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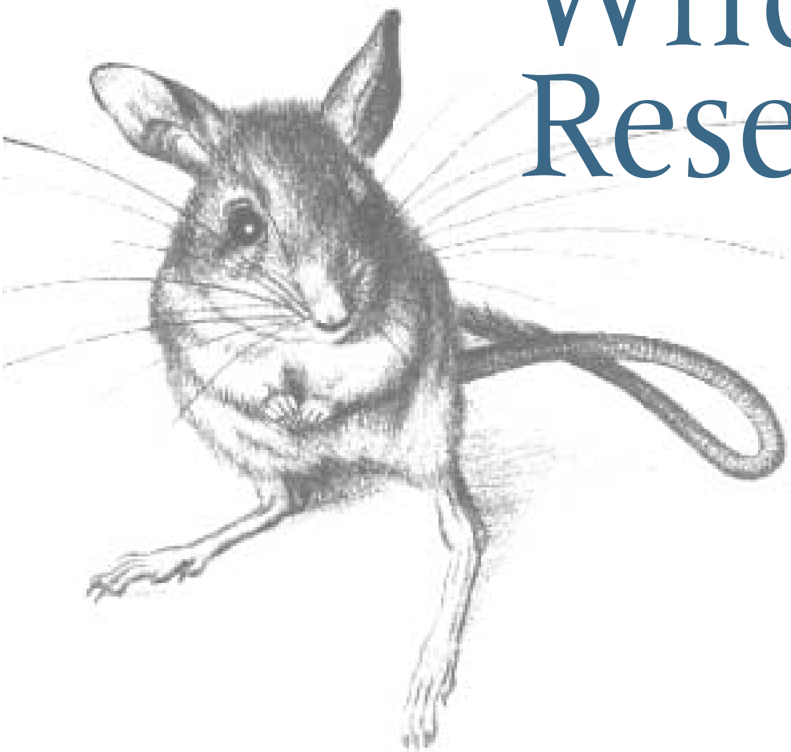

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The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory

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Abstract. In most areas of Australia, mammals constitute the staple diets of cats, foxes and dingoes. In central Australia the abundance of mammals is often too low to meet the dietary requirements of these carnivores and yet populations of cats, foxes and dingoes persist. To investigate alternative feeding strategies of cats, foxes and dingoes in arid environments, their diets were monitored in relation to prey availability in two areas of the Tanami Desert where rabbits do not occur. Dietary information was obtained by analysing predator scats collected between 1995 and 1997. Prey availability was monitored by track counts, pitfall trapping, Elliott trapping, and bird counts along walked transects. In contrast to dietary studies elsewhere in Australia, it was found that reptiles were an important component of the diets of predators in the Tanami Desert, and should be classified as seasonal staples. Birds increased in importance in the diets of cats and foxes during the winter, when reptiles were less active. There was considerable overlap between the diets of all three predators, although dingoes ate more large prey items (e.g. macropods) than the other two predators. Results highlight the opportunistic feeding habits of cats, foxes and dingoes and show that, although mammalian prey are less important in central Australia than has been found elsewhere, species that are vulnerable to extinction, such as the bilby (*Macrotis lagotis*), mulgara (*Dasycercus cristicauda*) and marsupial mole (*Notoryctes typhlops*), are also consumed by these predators.

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 (*Oryctolagus 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

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persist in the Tanami Desert (Gibson 1986; Lundie-Jenkins *et al.* 1993; author's unpublished data). This paper investigates the feeding habits of cats, foxes and dingoes in relation to prey availability at two sites in 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.

Methods

Study area

The study was conducted in two areas, approximately 400 km apart (Fig. 1). The northern study area, 'Tennant', was situated in the northern Tanami Desert, 200 km north-west of Tennant Creek (19°12′S, 132°40′E). The southern study area, 'Kintore,' was located approximately 450 km north-west of Alice Springs at the intersection of the Tanami, Great Sandy and Gibson Deserts (22°51′S, 129°57′E). The entire study region is Aboriginal Freehold land, and is sparsely populated and undeveloped.

