

The feeding ecology of the dingo

III. Dietary relationships with widely fluctuating prey populations in arid Australia: an hypothesis of alternation of predation

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Summary. Changes in the diet of dingoes (*Canis familiaris dingo*) in response to measured fluctuations of prey populations were followed over 7 years. The study began after great rains had broken a long drought. Eruptions of rodents and rabbits followed, but some prey were always either relatively abundant (live cattle) or scarce (red kangaroo, lizards, birds). Cattle carcasses were increasingly available during a subsequent drought. Small and medium-sized prey, rodents (26%), lizards (12%) and rabbits (56%) were preferred, probably because they were easily caught. Only rabbits were eaten consistently regardless of density. By contrast, large prey were eaten in relatively large amounts only during drought, with initial emphasis on red kangaroos (15% overall) and then cattle (17%) mostly as carcasses. The diet was functionally related to the respective abundances of all major prey species, but the relationship shifted during drought when predation on low populations was most severe. There was evidence that growth of resurging prey populations were suppressed by predation. Diets of dingoes did not differ significantly with age or sex. An hypothesis of 'alternation of predation' is presented: dingoes feed sequentially on prey of increasing size (rodents, rabbits, red kangaroos, cattle) in response to rainy periods and subsequent droughts, meanwhile always concentrating on the staple prey (rabbits). The fluctuating abundances of small and medium-sized prey determined not only their own relative availabilities but also that of large prey, and hence determined the diet of the dingo at any time. Prey availability (catchability, accessibility) appeared to be more important than prey abundance (numbers, biomass), and the dingo's flexible social organisation allowed versatility in hunting strategies and defence of resources. We conclude that dingoes do not always forage most efficiently as optimal foraging models predict because of the constraints imposed by the capricious environment in arid Australia, where prey availability fluctuates greatly and becomes limited and clumped in drought, so that dingoes may be faced with outright starvation. Instead we conclude that dingoes utilise a conservative feeding strategy and adopt any behaviour which provides at least a threshold quantity of energy or nutrient as part of a trade-off with other competing ecological requirements.

Key words: Foraging – Alternation of predation – Prey availability – Dingo – Desert

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Given a wide range of nutritionally palatable prey, all fluctuating in density more or less independently of each other, and with different spatial distributions, how does the diet of a predator change?

Various 'optimal foraging' models have been proposed which attempt to predict predator diet and foraging behaviour (see reviews in Pyke et al. 1977; Krebs et al. 1983; Pyke 1984). All are based on the tenet that natural selection ultimately favours individuals which select prey that convey the maximum nett benefit per effort (usually expressed as energy per time). They also assume that predators can make 'optimal decisions' in choosing prey, in utilizing prey patches and in hunting strategies. In early studies (e.g. Krebs et al. 1977; Krebs 1978), tests of the predictions of 'optimal diet' models were conducted under carefully controlled and/or simple environments where predators had limited prey choice, and restricted use of hunting strategies, and where they were essentially free of other competing ecological requirements.

Recently the underlying assumptions and theoretical predictions for predators in complex multfood systems have been questioned (e.g. see review in Schluter 1981; also Lacher et al. 1982; Lucas 1983) and alternative models have been proposed (e.g. Janetos and Cole 1981; also see Simon 1956). In particular, the assumptions that predators perceive the environment as 'fine grained' and stable are unrealistic given the spatial heterogeneity of natural environments, their unpredictability and stochastic characteristics (Oaten 1977; Stephens and Charnov 1982). Moreover, diet choice is influenced by factors other than calory intake (Goss-Custard 1977; Westoby 1978), especially intraspecific competition (Milinski 1982), age and experience (Sih 1982), hunger (Richards 1983) and hunting strategies (Winterhalder 1983).

There has been little research on social mammalian predators exploiting a wide range of prey in terms of both species composition and body size (but see Newsome et al. 1983b). In a review by Krebs et al. (1983) involving 89 studies pertinent to optimal foraging theory, only 17 concerned mammals, none of which were social carnivores. Further we know of no studies conducted in desert environments where there may be gluts of food or prolonged periods of extreme shortage during which the problem of starvation is real.

