 4 cats) and 1.72 ± 0.39 km (n = 5 based on 3 cats) for females, but the difference was not significant (P =0.34).

With the exception of females with kittens, the cats at our study site did not consistently return to the same den, but instead had a series of temporary shelters. Most shelters were inside large spinifex hummocks but cats were occasionally found in disused bilby holes. No cats were found in tree hollows but the Aboriginal trackers stated that they had obtained cats from trees on other occasions. During pursuit, cats did not climb trees as a means of escape. Both bilby holes and tree hollows were a rare resource in the study area.

Table 1. Summary of cat tracking data

CAT ID.	sex	date	total distance travelled	daily range width	no. of prey consumed: reptiles	mammals	birds
1	f	18-Sep-97	2.01	1.15	1	2	
2	f	22-Sep-97	2.55	1.88		1	
3	m	24-Sep-97	2.87	1.95	3	1	
3	m	25-Sep-97	6.10	3.90	6	1	
3	m	12-Oct-97	2.47	1.20	6		
3	m	13-Oct-97	2.30	1.36	2		
4	m	14-Oct-97	6.06	3.00	5	1	
4	m	18-Oct-97	3.93	2.16	1	2	
4	m	20-Mar-98	2.74	1.90	1	1	1
4	m	21-Mar-98	2.18	1.40	2		1
4	m	22-Mar-98	4.50	3.10	2		
5	m	10-Jun-98	10.01	5.00		2	
6	m	11-Jun-98	1.80	1.10		1	
6	m	12-Jun-98	1.10	0.50			
6	m	15-Jun-98	2.70	1.50			
4	m	17-Jun-98	10.10	5.20		2	
7	f	14-Jun-98	3.20	1.50			
7	f	15-Jun-98	3.20	2.10		2	
7	f	16-Jun-98	5.40	1.96			1
		mean	**3.96**	**2.20**			
		std deviation	**2.56**	**1.29**			

Prey consumption (in relation to prey availability)

Although this was a relatively short study, there were considerable fluctuations in the availability of prey groups during the study period (Fig. 5). Reptiles were most abundant in the spring survey and least abundant in winter. Birds remained relatively uncommon during the study period but were most abundant in the summer. Small mammals were initially rare but increased in abundance in the winter survey.

Only two scats were found that could be used to verify the accuracy of interpretation of the cats' predatory behaviour from the tracks. Scat 1 was collected in the first week of the tracking study and revealed a track interpretation accuracy of 60%. Scat 2 showed a track interpretation accuracy of 83% (Table 2).

Table 2. A comparison of prey consumption data obtained from track interpretation and scat analysis.

Cat	Date	Track data	Scat data	Accuracy
0.982	Sept-97	1 dasyurid	1 dasyurid + 1 rodent	
(Scat 1)	(Track data from day 1	3 lizards	2 lizards	60%
	2 scats found on day 2)		1 bird	
1.038	Mar-98	1 rodent	1 rodent	
(Scat 2)	(Track data from days 1-2	2 birds	2 bird's beaks	83%
	1 scat found on day 3)	3 lizards	2 lizards + 1 snake	

Assuming that the interpretation of predatory behaviour from the tracks is reasonably accurate, cats appeared to prey on reptiles in proportion to their relative availability (Fig. 5). When reptiles were abundant, they were the most frequently consumed prey items. There was some evidence that bird consumption was related to bird abundance (Fig. 5), but data for the tracking period when birds were most abundant was limited to only three 24-h sessions, all from the same cat. Additional evidence of bird hunting was seen in winter 1997, when six of the cats were caught. Budgerigars (*Melopsittacus undulates)* were particularly abundant at that time (Paltridge and Southgate 2001), and one cat consumed three budgerigars within a kilometre, before its capture, judging by the remains found along its trail. Small mammals were apparently eaten in all seasons, regardless of their relative abundance.