The region's climate is semi-arid, with very hot summers and mild winters. Mean daily minima and maxima for the hottest month (January) and the coldest month (July) are 25–37°C and 12–24°C for Tennant and 21–36°C and 4–20°C for Kintore. Annual mean rainfall is higher at Tennant (422 mm) than at Kintore (321 mm). Most rain falls during the summer months. Rainfall data were provided by the Bureau of Meteorology (Darwin).

Both study areas comprise predominantly sandplain habitat, dominated by a mixture of spinifex species (*Triodia pungens* and *T. basedowi* at Tennant, and *T. pungens* and *T. schinzii* at Kintore) with an overstorey of scattered shrubs including species of *Grevillea*, *Eucalyptus and Acacia*. Palaeodrainage channels, characterised by the presence of *Melaleuca* spp., also occur in both areas. Low parallel sand dunes, approximately 1 km apart, dissect the sandplain at Kintore, but are infrequent at Tennant.

Each study area contained three randomly selected monitoring sites, at least 20 km apart. Each site consisted of two study plots, approximately 4 km apart, one plot located in sandplain habitat and the other in palaeodrainage line habitat.

The study commenced at Tennant in September 1995, during fairly average seasonal conditions. Both 1995 and 1996 had slightly less than average rainfall, but 616 mm of rain fell during the 1996–97 summer, resulting in an annual total rainfall well above the mean of 422 mm for 1997. Seasonal conditions were very dry at Kintore when the study commenced in May 1996, as only one of the previous five years had received more than the mean rainfall. During 1996, the Kintore sites received only half (165 mm) of their annual average rainfall. However, good summer rains fell in early 1997, and the annual total for 1997 was 454 mm.

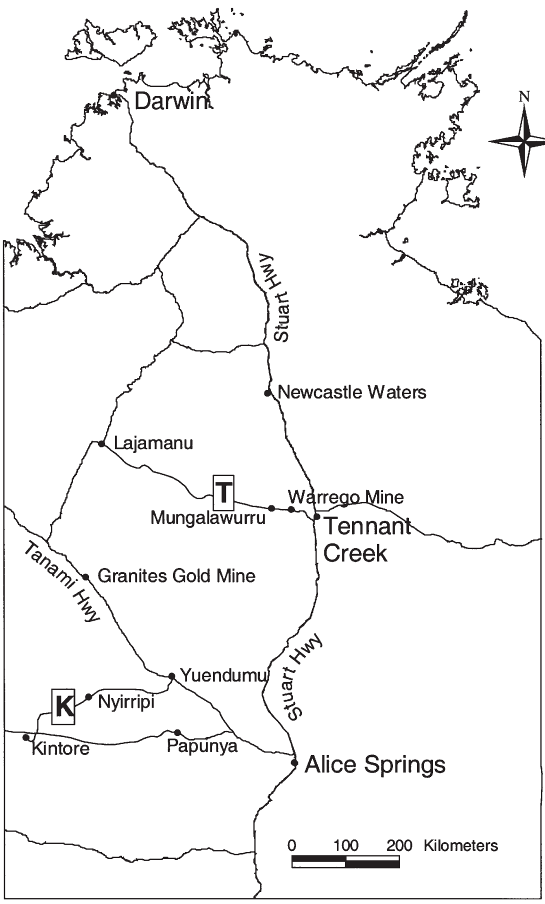

Fig. 1. Map of the Northern Territory showing location of the two study areas, Kintore (K) and Tennant (T).

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. Monitoring of prey was carried out over three days at each site.

The abundance of invertebrates, reptiles and small mammals was 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 10×50 binoculars. Perpendicular distances from the transect line to the birds were estimated with the intention of determining actual densities. However, counts were often too low for density estimation using line transect methods (Laake *et al.* 1991) and only counts-per-kilometre data are presented here. 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.

Scat analysis

Predators scats were collected along the tracking transects to determine diet. In addition, approximately 6 person-hours per study plot (36 person-hours per survey) were dedicated to searching for predator scats. 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.

Prey remains were initially sorted under a dissecting microscope and identified to the lowest possible taxonomic level. Reptiles were classified to 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.; zebra finches, *Taeniopygia guttata*) could be identified. Small mammals could often be distinguished by their 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-sized and large mammals were usually classified to 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.

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 × estimated mass of prey item)/(total number of prey items × 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 given 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 on the basis of 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 studies of predator diets (Croft and Hone 1978; Catling 1988; Jones and Coman 1992; Corbett 1995) but this method tends to over-represent 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 biased towards larger prey species.