One aim of the long term field study (7 yr) reported here was to fill that gap. Dingoes (*Canis familiaris dingo*)

are predators which may hunt in socially integrated groups or alone (Corbett and Newsome 1975; Newsome et al. 1983b) and which can catch large as well as small prey. Dingoes are also highly mobile (unpublished data) and are able to exploit widely separated prey patches. We examine the diet of the dingo in relation to the availability of a wide range of prey (insects to cattle) including eruptive species. This study began soon after great rains had broken a severe drought. Subsequently the weather became increasingly arid. This pattern provided a natural experiment causing some prey populations to fluctuate widely and inversely to others. Against this background we discuss the accuracy of 'optimal foraging theory' predictions and focus on Murdoch's (1969) concept of 'prey switching'. Extension of this concept has given rise to the hypothesis of 'alternation of predation' on the most available prey.

Methods

Study area

The study was conducted on Eraldunda pastoral lease (6705 km²; 25°S, 135°E) situated about 200 km SSW of Alice Springs township in central Australia (Fig. 1). Mostly Shorthorn and Hereford cattle (*Bos taurus*) were run. There were also small numbers of feral horses (*Equus caballus*) and donkeys (*E. asinus*), but no sheep (*Ovis aries*). The general region possesses an impressive array of vertebrate fauna, about 18 spp. native mammals, 5 spp. introduced mammals, 107 spp. birds and 50 spp. reptiles (Hooper et al. 1973). Habitats can be grouped into 4 basic associations (Fig. 1) based on Perry et al. (1962):

- Sparse shrublands (mainly *Acacia aneura*) over short grasses (*Aristida* spp., *Enneapogon* spp.) and forbs on red clay sands and sandy calcareous soils.
- Open chaenopod pasture lands (*Bassia* spp., *Maireana* spp., *Atriplex* spp.) with occasional hills and rocky plateaux of stone mantled calcareous soils.
- Plainslands with numerous ephemeral salt lakes and pans sometimes fringed with samphire (*Arthrocnemum* spp.).
- Desert dune fields and plains of red sands and red

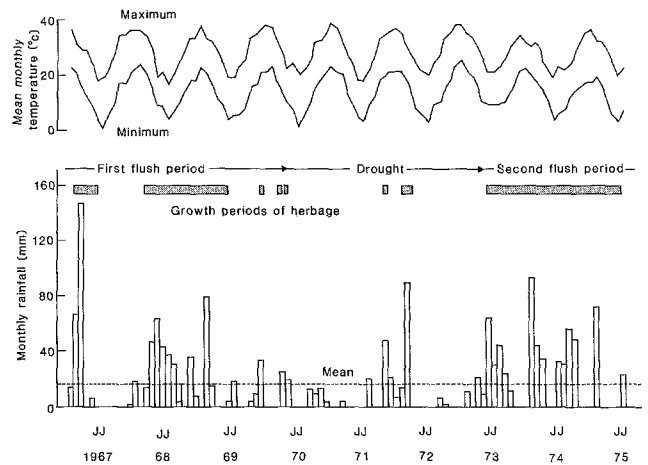


Fig. 2. Monthly rainfalls, mean monthly temperatures, periods of herbage growth, and flush and drought regimes at Eraldunda, 1967–75. Temperature records are the nearest available to Eraldunda, from Alice Springs airport

clayey sands dominated by spinifex (*Triodia* spp.) but with scattered stands of desert poplars (*Codonocarpus cotinifolius*) and desert oaks (*Casuarina decaisneana*).

The climate is semi-arid to arid (Meigs 1953). Day temperatures are generally high in summer (Fig. 2), but sub-zero night temperatures regularly occur in winter. The characteristically low rainfall (annual mean, 173 mm) is irregular and there may be prolonged periods of drought as during the study period (Fig. 2). In this study we refer to 2 major climatic regimes – flush and drought. The former were periods favouring pasture growth as during the early and late study years (Fig. 2) where durations were calculated from rainfall using Newsome's (1966) method. The intermediate drought between mid 1970 to mid 1973 was broken briefly in the summer of 1971–72 resulting in a brief resurgence in numbers of small and medium-sized prey. There was never a shortage of drinking water because 27 cattle bores and catchment dams have been sunk on the property and there are a few natural springs. All are referred to as watering points.