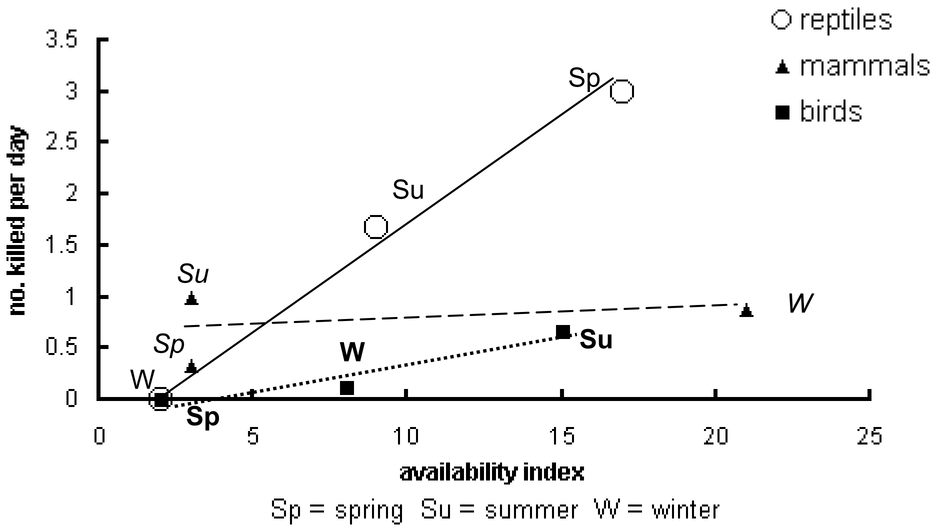

Fig. 5. The effect of prey availability on kill rates by cats. Prey availability data are based on number of captures per 180 trap nights (reptiles and small mammals) and counts per km of transect (birds).

Hunting behaviour

Cats appeared to use slightly different techniques for hunting reptiles and small mammals. The tracks indicated that cats often used a "sit-and-wait" approach for capturing small mammals, as many pounces on small mammals were preceded by sitting-down tracks. There was no sitting down or even standing still prior to catching most species of lizards however, and we have termed the lizard-hunting strategy the "random-search-and-pounce" technique. Cats rarely ran to chase prey, and the majority of chases covered less than 2 m. The longest chase observed in the tracks was when a cat ran 40 m down a sandhill in pursuit of a spinifex hopping-mouse, which apparently escaped.

Infanticide

Three examples of apparent infanticide were observed during the study. Three very young kittens (less than 1 week old) belonging to female 1.118 were found in a spinifex hummock several days after the mother was radio-collared in August 1997. The day after disturbing the kittens we returned to find that two of the kittens had been killed and the third moved to another location, 200 m away. No sign of any other predators was found near the dead kittens. A second female cat appeared pregnant when captured in August 1997. One month later she was tracked down to a hummock of spinifex where a young kitten was seen on top of the spinifex hummock. Several hours later it was still there (alive and actively calling) so we retrieved it and placed it inside the spinifex hummock. The following day we tracked the mother to a new location, 1.5 km from the original den. The kitten had been carried to this location but was dead. The following day all that remained was the head. Only cat tracks could be found, indicating that the mother had eaten the kitten. A third case of apparent infanticide was observed that was independent of human disturbance. At a site approximately 100 km from the main study area, a pair of adult cats were killed for meat in February 1997. The female cat was lactating and her tracks were traced back to a den. Outside the den were two freshly dead kittens. One was intact but the other had been eaten except for the head and two legs. Again only cat tracks were visible at the site.