The 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. Although some categories are broader than others, they represent functional groups of similar-sized species that cannot easily be further distinguished in scat analysis. Most categories include 1–3 species (with the exception of birds which is much broader); however, most birds consumed by predators would probably be one of five 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) on the basis of their estimated biomass, as described above. 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.

Results

A total of 74 cat scats, 51 fox scats and 75 dingo scats were analysed from Tennant and 68 cat scats and 75 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 list of prey species found in scats and their overall frequency of occurrence is presented in the Appendix.

The diets of all three predators contained a combination of mammals, birds, reptiles and invertebrates (Fig. 2*a–c*). The *t*-tests found no 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. 2*a*) but the increase in reptile consumption in the summer was significant only 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 significant only at Tennant ($z = 2.4$, $P < 0.05$).

Foxes consumed invertebrates more frequently than either of the other two predators (Fig. 2*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 significant only at Kintore ($z = 2.1$, $P < 0.05$).

Dingo diet was consistently dominated by reptiles, regardless of season (Fig. 2*c*). Invertebrates were rarely eaten by dingoes.

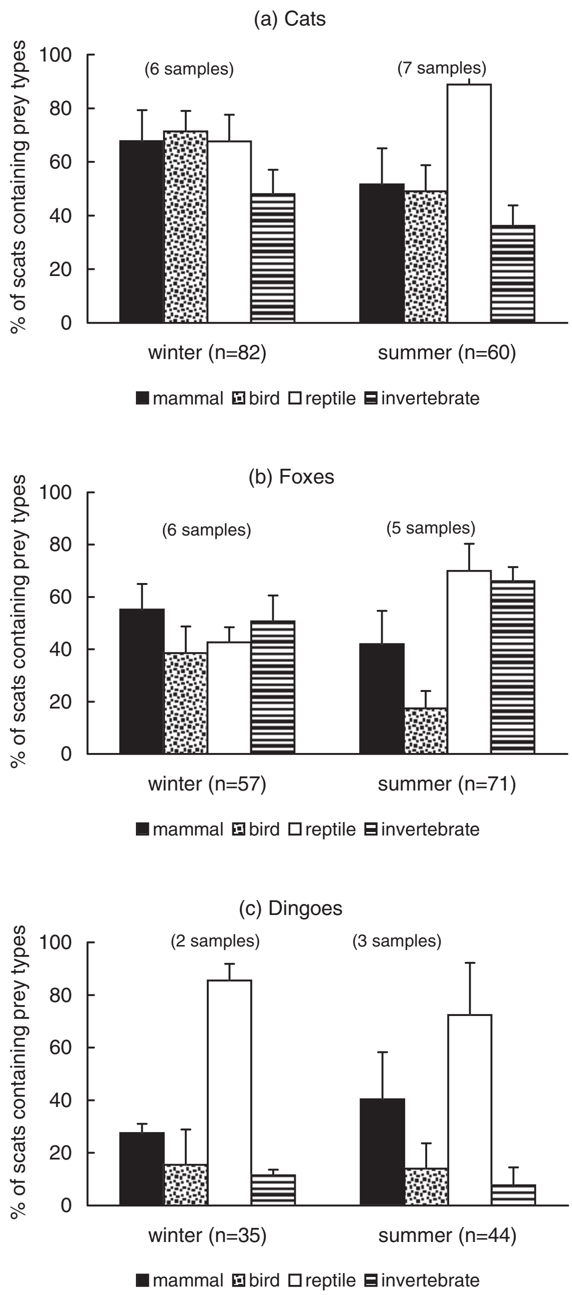

Fig. 2. Frequency of occurrence of prey types in predator scats collected during winter (May–September) and summer (October–April). Data are means (± standard error) of the results of multiple surveys conducted in both study areas. Number of samples refers to the number of surveys where at least five scats were collected, 'n' refers to the total number of scats collected in each season.

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). 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).