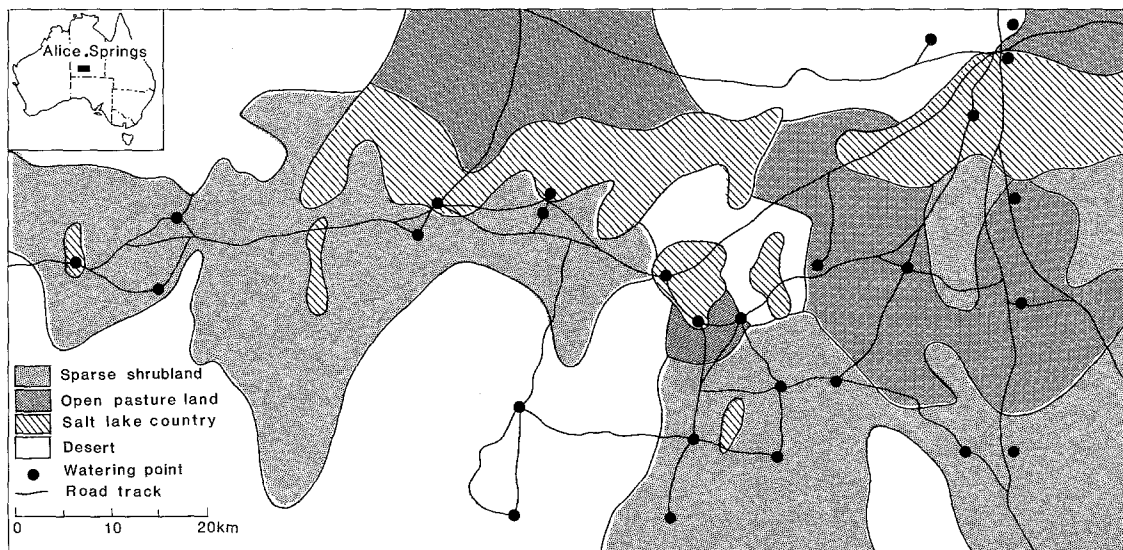


Fig. 1. Eraldunda study area, central Australia

Sampling and analysing dingo stomach contents

Between April 1968 and August 1974, 21 sampling trips were conducted on Erldunda, 10 during flush periods and 11 during drought (see Table 1 below). Each trip lasted about 10 days. Most dingoes were foot-trapped in Oneida No. 14 jump-traps, and some were shot. At post-mortem, stomach contents were weighed and preserved in 10% neutral buffered formalin. Other biological material was collected including eye lenses for estimating ages.

In the laboratory, the contents of each stomach were flushed through coarse and fine grain sieves and items were separated, towelled dry and weighed (g), and identified.

Identifying and analysing prey remains

Mammals were identified mostly on hair structure (as Corbett 1974). Other mammalian remains and those of birds, reptiles and insects were identified by comparison with known specimens or by specialists. The remains of cattle were judged as recently eaten or eaten as carrion based on presence or absence of bloody meat and maggots, or putrid ingesta and dried skin respectively. About half of the stomachs containing cattle could not be so classified and were recorded as indeterminate. As we could not distinguish between calf and adult cattle remains in stomachs except in a few cases, results are lumped. For the red kangaroo (*Macropus rufus*), most remains in stomachs appeared to be fresh, and carrion was not distinguished, nor adult and young.

Two methods of analysis were used, frequency of occurrence and wet weight. The former was the proportion of stomachs containing a particular prey species (e.g. rabbit), or a suite of prey species of similar size (e.g. rodents), or prey of different size within the same taxon (e.g. birds). The latter method expressed the wet weight of dietary items as a percentage of the total wet weight of remains. Both methods indicate the range of dietary items eaten, but frequency of occurrence tends to over-emphasise items which occur frequently but in very small amounts (e.g. rodents) and *vice-versa* for large amounts (e.g. kangaroos) (Lockie 1959; Floyd et al. 1978). The problems associated with weight are exactly opposite.

