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Similarities and Contrasts in the Diets of Foxes, *Vulpes vulpes*, and Cats, *Felis catus*, Relative to Fluctuating Prey Populations and Drought

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Abstract

The diets of the fox, *Vulpes vulpes*, and feral cat, *Felis catus*, were studied at Yathong Nature Reserve in semi-arid western New South Wales. The overall occurrence of rabbit was 45·1% in stomachs of foxes and 54·0% in cats, representing 51·3 and 82·6% respectively of the weight of stomach contents. Both predators exhibited a functional response to rabbits, *Oryctolagus cuniculus*, (their staple prey) during the rabbit breeding season. Predation on rabbits was greatest on an increasing prey population during good pasture conditions and a decreasing population during drought. After the rabbit breeding season, diet changed to other prey and resulted in an annual prey cycle which was similar for foxes and cats. Both predators successfully co-exist in the semi-arid environment by primarily utilising different age groups of the same staple prey and to some extent different supplementary prey. Foxes mainly ate adult rabbits and cats young rabbits. During the drought foxes preyed heavily on adult rabbits; cats ate some rabbits but relied heavily on other food sources. The supplementary prey of foxes were invertebrates, birds, reptiles and carrion; small mammals and fruits opportunely eaten. Invertebrates, birds, reptiles and small mammals were supplementary prey for cats with carrion opportunely eaten.

Introduction

Many studies have reported on the diet of the red fox, *Vulpes vulpes*, and the feral cat, *Felis catus*, in Australia (McIntosh 1963; Martensz 1971; Norman 1971; Coman and Brunner 1972; Coman 1973; Ryan and Croft 1974; Bayly 1976; Croft and Hone 1978; Seebeck 1978; Jones and Coman 1981; Triggs *et al.* 1984). Both species are considered to be opportunistic predators and scavengers with the rabbit, *Oryctolagus cuniculus*, as the main prey in most studies. However, where rabbits are uncommon, such as in the remote forests of south-eastern Australia and the alpine zone, the incidence of rabbit in the diet is greatly reduced (Coman 1973; Green and Osborne 1981; Jones and Coman 1981; Triggs *et al.* 1984).

Only one study has compared diet with prey availability. Green and Osborne (1981) found that in the Kosciusko National Park foxes showed strong seasonal trends in their diet, with insects common in the snow-free months and small mammals the staple prey when snow was present. Rabbits were uncommon at their study site. In South Australia, Bayly (1978) found that rabbits were the most important dietary item for foxes and cats, although their diets differed significantly with foxes showing a much higher incidence of scavenged food.

This study was part of a larger one designed to test the effect of predator removal on prey populations (A. E. Newsome, I. Parer and P. C. Catling, unpublished). Stomach contents of foxes and cats obtained over a two-year period in that study are examined here for dietary differences between predators, age groups and seasons, and in relation to changes in the numbers of the major prey, the rabbit.

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Methods

Study Area

The study was carried out in mid-western New South Wales in Yathong Nature Reserve (33°45'S., 145°30'E.), an area of about 107 000 ha comprising three former grazing properties. The vegetation was cleared grassland and adjacent woodland; Parer and Libke (1985) gives a detailed description. The climate is semi-arid with an annual rainfall of 200–350 mm (range 155–881 mm). The study began in good pasture conditions in June 1981 following two drought years in 1979–80 and finished in a drought in early 1983. Rabbit numbers had been extremely high in late 1979 but crashed by early 1980 due to the drought so that numbers at the commencement of this study were very low.

Predator Collection, Age Determination and Dietary Identification

Predators were shot at night with the aid of spotlights, for one week in every 2–3 weeks between June 1981 and June 1983. A total of 288 foxes and 112 cats were collected. After collection they were weighed, their head and body lengths were measured and the skulls cleaned and retained. Stomach contents were weighed and stored in 10% formalin. In the laboratory, contents were sorted macroscopically into species, weighed, and hair samples were prepared for microscopic identification by the method of Newsome *et al.* (1983). If larvae of blowflies (Calliphoridae) were present the contents were considered to be carrion. Goats, *Capra hircus*, were also considered to be carrion as they were shot by us to attract predators. Kangaroos (*Macropus* spp.) were also classified as carrion as some illegal shooting took place in the reserve, and also many died in late 1982 as a result of the drought. Birds were identified by microscopic and macroscopic comparison of the feathers (Brom 1980).