At Tennant, the abundance of small mammals declined throughout the study period, rising slightly in the final survey (Fig. 4). Bird abundance peaked twice during the

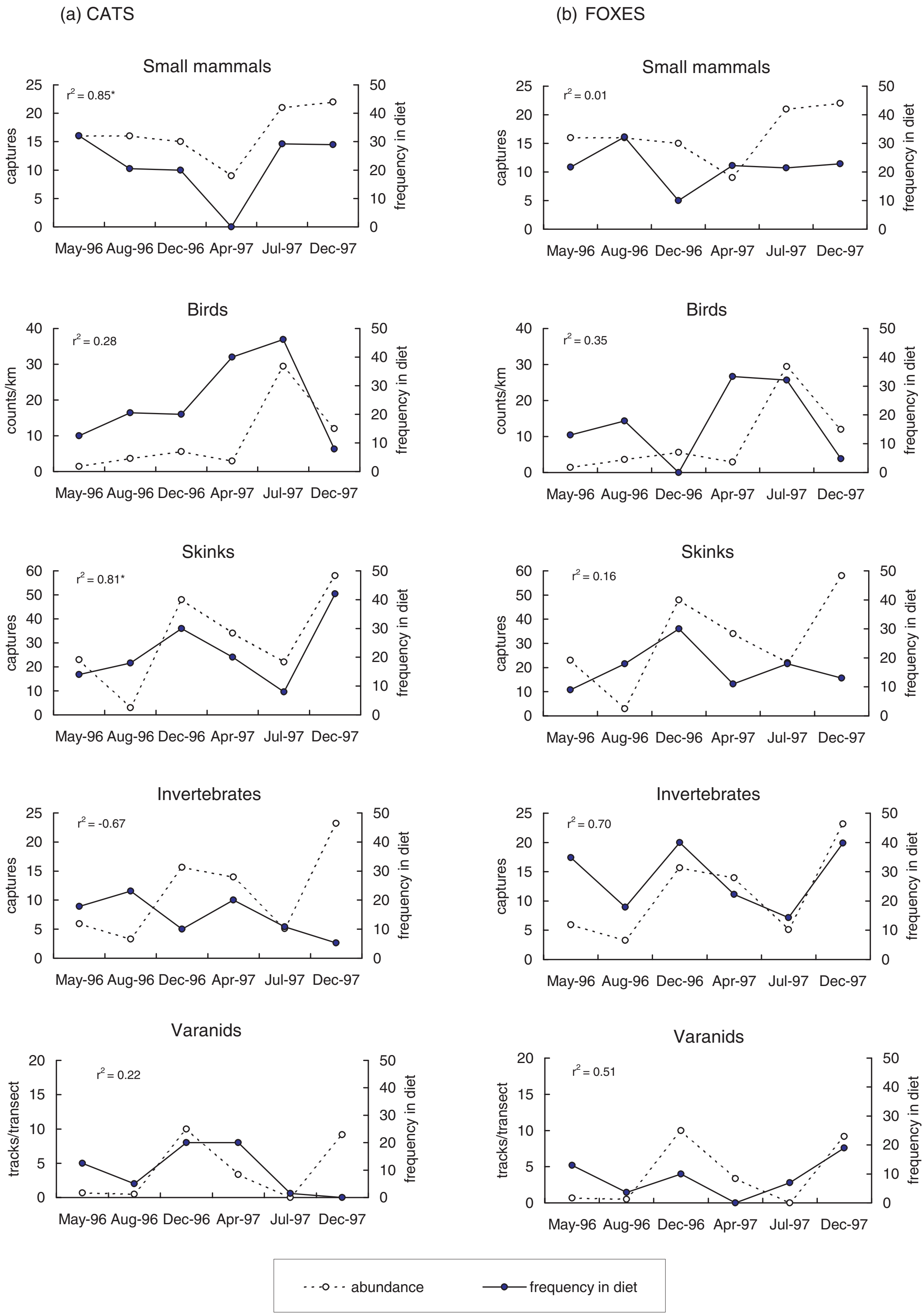

Fig. 3. The relationship between the relative abundance of the five most frequently consumed prey and their numerical frequency in the diets of cats and foxes at Kintore. Consumption, shown on the secondary *y* axes, is expressed as the numerical frequency of prey items in the diet. Breaks in the lines indicate missing data. (Asterisk indicates that Pearson correlation coefficient r^2 is significant at the 0.05 level; captures = animals caught per 1080 trap-nights; tracks/transect = mean proportion of 500-m cells with tracks per transect).