Indices of prey abundance

Early results suggested that dingoes ate particular species (as below) more frequently than others and so attempts were made to estimate their abundances in the same general areas where dingoes were trapped. All values were expressed as mean \pm standard error. The one set of data for the false break in the drought are included in the totals only. Methods were as follows:

Small mammals (rodents, marsupial mice). Two methods were utilised: spotlight counts and live-trapping, both along standard transects. The counts were made within a band of about 50 m when driving at night between watering points. A total of 21 counting surveys were conducted over 1355 km (65 ± 14 km/survey), 12 in flush periods (912 km, 76 ± 21 km/survey) and 8 in drought (416 km, 52 ± 17 km/survey). Abundance was recorded as the number of small mammals/10 km/survey. Elliott live-traps baited with rolled oats and bird seed were set in up to 3 grids, each of 20 traps, for up to 10 days during field trips. Grids were in two lines

with approximately 10 m between traps. A total of 21 trapping surveys were conducted (total 2389 trap-nights, 114 ± 16 /survey), 11 in flush periods (1270 trap-nights, 116 ± 19 /survey) and 9 in drought (819 trap-nights, 91 ± 22 /survey). Abundance was recorded as the number/100 trap-nights/survey.

The above methods provided quite different indices of small mammal abundance (see results below). Hence a mean index of abundance was derived by combining transect and trapping data as follows. Each of the two estimates at any time was divided by the greatest value recorded during the entire study and expressed as a percentage, and then a mean index was calculated for each pair of percentages.

Rabbit (Oryctolagus cuniculus). Spotlight counts were similarly run but rabbits were counted in a wider band of about 100 m. A total of 21 counting surveys were conducted over 1555 km (74 ± 13 km/survey), 11 in flush periods (1007 km, 50 ± 13 km/survey) and 8 in drought (352 km, 44 ± 13 km/survey). Abundance was recorded as the number of rabbits/10 km/survey.

Red kangaroo (Macropus rufus). We recorded all red kangaroos seen in a belt about 300 m wide when driving along transects during the day, at dusk and at night. A total of 21 counting surveys were conducted over 2713 km (129 ± 17 km/survey), 11 in flush periods (1485 km, 135 ± 31 km/survey) and 8 in drought (928 km, 116 ± 20 km/survey). Abundance was expressed as the number of red kangaroos/100 km/survey.

Cattle (Bos taurus). The number of dead cattle were counted along roads and within about 1 km radius of watering points (7 ± 1 waters/survey). Abundance was expressed as the total number of carcasses/survey (total 15 surveys, 5 in flush periods, 8 in drought). The number alive was obtained per year from official records of the Northern Territory Department of Primary Production (C Rydeout, pers. comm.). Incidents of dingoes attacking cattle or of cattle wounded by dingoes were recorded and expressed as a total for each field trip.

Lizards. Holes which appeared to be occupied by the small lizard (*Amphibolurus nuchalis*) were dug out on 20 quadrats each approximately 0.2 ha and spaced approximately 0.8 km apart. Digging ceased when 10 lizards were captured, or when all the holes on 20 quadrats were dug out, whichever was first. All captured lizards were identified before release. A total of 16 surveys were conducted and a total of 1961 holes were dug out in 46 ha (3 ± 0.3 ha/survey, 123 ± 16 holes/survey, 63 ± 9 holes/ha). Respective values for 6 surveys in flush periods were: 2 ± 0.4 ha/survey, 101 ± 24 holes/survey, 85 ± 22 holes/ha; and for 8 surveys in drought: 4 ± 0.1 ha/survey, 112 ± 17 holes/survey, 29 ± 2 holes/ha. Abundance was recorded as the number (and species) of small lizards/ha/survey.

Large dragons (*Amphibolurus vitticeps*) and monitors (*Varanus gouldii*) were recorded whenever seen while driving along roads and at watering points during the day. In 19 surveys there were 150 recording days (8 ± 1 days/survey), in 9 surveys in flush periods, 66 days (7 ± 1 days/survey), and in 8 surveys in drought, 64 days (8 ± 1 days/survey). Abun-

Table 1. The frequency of various prey in stomachs of 285 dingoes at Eridunda during different periods between 1968–74^a