DISCUSSION

The collaboration between contemporary scientific techniques and Aboriginal skills and knowledge was integral to the success of this study. Aboriginal tracking expertise facilitated initial capture of the cats as well as subsequent interpretation of the behaviour of the radio-collared animals from their tracks. Whilst it is unrealistic to attempt to compare capture rates of cats across widely differing situations (cat densities, food availability, familiarity with humans), the capture of 17 cats in 23 days is quite efficient relative to other studies of feral cats at similarly low densities (less than 1 cat per square km, Paltridge unpublished data). For example, a simultaneous study testing the effectiveness of cat traps at another site in central Australia (dePreu and Edwards, unpublished data), achieved a trap success rate (animals caught per trap-night) of only 0.2% (2 cats in 12 days) and, in central New South Wales, the trap success rate was 1.1% (Molsher 1999). A rate of 1.1% would require the use of 67 traps per night to obtain as many cats as we captured in a 23 day period. The highest trapping rates reported for arid zone feral cats, are from another site in central Australia, where 10% trap success rate was recorded on one survey but the average trap success rate between 1991 and 1993 was about 4% (from Gibson *et al*. 1995). This earlier study also involved collaboration with Aboriginal trackers.

The employment of Aboriginal trackers to eradicate cats from localised areas should not be discounted as a valuable tool in integrated cat control programs. Whilst broad-scale baiting is currently the only potential method for controlling cats over large areas (Short *et al*. 1997; and even this has not yet been convincingly demonstrated), Aboriginal trackers could be used to eliminate cats from core areas, such as around isolated populations of threatened species. These core areas could then be protected from recolonisation by baiting a buffer zone in the surrounding area. The advantage of the tracking technique is that every last cat in a defined area can be sought out, whereas baiting programs are likely to only remove a fraction of the cats in an area. Also, baiting is only effective during times of food shortage for cats (Short *et al*. 1997), whereas Aboriginal trackers can obtain cats at any time. Finally, baiting is not target specific so in areas where dingoes and cats coexist, it is more likely to result in the poisoning of dingoes than cats. Reduced predation and competition from dingoes may then allow an increase in cat populations (Pettigrew 1993, Lundie-Jenkins *et al*. 1993).

The combined tracking technique was a successful method of mapping the movement patterns of cats in central Australia. The distance moved by a cat in a 24-hour period could be accurately mapped in 2-4 hours, rather than the round-the-clock monitoring that would have been required if radio-tracking was used in isolation. The method was reliable because each cat had a unique radio-transmitter frequency that was always checked at the end of the tracking session, ensuring that the same individual had been followed from its initial location. The main disadvantage of the sand-tracking technique is that it is dependent on fine weather: rain and excessive wind render tracks unreadable. Radio-telemetry is also affected by climatic conditions, but to a lesser degree and it is still possible to detect animals during rainy conditions.

Because of the intensive data collection required to monitor 24-hour home ranges, using standard radio-tracking techniques, there is little information available on daily movement patterns of cats in other areas. Most cat behaviour studies have investigated only long-term home ranges, however a study in semi-arid woodland habitat in central Australia analysed the 24-hour home ranges of 4 male cats (Edwards *et al*. 2001). Using the smallest area that encompassed 95% of data points per sample, they obtained a mean daily estimate of 250 ha. A map for one of the cats indicated a mean daily home range width of approximately 1.6 km, slightly less than the current study.

There was insufficient data to draw solid conclusions about the effect of sex and season on 24-hour distances travelled by cats. However, the data suggest that on most days males and females travelled over similar distances, with males occasionally making long-distance excursions, covering more than 5 km in a 24 hour period. Other studies into the long-term home ranges of cats have found that male home ranges are on average 3.5 times larger than females living under the same ecological conditions (Bradshaw 1992, Konecny 1987a).

Although the cats that we tracked appeared to have been hunting alone, in 9 of the 19 tracking sessions we encountered the fresh tracks of another cat in close proximity to the tracks of a radio-collared individual, suggesting that there is some overlap in home ranges. In Scotland, European wildcats were rarely detected in the same area at the same time; the exception was a female in oestrous that was regularly found in the company of a male during a two week period (Corbett 1979).