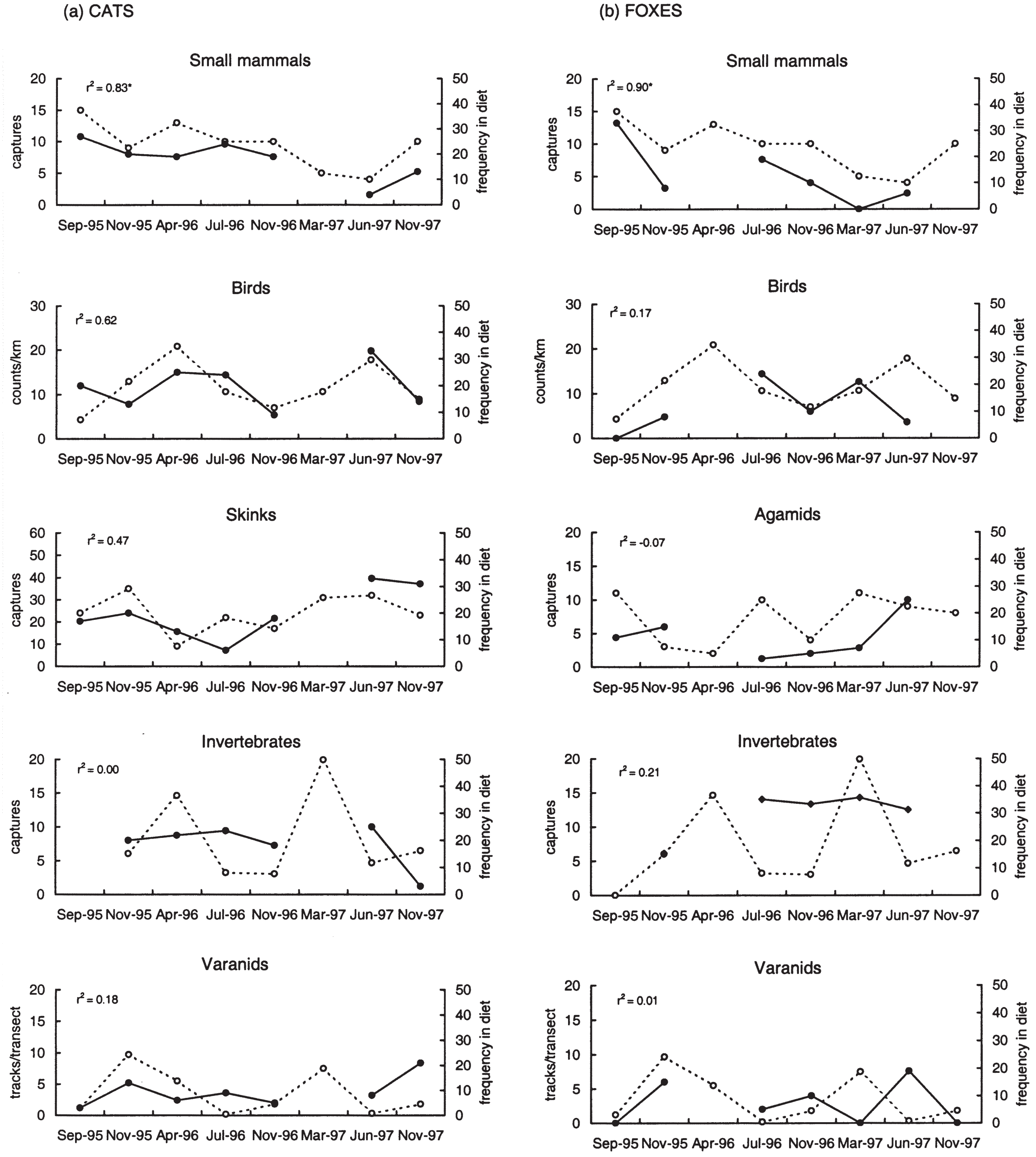

Fig. 4. The relationship between the relative abundance of the five most frequently consumed prey and their numerical frequency in the diets of cats, foxes and dingoes at Tennant. Consumption, shown on the secondary *y* axes, is expressed as the numerical frequency of prey items in the diet. Breaks in the lines indicate missing data. (Asterisk indicates that Pearson correlation coefficient r^2 is significant at the 0.05 level; captures = animals caught per 1080 trap-nights; tracks/transect = mean proportion of 500 m cells with tracks per transect).