Dietary items (Sample No.)	No. of occurrences				
	Mean adult body weight kg	Apr./June 1968 (1)	Jan./Mar./May 1969 (2)	Sept./Dec. 1969 (3)	Apr. 1970 (4)
Large mammals, total		8	3	3	2
Total cattle <i>Bos taurus</i>	254.00 ^b	7	3	1	1
Fresh remains		1			1
Carion remains		3			
Indeterminate remains		3	3	1	
Red kangaroo <i>Macropus rufus</i>	48.00	1		2	1
Horse <i>Equus caballus</i>	254.00 ^b				
Euro <i>M. robustus</i>	25.00				
Medium-sized mammals, total		20	28	12	20
Rabbit <i>Oryctolagus cuniculus</i>	1.43	20	28	12	20
Feral cat <i>Felis catus</i>	4.00				
Small mammals, total		44	8	3	0
Brown hopping mouse <i>Notomys alexis</i>	0.03	13	3		
Indeterminate <i>Notomys</i> spp.		9	1	1	
House mouse <i>Mus musculus</i>	0.01	9	1		
Sandy inland mouse <i>Pseudomys hermannsburgensis</i>	0.01	6	1		
Forrest's mouse <i>Ps. forresti</i>	0.02	1			
Indeterminate <i>Ps.</i> spp.		2			
Long-haired rat <i>Rattus villosissimus</i>	0.16	2	1	1	
Rodent, indeterminate spp.		2	1	1	
Dunnart, indeterminate <i>Sminthopsis</i> sp.	0.02				
Lizards, total		2	0	1	0
Central netted dragon <i>Amphibolurus nuchalis</i>	0.02	1			
Bearded dragon <i>A. vitticeps</i>	0.26	1			
Sand monitor <i>Varanus gouldii</i>	2.90				
Short-tailed monitor <i>V. brevicaudata</i>	0.03				
Leonhard's skink <i>Ctenotus leonhardii</i>	0.01				
Lizard, indeterminate sp.				1	
Birds, total		4	3	0	0
Crow/Raven, indeterminate <i>Corvus</i> spp.	0.60	2	1		
Zebra finch <i>Peophila guttata</i>	0.01	2			
Whiteface, indeterminate <i>Aphelocephala</i> sp.	0.01		1		
Richard's pipit <i>Anthus novaeseelandiae</i>	0.03				
Budgerigar <i>Melopsittacus undulatus</i>	0.03				
Emu <i>Dromaius novaehollandiae</i>	33.00		1		
Insects, total		0	0	0	0
Beetle, undetermined spp.	<0.01				
Grasshopper, undetermined spp.	<0.01				
Undetermined insect sp.					
Others, total		0	0	0	0
Fat, meat, bone; indeterminate					
Berries, undetermined sp.					
No. of stomachs with dietary items used in analyses		52	34	15	22
Total no. of stomachs sampled		58	49	18	31
No. empty stomachs or containing non-dietary items ^c		6	15	3	9

^a Data for some field trips are lumped to provide adequate sample sizes. Samples 1–5, 12 collected during flush periods; 6–8, 10–11 during drought; and 9 during the false break in the drought

^b Mean composite weight for adult, yearling and young

^c Dingo, detritis

No. of occurrences								Total sample 1968-74	
June/Sept. 1970 (5)	Dec./Feb. 70/71 (6)	June 1971 (7)	Dec./Feb. 71/72 (8)	May/Sept. 1972 (9)	Dec./Feb. 72/73 (10)	June 1973 (11)	Aug. 1974 (12)	Occurrence %	Weight %
6	6	19	15	6	20	5	1	33.0	25.5
1	0	10	9	2	12	1	1	16.8	15.4
		1	2		1			2.1	
		3	3	2	5	1	1	6.3	
1		6	4		6			8.4	
4	6	8	6	4	8	3		15.1	8.8
		1				1		0.7	
1								0.4	
9	13	11	9	15	10	6	9	56.8	62.9
8	12	10	9	15	10	6	9	55.8	61.0
1	1	1						1.1	
0	0	0	0	3	11	5	2	26.7	7.6
						1		6.0	
				2	7	3	2	3.9	
					1			8.4	
								2.8	
				1				0.4	
								1.1	
								1.4	
					3			2.5	
						1		0.4	
0	0	0	4	5	16	6	0	11.9	3.6
			3	5	13	6		9.8	3.0
			1					0.7	
					1			0.4	
					1			0.4	
					1			0.4	
0	1	0	1	1	1	0	0	3.9	<0.1
	1							1.4	
				1				1.1	
								0.4	
					1			0.4	
			1					0.4	
								0.4	
0	1	0	0	1	4	0	0	2.1	0.1
	1			1	1			1.1	
					2			0.7	
					1			0.4	
1	0	0	0	1	0	0	0	0.7	0.4
1								0.4	
				1				0.4	
15	19	26	22	23	33	14	10	285	
23	34	35	30	35	42	18	13	386	
8	15	9	8	12	9	4	3	101	

dance was expressed as the number of large lizards/day/survey.