The time of closure of sutures in the skull were used for classifying foxes into the following age groups: <9 months, 9 months–2 years and >2 years (Harris 1978). As it was not possible to age cats from skulls, they were divided by weight into immature animals (females <2·2 kg, males <3·5 kg) and adults (Jones and Coman 1982).

Estimates of Rabbit Numbers

Rabbit numbers were monitored every 6–8 weeks by noting changes in the mean number of used burrow entrances in 8 areas (335 marked warrens with over 3500 entrances). The census method is a good indicator of the number of rabbits in a warren (Myers *et al.* 1975).

The Age of Rabbits in the Stomachs

Ingested rabbits were aged as <50, 50–80 days and >80 days by comparing measurements of body pieces such as ears and feet in the stomachs with measurements from rabbits of known age (I. Parer, personal communication).

Results

Overall Diet

The appendix presents the percentage occurrence of all species found in fox and cat stomachs.

(i) *Foxes*

Foxes ate 57 species representing 4 groups of prey as well as plants. The number of species, percentage occurrence and percentage weight for the major groups were respectively, for mammals (13; 81·6; 90·8), invertebrates (11; 70·1; 11·8) amphibia and reptiles (16; 23·3; 3·1), birds (15; 18·0; 3·1), and plants (2; 14·9; 0·01). By far the most important single item was rabbit with an occurrence of 45·1% and an occurrence by weight of 51·3%.

(ii) *Cats*

Cats ate 48 species representing 4 groups of prey. The respective values for cats were: mammals (10; 80·5; 87·2) invertebrates (10; 42·5; 1·5), reptiles (17; 30·1; 4·7), and birds (10; 21·2; 6·6). No vegetable matter was eaten. As with foxes, rabbit was the most important single item with an occurrence of 53·0% and an occurrence by weight of 82·6%.

Seasonal Changes

(i) *Foxes*

The percentage occurrence and percentage weight of the major groups of prey are presented seasonally in Fig. 1. The seasonal trends for weight and occurrence were similar although the weight contribution was generally low for some groups, e.g. invertebrates.