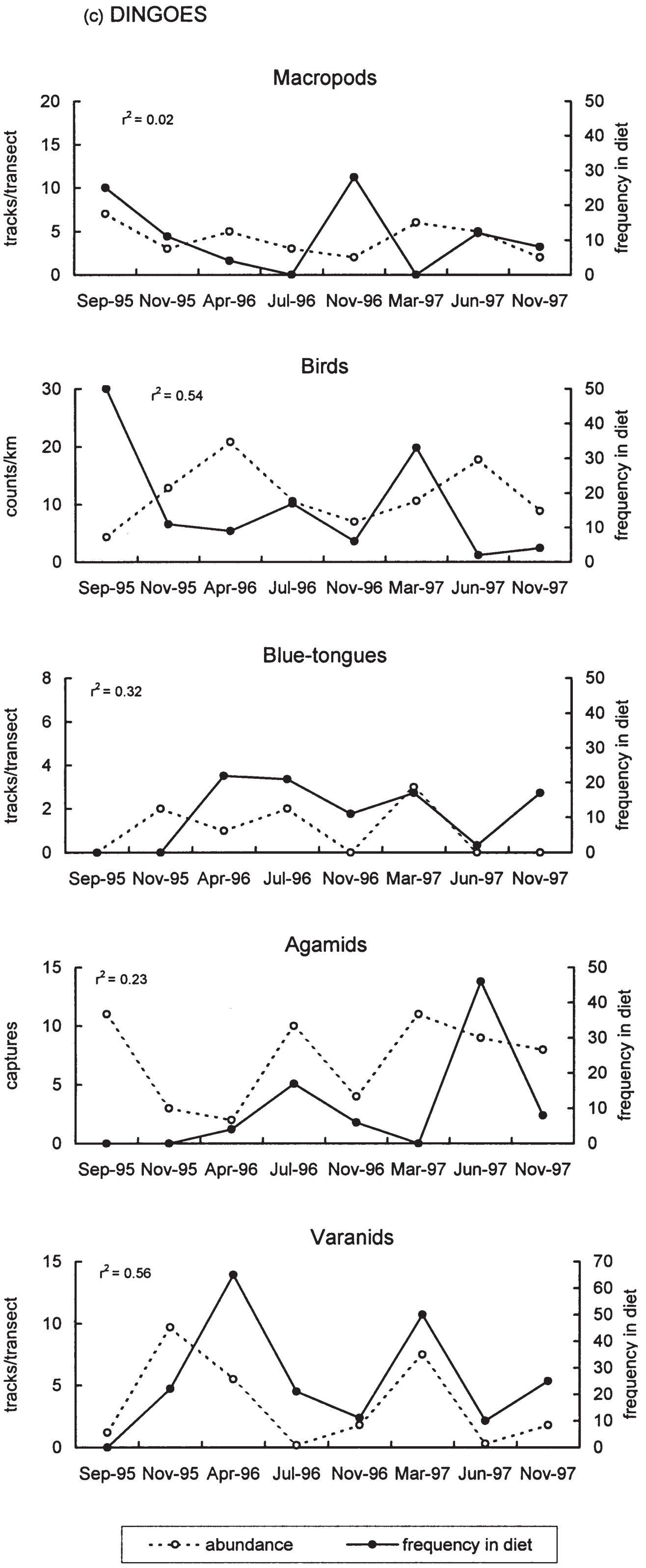

Fig. 4. (continued)

study period, first in April 1996 and again in June 1997, both in response to good rainfall. 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. 4).

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 was strongly correlated with their field abundances ($P < 0.05$) (Fig. 3*a*). Small mammals were consistently eaten by cats, except in April 1997, when birds became important in the diet. Birds continued to dominate cat diets at Kintore in July 1997, 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. 4*a*).