Birds. We assumed that fluctuations in the number of zebra finches (*Peophila guttata*) were representative of small passerine birds. The number seen in shrubs and trees near

watering points were estimated usually during the hot mid-day period when they congregated near water. A total of 18 surveys were conducted (7 ± 1 waters/survey), 8 in flush periods (7 ± 1 waters/survey) and 8 in drought (7 ± 1 waters/survey). Abundance was expressed as the number of zebra finches/water/survey.

Estimating prey biomass

Biomass for each prey species was estimated each trip by multiplying abundance indices by respective mean weights (see Table 1 below). Extrapolations were made for the entire cattle station, assuming the representativeness of respective surveys. The elaborate road network allowed us to sample most of the study area except for some desert habitats (see Fig. 1). We usually worked on about half the study area and alternated between halves on successive trips. We also assumed that most cattle died near watering points.

Diets by age-class and sex of dingoes

Dietary frequencies were compared from the same sample. Age was estimated from eye lens weight (unpublished data) using the equation calculated by the late ML Dudzinski (in Corbett 1974).

Statistical analyses

Most comparisons of diet and prey abundance were analysed using non-parametric statistics (Siegel 1956) and all tests are one-tailed. U and z refer to the Mann-Whitney U test and r_s to the Spearman Rank Correlation Coefficient. Otherwise, r refers to Pearson's Correlation Coefficient and χ^2 refers to the Chi-square test.

Results

A total of 386 dingo stomachs were obtained. Of these, 59 (15.3%) were empty and 42 (10.9%) contained only non-dietary items, leaving 285 (73.8%) for analysis. Data were lumped to provide 6 major samples for flush periods, 5 for drought and 1 sample during the false break in the drought. Values are presented as mean \pm standard error/sample.

Diet overall

A list of all dietary items is given in Table 1. Inherent biases between the 2 methods of analyses appear to be minimal for this study. There are significant correlations between the percentages of wet weight and frequency of occurrence for most of the major dietary items (rabbit, $r_s=0.879$, $P<0.01$; cattle, $r_s=0.593$, $P<0.05$; red kangaroo, $r_s=0.791$, $P<0.01$; lizards, $r_s=1.000$, $P<0.05$), but not for small mammals ($r_s=0.366$, $P>0.05$) and birds ($r_s=0.371$, $P>0.05$) which were under-represented by weight and over-represented by occurrence. Most results were analysed therefore as percent occurrence.

For the total sample, the most common species eaten was rabbit (56% occurrence) followed by cattle (live 2.1%, dead 6.3%, indeterminate 8.4%), then red kangaroo (15%). Small mammals (27%) were eaten more frequently than lizards (12%), birds (4%), and insects (2%).

Diet relative to prey abundance (Figs. 3, 4)

Rabbit. Numbers fluctuated greatly but were always present averaging $29 \pm 8/10$ km over 21 surveys (Fig. 3a). More rabbits were seen during flush periods than drought (respective means $50 \pm 13/10$ km, $n=11$; and $5 \pm 1/10$ km, $n=8$; $U=0$, $P<0.001$).

Rabbits were a feature of dingo diet in all 12 samples, varying between 30–91% occurrence (mean $60 \pm 6\%$, Fig. 3a); but more dingoes ate rabbits in flush periods than