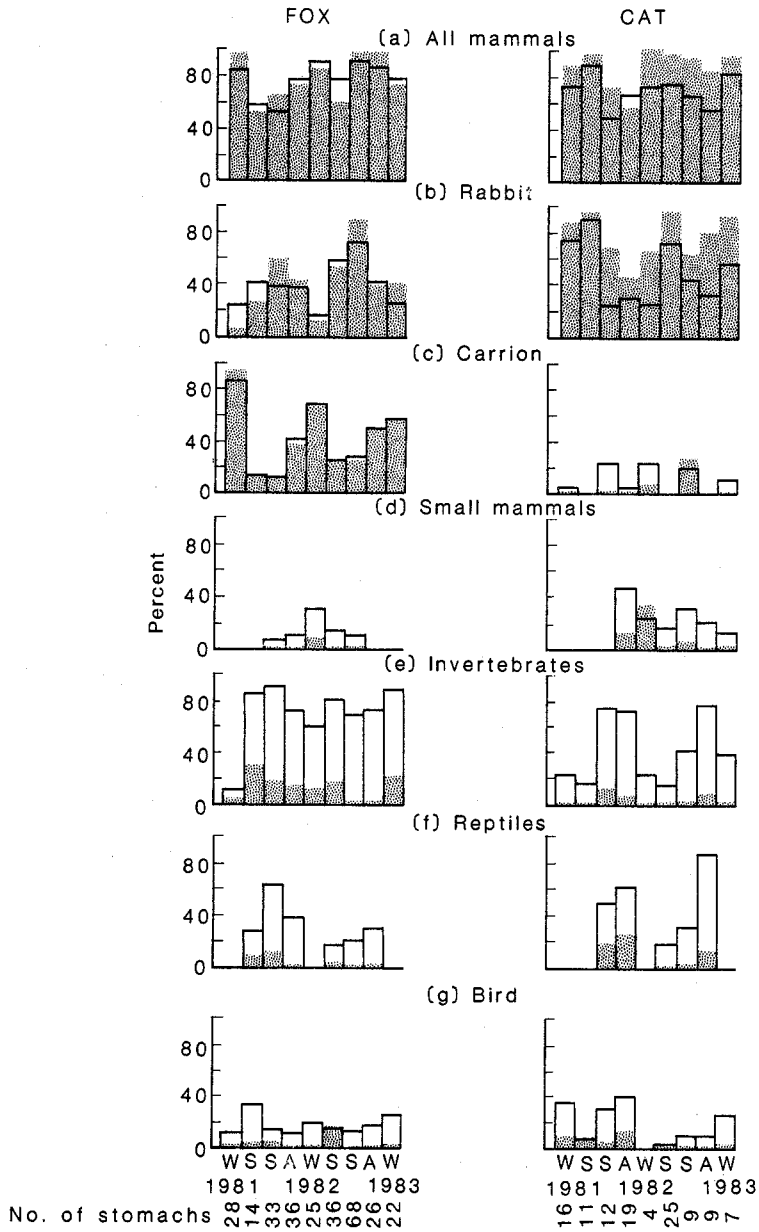

Fig. 1. Seasonal changes (winter, spring, summer, autumn) in the percentage occurrence (open) and percentage weight (stippled) of the major groups of prey found in fox and cat stomachs: (*a*) all mammals, (*b*) rabbit, (*c*) carrion, (*d*) small mammals, (*e*) invertebrates, (*f*) reptiles, (*g*) birds.

The most important group was mammals which were eaten consistently in all seasons (Fig. 1*a*). Rabbit was the most abundant species, with the highest occurrence in spring and summer and the least in winter when the incidence of carrion was at its highest (Fig. 1*c*).

Small mammals only occurred in the diet from the summer of 1981–82 until the summer of 1982–83 (Fig. 1*d*); they were most abundant (32%) in the winter of 1982. Invertebrates showed a high occurrence throughout the study [except for the first winter 14·3% (Fig. 1*e*)]; there were seasonal differences for the different species. Caterpillars (Family Geometridae) were eaten mainly during the flush periods (spring 1981, winter/spring 1982 and winter 1983) when they became very obvious on the pasture. The highest incidence of grasshoppers in the diet occurred during spring/summer. Spiders, beetles, centipedes, and scorpions were eaten mainly during the warmer months. Ants were also found in the stomachs but may have been ingested while eating other prey.

Reptiles were most common in the diet in summer and autumn of both years (63·6, 38·9 and 20·6 and 30·8% respectively). The weight of reptile in the stomach was generally low although it did reach 12·1% in the first summer (Fig. 1*f*). No reptiles were eaten in any of the three winters of the study.

Birds were consistently eaten, ranging in percentage occurrence from 13·9 to 35·7%, but their weight contribution was low except in spring 1982 when it reached 18·8% (Fig. 1*g*). About 115 bird species are found in the different vegetation strata in Yathong Nature Reserve (I. Mason, personal communication) with 43 species spending most of their time in the lower vegetation strata; of those 10 (23·3%) were taken by foxes (32 incidences). Of the 72 species which spend most of their time in the upper vegetation strata, only 5 species (6·9%) were taken by foxes (8 incidences).