Consumption of invertebrates by foxes 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*b*). Small mammals were eaten consistently by foxes, except in December 1996, when the 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 is likely that birds had already started increasing at this time. Flocks of 12–20 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 the relative abundance of small mammals ($P < 0.05$) (Fig. 4*a*, *b*). The relative abundances of the remaining prey categories were tracked more closely by cat diets than fox diets (Fig. 4*a*, *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. 4*c*). When varanids were scarce, they were replaced in the diet by either blue-tongued lizards (*Tiliqua multifasciata*) or agamids.

Index of Relative Importance

Tables 1–5 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 1–5).

Table 1. 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 are also ranked during each survey according to the IRI values for that survey

Prey	IRI	Rank per survey					
		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 2. Importance of prey categories in the diet of foxes 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

Prey	IRI	Rank per survey					
		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	–

Birds contributed more to the diet of cats at Kintore than any other prey category (highest pooled IRI score), but ranked first only in the winter surveys (Table 1). 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 1). 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 2). However, birds were the major prey 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). As was the case at Kintore,

Table 3. Importance of prey categories in the diet of cats at Tennant, 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

Prey	IRI	Rank per survey							
		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 4. Importance of prey categories in the diet of foxes at Tennant, 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

Prey	IRI	Rank per survey							
		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	–		–	–

Table 5. Importance of prey categories in the diet of dingoes at Tennant, 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

Prey	IRI	Rank per survey							
		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	–

varanids were ranked first 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.

Invertebrates were ranked the most important prey in the diet of foxes at Tennant in all but one survey (Table 4). Varanids were the second most important prey category, followed by birds, rodents and agamids.

Dingo diet at Tennant was dominated by varanids (Table 5), 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 5).

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 42 of 74 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 = 50) 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.

Dietary overlap between species.

There was considerable overlap in the diets of cats, foxes and dingoes (Table 6), with greater overlap occurring between cats and foxes than between cats and dingoes or foxes and

Table 6. Dietary overlap between cats, foxes and dingoes at the two study sites
Subscripts indicate the study sites: K, Kintore; T, Tennant

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 7. Percentage of prey items taken by cats, foxes and dingoes in three size classes
Size classes: small (<100 g), medium-sized (100–1000 g) and large (>1000 g)

Size class of prey	Tennant Cat	Tennant Fox	Tennant Dingo	Kintore Cat	Kintore Fox	Kintore Dingo
Small	87	80	48	92	86	–
Medium	11	16	36	7	14	–
Large	2	4	16	1	0	–

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 6).

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

Discussion

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. ‘Opportunistic 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 (Southgate and Masters 1996; Paltridge and Southgate 2001), 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.

Importance of reptilian prey

When biomass of prey was taken into account, the varanids (in most cases the sand goanna, *Varanus gouldii*), 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 three of the six 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 (Paltridge and Southgate 2001), 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 north 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 studies of fox diets conducted throughout Australia (Marlow 1992), the 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 were rarely eaten by cats (Fitzgerald and Turner 2000).

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 rainfall (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 (Paltridge and Southgate 2001) and it is during these times that predators may struggle to meet their nutritional requirements.

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 found 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 numbers of small mammals were low during the study period, despite considerable rain falling 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 occurred during periods when most other prey species were 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.

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 (Appendix). Most studies of cat diet have shown invertebrates to be a consistent but overall fairly minor dietary item (Pearre and Maass 1998; Fitzgerald and Turner 2000), 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 have also been found to be important prey for canids in the Namib and Sonoran Deserts (Bothma *et al.* 1984; Hernandez *et al.* 1994).

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 did foxes or cats. Some degree of size partitioning of prey 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 the greater consumption of birds and reptiles by cats and the 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 (Paltridge and Southgate 2001).

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 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 occurs only 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), 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).

Predation on vulnerable species

Predation by cats and foxes 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, the mulgara and the 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 take only young animals. Bilbies and mulgaras both occurred rarely 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 as consuming marsupial moles, but fox scats contained the highest proportion of this species.

Given the information we have on predator diets 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 droughts, 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, the mulgara and the marsupial mole – may not be secure.

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Appendix 1. Frequency of occurrence of prey species found in cat, fox and dingo faecal pellets, at two study areas in the Tanami Desert, 1995–97

Order and species	Tennant Cat n = 76	Tennant Fox n = 53	Tennant Dingo n = 77	Kintore Cat n = 70	Kintore Fox 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
Invertebrata					
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