In some environments cats (particularly males) have been found to maintain exclusive territories by actively patrolling their boundaries and aggressively chasing away intruders (Langham and Porter 1991) or advertising their boundaries with prominently deposited scats (Corbett 1979, Molsher 1999), but there was no evidence of such behaviour in the Tanami Desert during this study. The majority of scats were buried and no evidence of fighting or interspecific chasing was gleaned from the tracks. While territoriality is viewed as advantageous in situations with low resource levels (Corbett 1979, Konecny 1987a), in extremely resource-poor environments overt territorial defence may be too expensive to maintain (Konecny 1987a). Where cats tolerate overlap in home-ranges, other olfactory cues, such as spray marking, can be used to alert conspecifics to the recent passage of individual cats (Corbett 1979, Konecny 1987a). This may prevent unwanted encounters between animals; alternatively it may help an oestrous female attract a mate. Spraying was recorded during five tracking sessions in the current study, including three male cat tracking sessions and two female cat tracking sessions.

The width of the home range encompassed in a 24 hour period can be used to interpret the results of track counts along freshly prepared transects. On average, cats did not exceed a distance of 2.2 km from their starting point within a 24 hour period. Thus, at this site, fresh tracks that are greater than 2.2 km apart are considered likely to belong to different individuals. Fresh tracks that are less than 2.2 km apart may be judged to belong to the same cat, unless the size of the paw prints indicates that different sized individuals are present in the area. This method has been used to evaluate an index of relative abundance of cats in the Tanami Desert (chapter 4).

We can be less certain as to the accuracy of the predation activities interpreted from the tracks. In some cases the results of an attack on prey were obvious, particularly if the cat had only partially consumed the prey and some remains were visible, for example the head of a mouse or the wing of a budgerigar. In most cases, however, there were no remains, and when the pouncing tracks were close to a clump of spinifex it was sometimes difficult to determine whether the prey's tracks continued on or ended at that point. Even assuming that most of the pounces were successful, prey intake did not often appear to meet the 200g that has been estimated as the daily requirement of an adult cat (Scott and Scott 1967), which suggests that some predation events may have been missed during tracking. This seems unlikely however, as a pounce on prey was quite an aberration in the otherwise single line of equally spaced tracks. In Africa the accuracy and reliability of track interpretation by Ju/'Hoan trackers was assessed by testing their interpretation of animal activities that had previously been witnessed and recorded by a scientific observer (Stander *et al*. 1987). The cryptic behaviour of feral cats coupled with intrinsically poor visibility in spinifex grassland habitat renders this method of validation impossible, and we can only resort to scat analysis. Unfortunately only two scats were found that could be used to check the accuracy of the track interpretation. To be a scientifically accepted technique for measuring functional response, our method of interpreting prey consumption from tracks will require additional testing.

Other studies (Liberg 1984, Konecny 1987b) that have tried to evaluate food consumption of cats from scat analysis have assumed that approximately one scat sample is produced per day. This was not the case during our study, as scats were found during less than half the 24 h tracking periods, suggesting that scats were only produced every second day. Although cats often bury their scats in central Australia, the raking marks and resulting mound of sand at a fresh defecation are quite obvious and would not have been missed during a tracking session.

Assuming reasonable accuracy in the prey consumption data, our results illustrate the importance of reptiles in the diet of cats during the warmer months. This is consistent with other studies of cat diet in central Australia which have found small mammals to be consumed throughout the year, while birds and reptiles are seasonally important prey items, in winter and summer respectively (Paltridge *et al*. 1997, Paltridge 2002).

Two general hunting strategies have been identified within the hunting behaviour of cats, one mobile and the other stationary (Corbett 1979). The mobile strategy is more opportunistic (Fitzgerald and Turner 2000): cats conduct a roving search, pursuing prey as they are encountered. The stationary strategy involves cats targeting potentially profitable sites and waiting in ambush for prey to emerge (Corbett 1979). This technique may be more profitable when hunting larger, group-living prey such as rabbits, but is also suitable for burrowing rodents (Leyhausen 1979). In our study 'sitting-down' tracks were sometimes associated with a pounce on a small mammal or the communally living Nocturnal Desert Skink (*Egernia striata*). For other lizard species, however, cats employed a mobile hunting strategy. The random-search-and-pounce technique appeared to involve little stalking, just a sudden pounce when a prey item was detected. Cats rarely ran in pursuit of prey over large distances with most chases covering less than 2 m. In the spinifex grasslands of our study site, the spatial patterning of the spinifex clumps was such that prey were almost always within 2 m of the refuge of spinifex. After 2 m the cat has either caught the prey or it has escaped into this refuge (or flown away, in the case of birds).