(ii) *Cats*

The seasonal occurrence and weight contributions of the major groups in cat stomachs are presented in Fig. 1. As with the fox, mammals and invertebrates occurred consistently (Figs 1*a* and 1*e*). However, the weight contribution of invertebrates was generally small. Rabbit was by far the most important single item; occurrence peaked each spring (90·9% and 72·0%) at much higher levels than at other times (Fig. 1*b*). Incidence of carrion reached 25% in the summer of 1981–82 and the winter of 1982 but was generally low in occurrence and weight (Fig. 1*c*).

Invertebrates and reptiles were well represented in the diet in the summer and autumn of each year. No reptiles occurred in the diet in winter.

Birds were present in the diet in most seasons and reached a peak in autumn 1982 (42·1%) but were not eaten in the winter of 1982 (Fig. 1*g*). Of the 115 bird species found at Yathong Nature Reserve, cats ate 7 species (16·3%) which frequent the ground and lower shrubs (17 incidences) but only 3 species (4·2%) which frequent the trees and upper canopy (7 incidences). There was no significant difference between foxes and cats in regard to the vegetation strata from which birds were taken ($\chi^2_1 = 0{\cdot}284$, $P > 0{\cdot}05$).

Small mammals did not occur in the diet until early in 1982 (47·4%) but they were then present for the rest of the study.

Functional Responses in the Diet

The percentages of weight and occurrence of rabbit in the stomachs follow the same trends (Fig. 1*b*), hence only percentage occurrence is considered for analysis and has been calculated as a running mean (weighted according to sample size).

The mean number of active burrow entrances peaked in September 1981 and September 1982 ($n = 198$ and 249 respectively) and was low in June 1981, April 1982 and February 1983 ($n = 26$, 108 and 26 respectively). The rabbit breeding season was measured by an increase in the mean number of used burrow entrances (June '81–Sept. '81; Apr. '82–Sept. '82; Fig. 3). As this value increased each winter/spring (Fig. 2), so also did the occurrence of

rabbit in the stomachs of foxes and cats (Figs 2 and 3), illustrating a functional response of predator to prey during the rabbit breeding season. When rabbits ceased breeding each year in summer/autumn the incidence of rabbit in the stomachs of foxes and cats decreased (Figs 2 and 3) and a change to other prey occurred. After the second breeding season rabbit numbers began to decline due to the drought, but the incidence of rabbit in stomachs remained high especially for the fox and then also declined (Figs 2 and 3).

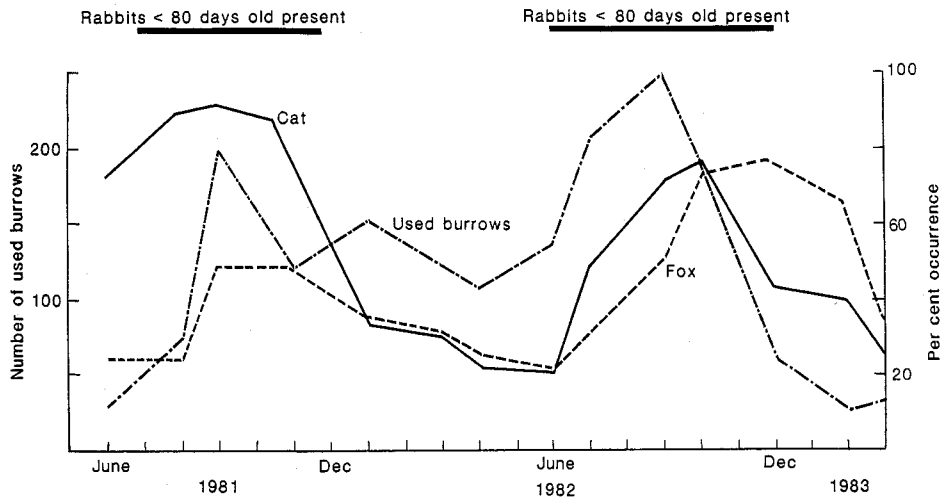

Fig. 2. Changes in the mean number of used burrow entrances (-·-·-) and the percentage occurrence of rabbit in the stomachs of foxes (dashed line) and cats (solid line).

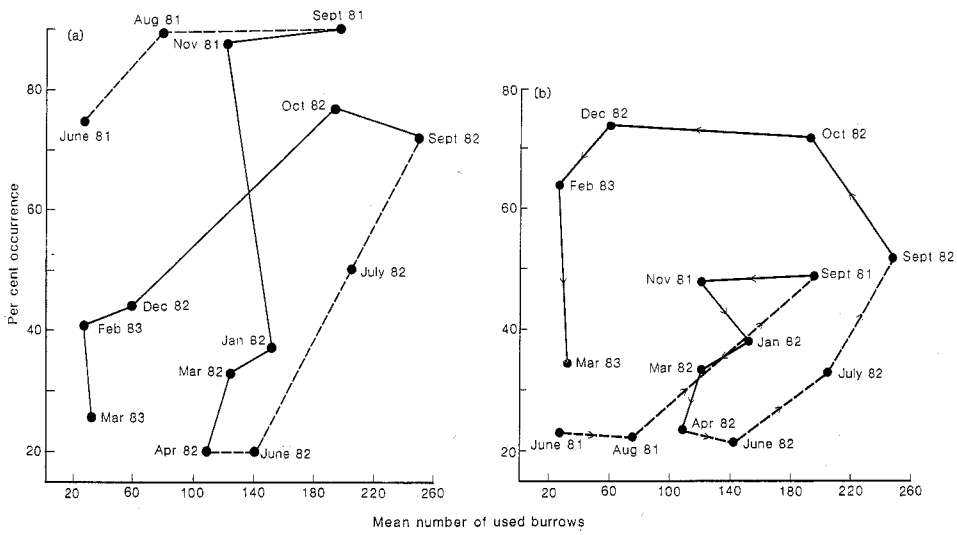

Fig. 3. Percentage occurence of rabbit in the stomachs of (*a*) cats and (*b*) foxes in relation to the mean number of used burrow entrances. Dashed lines represent a functional response to rabbits during the rabbit breeding season.

Diet and Age of Predator

Diets of different age groups were compared in summer and autumn when all age groups occurred simultaneouly.

There was no significant difference in diet composition between the youngest and oldest foxes. The 9–24 month age group ate less rabbit than the >24 months age group ($\chi^2_1=4\cdot24$, $P<0\cdot05$) (Table 1). There was no significant difference for any of the major groups between immature and mature cats (Table 1).

Table 1. Percentage of fox and cat stomachs containing the major groups of prey in relation to age of predator shot during summer/autumn

Foxes 9–24 months *cf.* foxes >24 months for rabbit: $\chi^2_1=4\cdot24$, $P<0\cdot05$; Immature foxes *cf.* immature cats for reptile: $\chi^2_1=4\cdot74$, $P<0\cdot05$; Immature foxes *cf.* immature cats for small mammal: $\chi^2_1=12\cdot29$, $P<0\cdot001$; Mature foxes *cf.* mature cats for bird: $\chi^2_1=4\cdot41$, $P<0\cdot05$; Mature foxes *cf.* mature cats for small mammal: $\chi^2_1=6\cdot72$, $P<0\cdot01$; Mature foxes *cf.* mature cats for rabbit: $\chi^2_1=4\cdot69$, $P<0\cdot05$

Prey group	Foxes			Cats	
	<9 Months	9–24 Months	>24 Months	Immature	Mature
Invertebrate	77·0	63·6	66·7	80·0	62·1
Reptile	30·4	54·5	50·0	55·0	62·1
Bird	15·6	9·1	16·7	15·0	37·9
Small mammal	5·9	9·1	5·5	30·0	34·5
Carrion	27·4	36·4	27·8	10·0	13·8
Rabbit	53·3	27·3	66·7	35·0	24·1
No. of stomachs	135	11	18	20	29