Cats are not adapted to long-distance running, either to chase prey or escape predators (Kleiman and Eisenberg 1973), a trait which makes them vulnerable to predation by foxes and dingoes as well as experienced Aboriginal trackers. The cheetah is the only felid that has evolved as a long distance runner (Kleiman and Eisenberg 1973).

Most movements of cats in a 24 h period followed approximately linear routes. Cats did not usually loop around during hunting, and did not return to their starting point during the 24 hours. It has been suggested that the shape of a cat's daily movement path reflects the availability of resources (Konecny 1987a), with linear movement patterns occurring when there is low abundance of prey. In situations of higher prey abundance, encounter rates between predator and prey are higher, and as prey are either consumed or alerted to the presence of the cat, there is a greater rate of renewal of resources, making it more profitable for a cat to retrace parts of the path already traversed that day (Konecny 1987a).

It is possible that the movement patterns of cats in this study may have been altered as a result of disturbance, as our tracking method is more intrusive than remote radiotelemetry. However, we believe our level of disturbance was minimal, as we rarely flushed the cats from their day-time shelters. Our interference may have contributed to the deaths of several kittens however, as a mother cat disturbed at her nest may be inclined to move the litter to a new location (Leyhausen 1979). One cat moved one of three kittens to a new shelter 200 m away but the other two were left dead outside the original nest. Another female carried her kitten 1.5 km after being disturbed. Whether the kitten's death was an accident resulting from being carried for such a long way is unknown, but by the following day, the mother appeared to have eaten it. The third case of kitten mortality happened prior to any human intervention and may have been a result of male infanticide; a male cat was found with the mother of the kittens shortly after their death. Infanticide, which is common in lions, has occasionally been recorded in cats (Bradshaw 1992). Cessation of lactation brings females into oestrous more rapidly, which may be advantageous to the males if they did not sire the kittens (Bradshaw 1992). Dead kittens are usually eaten by their parents (Leyhausen 1979).

The combined sand-tracking/ radio-tracking technique could be utilised as a research tool to study the behaviour of a variety of species in the 2 million square km of sandy desert country of inland Australia. For example, the technique could be employed to provide information on the daily movement patterns of foxes in non-rabbit areas of central Australia, which would facilitate interpretation of track-based count data (chapter 4). It would also be useful to determine home-range size and foraging behaviour of wild bilbies in central Australia. The ability to relate extent and density of bilby diggings to a more quantitative index of abundance would improve monitoring programs for this threatened species. Increasing employment opportunities for Aboriginal People to collaborate with scientists in wildlife studies improves the chances that important traditional tracking skills will be maintained and valued by future generations.

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APPENDIX B

OCCURRENCE OF MARSUPIAL MOLE (*NOTORYCTES TYPHLOPS*) REMAINS IN THE FAECAL PELLETS OF CATS, FOXES AND DINGOES IN THE TANAMI DESERT, N.T.*

INTRODUCTION

Little ecological information has been collected on the Marsupial Mole, *Notorcytes typhlops*, since its discovery in 1888. The only field data published on the species this century has resulted from opportunisic encounters with the animal (Johnson and Walton 1989), and no reliable methods for capturing it or monitoring its abundance and distribution have been developed.

In 1920 a second species of Marsupial Mole, *Notoryctes caurinus*, was described from specimens collected in north-western Australia. The distributions of the two species have not been clearly differentiated however, and the two species are often regarded as synonomous (e.g. Johnson 1995). In this paper the potential for a second species was disregarded and reference is made only to *N. typhlops* due to the proximity of the study sites to the location of recent records of this species.

This paper reports on occurrences of *N. typhlops* in cat (*Felis catus*), fox (*Vulpes vulpes*) and dingo (*Canis lupus dingo*) faecal pellets collected in the Tanami Desert in the Northern Territory between 1995 and 1997, as part of a wider study into predator-prey dynamics of spinifex grasslands in the Tanami Desert.