However there were interspecific differences. Immature cats ate more reptiles ($\chi^2_1=4\cdot74$, $P<0\cdot05$) and small mammals ($\chi^2_1=12\cdot29$, $P<0\cdot001$) than immature foxes (Table 1). In summer/autumn, mature cats ate more birds ($\chi^2_1=4\cdot41$, $P<0\cdot05$) and small mammals ($\chi^2_1=6\cdot72$, $P<0\cdot01$) and less rabbit ($\chi^2_1=4\cdot69$, $P<0\cdot05$) than mature foxes (Table 1). In winter/spring, mature cats ate less invertebrate ($\chi^2_1=29\cdot55$, $P<0\cdot001$) and carrion ($\chi^2_1=27\cdot38$, $P<0\cdot001$) but more rabbit ($\chi^2_1=25\cdot41$, $P<0\cdot001$) than mature foxes (Table 1).

Table 2. Age of rabbits eaten by predators

$\chi^2_2=36\cdot40$, $P<0\cdot001$

Age of rabbit	Fox		Cat	
	Number	Percentage	Number	Percentage
<50 d (small kitten)	12	20·0	35	72·9
50–80 d (large kitten)	12	20·0	9	18·7
Adult	36	60·0	4	8·3
Number of observations	60		48	
Number of stomachs	58		41	

Age of Rabbit in the Stomachs

The most common body pieces used to age rabbits in stomachs were ears and limbs. There was no difference between predators in the incidence of specific body pieces. In many cases predators consumed ears and feet of rabbits intact and several cats ingested whole marsupial mice *Sminthopsis crassicaudata* up to 16 g in weight.

Despite the seasonal differences in the number of foxes and cats shot ($\chi^2_8=24\cdot38$, $P<0\cdot0001$) (Fig. 1) and eating rabbits ($\chi^2_8=36\cdot53$, $P<0\cdot001$), there appears a real

difference in the age of rabbits taken by foxes and cats. It was possible to determine the age of rabbits in 58 out of 130 fox stomachs that contained rabbit and 41 out of 61 cat stomachs. Some stomachs contained more than one age group. Foxes mainly ate adult rabbits (60·0%) with small kittens (20·0%), whereas cats ate mainly small kittens (72·9%) and few adults (8·3%) ($\chi^2_2 = 36{\cdot}40$, $P < 0{\cdot}001$) (Table 2).

Discussion

The analysis of stomach contents identifies predation as being greatest on an increasing prey population during good pasture conditions and a declining prey population during bad pasture conditions. Drought appears to induce predation on a declining population by reducing the amount of food and cover for rabbits and the amount of alternate prey for predators. During the drought of late 1982 and early 1983 when only adult rabbits were available and were declining, their occurrence in fox stomachs was much higher than at any other time. Their occurrence was also greater in cat stomachs compared with the same period the previous year. A recent related study (A. E. Newsome, I. Parer and P. C. Catling, unpublished) concluded that predators can inhibit the population growth of mammalian prey. However, the precise timing of the effects of predation could not be established as was done for cyclic mammals in North America (Pearson 1966, 1971; Fitzgerald 1977). There predation was most severe on a declining and low prey population.

Holling (1959) used 'functional response' to describe the relationship between the density of prey and the rate at which an individual predator consumes prey. For invertebrate predators, it is often initially a linear response which levels off at high prey density. For vertebrate predators the response is generally S-shaped, showing an initial lag in the response of the predator to increasing numbers of prey and a levelling off at high prey density. During the rabbit breeding season in winter/spring each year, foxes and cats exhibited a functional response to rabbits.

However, after the rabbit breeding season, the staple prey (rabbits) became less important and a change to supplementary prey occurred as it became abundant or available, as was the case for reptiles. Newsome *et al.* (1983) identified four categories of prey: staples, supplementary, opportune and scavenged. Staples are those on which predators can rely over time even though they may not always have the highest occurrence; supplementary are prey which may form the major proportion of the diet at times but are generally ancillary and may be unavailable or infrequently eaten at other times; opportune are those which although available were not eaten regularly or in large proportions or were infrequently available; and scavenged is a special category of opportune prey. In this study rabbits were considered staple for both predators. Supplementary prey were (in order of magnitude) invertebrates, reptiles, birds and small mammals for cats, and invertebrates, reptiles, carrion and birds for foxes. Opportune prey were carrion for cats and small mammals and fruits for foxes.

Seasonal changes from staple to supplementary prey resulted in an annual prey cycle which was similar for foxes and cats and could lead to competition. However, competition appeared to be offset by cats mainly eating young rabbits (in winter/spring) and foxes mainly eating adult rabbits (in spring/summer). Parer (1977), Jones (1977), Gibb *et al.* (1978), Corbett (1979) and Liberg (1984) also found cats to kill mainly young rabbits. Corbett (1979) concluded that the hunting techniques of cats did not appear to be adapted to exploiting adult rabbits, even though cats appeared to reside in rabbit warrens for some of the time at least. However, in sandy habitats foxes accounted for between 26 and 75% of a seasons's nestlings (Wood 1980). In this study, cats changed from mainly young rabbits in winter/ spring to invertebrates, small mammals and reptiles in summer/autumn when only adult rabbits were present. Similarly, foxes changed from mainly adult rabbits and invertebrates in spring/summer to carrion and invertebrates in autumn/winter.

Carrion was mostly eaten in the winter months, particularly by the fox. Other studies

have demonstrated that foxes eat significant amounts of carrion and refuse in winter (Englund 1965; Bayly 1978; Green and Osbourne 1981). Cats did not each much carrion; greatest occurrence of carrion by weight in cat stomachs was at the height of the drought when the availability of other prey was reduced. Similarly, during winter on Macquarie Island when the availability of other food was low, cats scavenged on carrion (Jones 1977).

Invertebrates were important, especially for foxes. In this and other studies, they were mainly eaten during the warmer months when generally most abundant (Coman 1973; Brunner *et al.* 1975; Fitzgerald and Karl 1979; Green and Osbourne 1981). In this study foxes ate substantial numbers of caterpillars which became abundant on the lush pastures in winter/spring.

Reptiles were eaten by both predators in spring, summer and autumn, a time when reptiles were most accessible; these findings are similar to those of Triggs *et al.* (1984). Cats ate a greater amount and a greater diversity of reptiles than foxes, especially during the drought; during the autumn of 1983, almost every cat stomach contained reptile.

It is doubtful if foxes and cats could exist in any numbers in this area without rabbits which are the important staple prey. In areas where rabbits are uncommon such as the coast and the Alpine region, small rodents and marsupials are the staple prey (Green and Osbourne 1981; P. C. Catling and A. E. Newsome, unpublished). Australian sheep-grazing areas lack the abundance and diversity of rodents and small marsupials found in forested areas. It would appear that foxes and cats successfully co-habit a semi-arid environment because they primarily utilize different age classes of the same staple prey and to some extent different supplementary prey.

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Appendix. Diets of the fox and feral cat at Yathong Nature Reserve