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As the article was written part-way through the study, results are based on a sub-set of the dataset presented in Chapter 3, hence there are inconsistencies in the frequency of occurence data between the two papers.

METHODS

Predator scats were collected from two areas of the Tanami Desert (Fig.1.) at four-monthly intervals, over a period of 18 months. The southern study area was approximately 400 km west of Alice Springs and the northern study area was approximately 200 km north-west of Tennant Creek. Both study areas comprise predominantly sandplain habitat, dominated by a mixture of spinifex species (*Triodia pungens, T. basedowii* and *T. schinzii*) with an overstory of scattered shrubs including species of *Melaleuca, Grevillea, Eucalyptus* and *Acacia*. Low sand dunes dissect the sandplain in the southern study area, but are infrequent west of Tennant Creek. Each of the two major study areas contained three sites, at least 20 km apart, giving a total of six sites.

Scats were classified as fresh, one week to 3 months old, 3-6 months and older than 6 months, according to colour, smell, apparent moisture content and surface deterioration. Prey remains were initially sorted under a dissecting microscope but a representative sample of all hair was cross-sectioned and examined under a compound microscope. Identification of *N. typhlops* hair made by comparison with reference material was simple because the hair occurs in bundles of 9-20 fine hairs around a single distinctively large and flattened guard hair (Spencer 1896) that is unmistakable in cross-section. Additional confirmation came from the presence of jaw fragments, claws and the heavily keratinised skin of the rostrum and tail of *N. typhlops* in some faecal pellets.

RESULTS AND DISCUSSION

Of 252 faecal pellets examined, 14 (5%) contained remains of *N. typhlops*. This included 9.8% of fox scats (n = 82), 2.7% of cat scats (n = 111) and 5.1% of dingo scats (n = 59). Remains of *N. typhlops* were found in faecal pellets from five of the six study sites. Four records were from a single sand dune which was believed to be a regular defecation site for a resident fox. Occurrences of *N. typhlops* in scats from the northern study area are at least two hundred kilometers further north than any previous records of this species in the Northern Territory (Fig. 1).

All but two of the predation events probably occurred between May and September based on the estimated age of scats. Collectors in 1895 also reported that winter was the best time for finding *N. typhlops*, particularly after rain. (Calaby 1996), and this was reiterated by Aboriginal informants on surveys in north-west South Australia (Baker and Nesbitt 1996).

It is uncertain whether predators were taking *N. typhlops* when on the surface or digging them up. The limited information on *N. typhlops* burrows suggests that animals may occur at relatively shallow depths (Johnson and Walton 1989) from which they could be dug by foxes. Foxes are accomplished diggers, and have been observed digging rabbit kittens from burrows (Newsome *et al*. 1989). Nor can it be confirmed that predators were actually killing *N. typhlops* or taking already dead animals. Foxes and dingoes are known to feed on animal carcasses but cats rarely scavenge in central Australia (Paltridge *et al*. 1997).

Despite spending considerable time in these study areas, where partciular attention was paid to track identification, both along set tracking transects and whilst hunting with Aboriginal people, no sign of *N. typhlops* was observed during the 18 month study period. However, tracks and burrow entrances from *N. typhlops* were observed approximately 50 km south of the southern study area, during the winter of 1996 (P. Bartlett pers. comm.). An additional twelve cat scats were collected from this location, but none of these contained remains of *N. typhlops*. During the same period (1995-1997), six individual *N. typhlops* were sighted along roads in Uluru National Park, which is about 300 km south-east of the southern location (J. Gillen pers. comm.). Extensive fauna surveys throughout the Tanami Desert in the 1980s failed to detecct sign of this animal using conventional survey techniques (Gibson 1986) but a number were collected by Aboriginal people in the Nyirripi region during that period.

Results of this project demonstrate the usefulness of predator faecal pellet analysis as a tool for detecting the presence of cryptic species during biological surveys. Without this tool, despite intensive trapping and tracking surveys over an 18 month period, *N. typhlops* would not have been recorded in the two study areas under investigation.

This study identifies predation by cats, dingoes and particularly foxes as a potential threatening process for *N. typhlops*, but until distribution and abundance of the species can be effectively monitored, the impact of this predation cannot be quantified. In the meantime, its status should be viewed with concern and effort directed at developing a monitoring program.

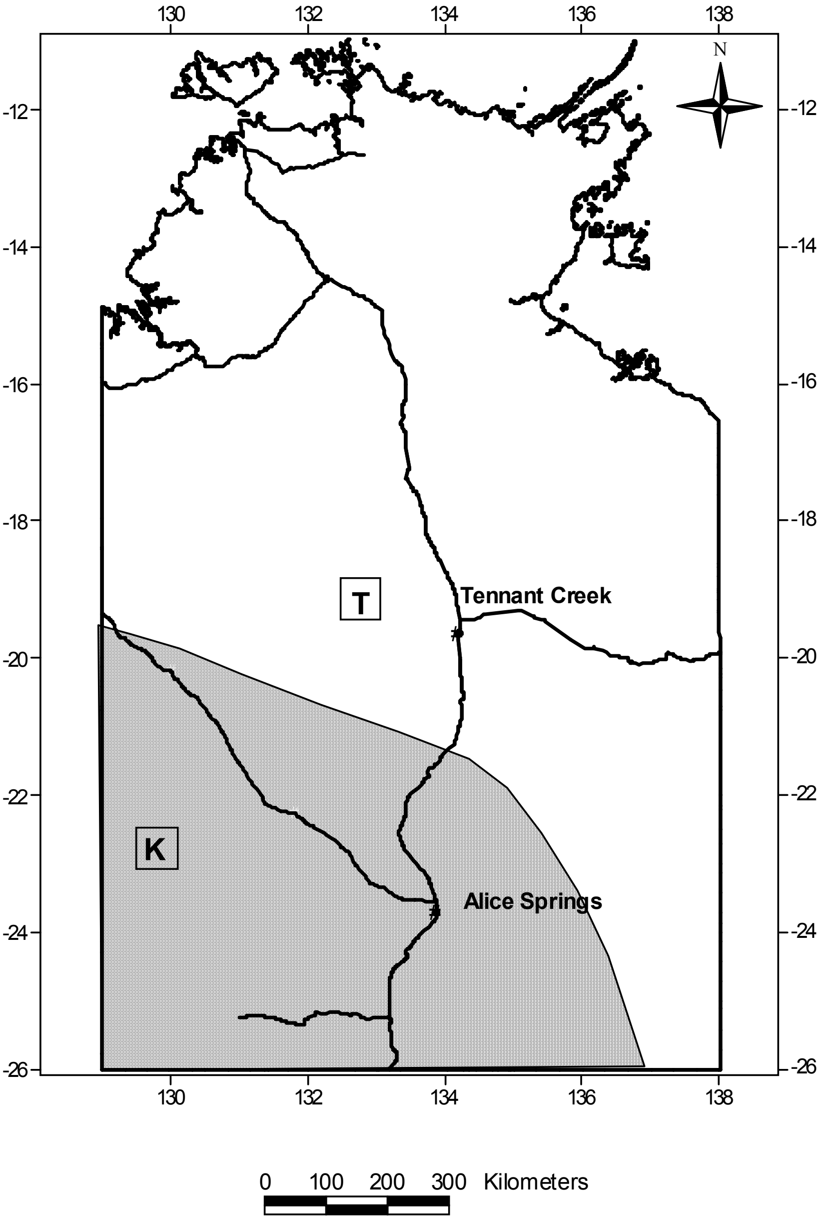

Fig. 1. Map of the Northern Territory showing location of the northern study area (T) and the southern study area (K) in relation to the previously known distribution of the Marsupial Mole in the Northern Territory (from the NT Parks and Wildlife Service Fauna Atlas database).

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