		Fox	Cat
Number of stomachs examined		288	112
Number of empty stomachs		7	9
Occurrence of listed species within stomachs		%	%
Plants		14·9	2·6
Burr medic	*Medicago denticulata*	1·7	–
Wilga seeds	*Geijera parviflora*	5·2	–
Plant indet.		8·3	2·6
Invertebrates		70·1	42·5
Scorpion	Scorpionida	13·2	3·5
Spider	Arachnida	30·2	25·7
Centipede	Chilopoda	21·9	7·1
Termite	Isoptera	–	0·9
Grasshopper and cricket	Orthoptera	32·3	28·3
Beetle	Coleoptera	34·4	5·3
Dermestid larvae	Coleoptera	1·4	–
Fly indet.	Diptera	1·4	6·2
Maggot	Diptera	3·1	–
Moth	Lepidoptera	4·2	4·4
Caterpillar indet.		24·3	4·4
Amphibia and reptiles		23·3	30·1
Frogs	*Limnodynastes interioris*	0·3	–
	Neobatrachus sudelli	0·3	–
Lizards	*Diplodactylus intermedius*	0·7	1·8
	Diplodactylus steindachneri	1·4	1·8
	Diplodactylus spp.	–	0·9
	Gehyra variegata	4·5	8·0
	Oedura marmorata	–	0·9
	Rhynchoedura ornata	6·9	4·4
	Underwoodisaurus milii	0·7	4·4
	Gekkonidae indet.	–	2·6
	Pygopus nigriceps	4·2	8·0
	Amphibolurus vitticeps	1·7	0·9
	Agamidae indet.	1·0	–
	Varanus gouldii	1·4	–
	Varanus spp.	0·3	0·9
	Cryptoblepharus carnabyi	–	0·9
	Ctenotus atlas	–	0·9
	Ctenotus regius	–	0·9
	Ctenotus spp.	–	0·9
	Egernia striolata	–	4·4
	Eremiascincus richardsonii	–	6·2
	Lerista muelleri	0·7	–
	Lerista punctatovittata	5·2	7·1
	Lerista spp.	1·0	–
	Scincidae indet.	0·3	–
Lizard indet.		0·7	–
Snakes	*Ramphotyphlops bituberculatus*	1·7	–
	Ramphotyphlops spp.	1·4	0·9
	Simoselaps australis	1·0	1·8
	Unechis spectabilis	0·3	–
	Elapidae indet.	0·3	–

Appendix (*continued*)

		Fox	Cat
Birds		18·0	21·2
Emu	*Dromaius novaehollandiae*	3·8	–
Brown goshawk	*Accipiter fasciatus*	0·3	–
Stubble quail	*Coturnix novaezealandiae*	0·7	1·8
Common bronzewing	*Phaps chalcoptera*	0·7	–
Crested pigeon	*Ocyphaps lophotes*	0·3	–
Galah	*Cacatua roseicapilla*	1·0	3·5
Mallee ringneck	*Barnardius barnardi*	0·7	2·6
Red-rumped parrot	*Psephotes haematonotus*	0·3	2·6
Blue-bonnet	*Northiella haematogaster*	–	1·8
Tawny frogmouth	*Podargus strigoides*	1·0	–
Red-capped robin	*Petroica goodenovii*	0·3	–
Grey-crowned babbler	*Pomatostomus temporalis*	0·3	–
Southern whiteface	*Aphelocephala leucopsis*	–	0·9
Noisy miner	*Manorina melanocephala*	1·0	2·6
Yellow-plumed honeyeater	*Lichenostomus ornatus*	–	0·9
Common starling	*Sturnus vulgaris*	0·3	–
White-winged chough	*Corcorax melanorhamphos*	–	0·9
Australian magpie	*Gymnorhina tibicen*	0·3	–
White-winged chough or Australian magpie indet.		2·4	0·9
Bird indet.		5·9	3·5
Egg shell		–	0·9
Mammals		81·6	80·5
Short-beaked echidna	*Tachyglossus aculeatus*	1·4	–
Fat-tailed dunnart	*Sminthopsis crassicaudata*	1·4	4·4
Common brushtail possum	*Trichosurus vulpecula*	0·3	0·9
Grey kangaroo	*Macropus giganteus* and *M. fuliginosus*	15·3	2·6
Red kangaroo	*Macropus rufus*	2·8	–
Kangaroo indet.	*Macropus* spp.	1·0	0·9
Lesser long-eared bat	*Nyctophilus geoffroyi*	0·3	1·8
Bat indet.	Chiroptera	0·3	0·9
House mouse	*Mus musculus*	4·2	8·8
Rabbit	*Oryctolagus cuniculus*	45·1	54·0
Feral pig	*Sus scrofa*	0·7	0·9
Ox	*Bos taurus*	0·7	0·9
Feral goat	*Capra hircus*	12·1	2·6
Sheep	*Ovis aries*	1·0	–
Bone and flesh indet.		6·2	–
Number of species identified		57	47