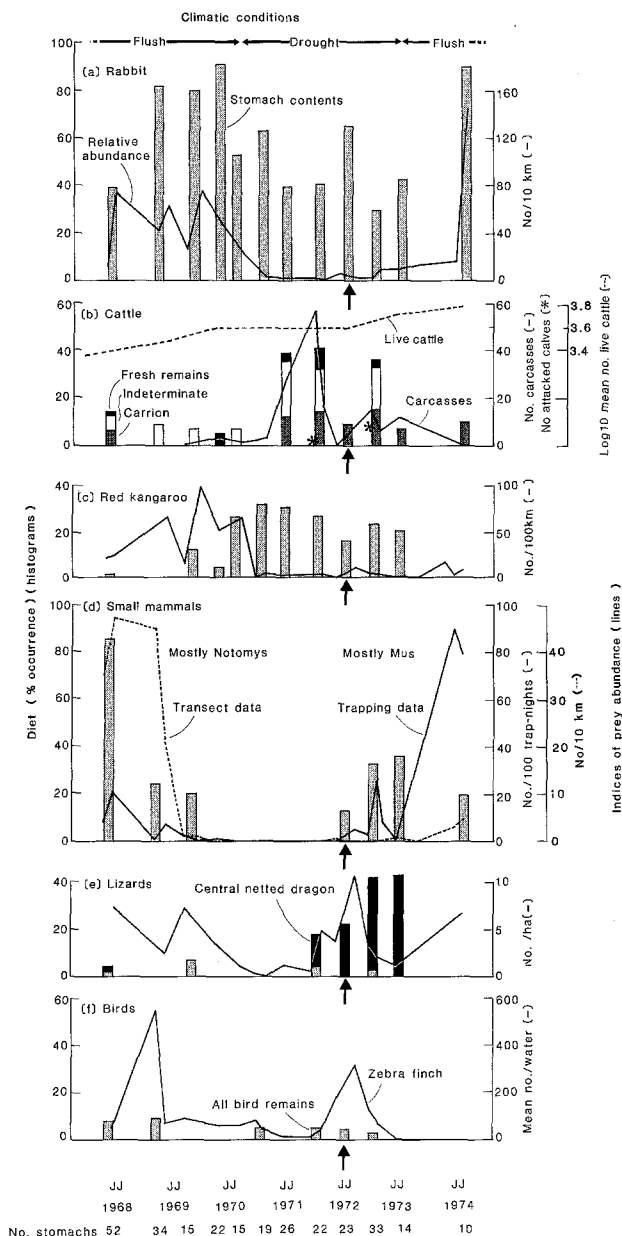


Fig. 3a-f. The frequency of prey remains in dingo stomachs (histograms) in relation to indices of prey abundance (line graphs) in flush periods and drought. The arrow indicates samples collected during the false break in the drought

drought (respective means $73 \pm 9\%$, $n=6$; and $43 \pm 5\%$, $n=5$; $U=4.5$, $P<0.05$). Despite a basically functional dietary response (Fig. 4a), Figure 3a indicates severe predation on rabbits during the drought. When hardly any rabbits were being seen, up to 63% of dingoes were eating them and never fewer than 30%.

Cattle. With the breaking of the severe drought of 1958–66, cattle numbers gradually increased from about 2500 head in 1968 ($0.37/\text{km}^2$) to about 6000 in 1974 ($0.89/\text{km}^2$) (Fig. 3b). Most calves are born between September and December and it is usual for about 24% of the herd to be less than 12 months of age (Petty et al. 1979). As shown in Fig. 3b also, more carcasses were seen during drought than flush periods (respective means 17 ± 8 , $n=5$; and

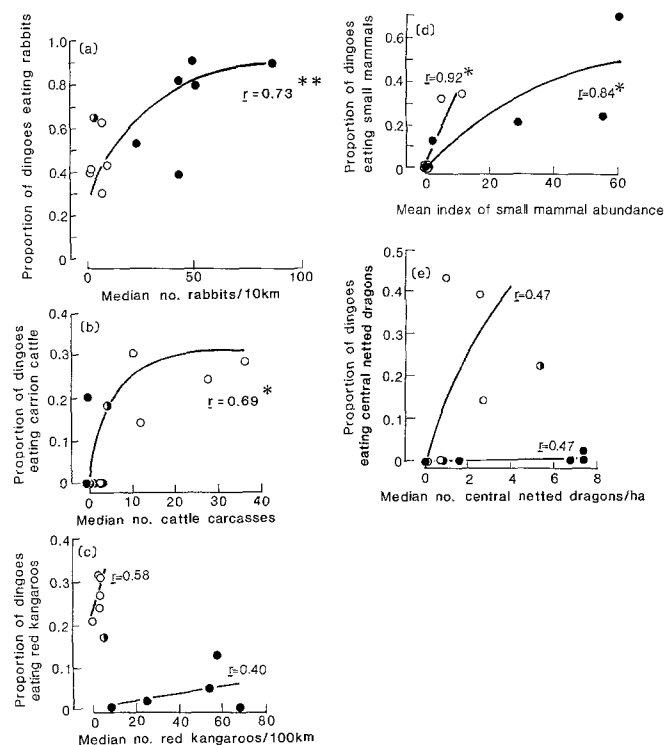


Fig. 4a-e. Functional responses during flush periods ●, drought ○, and the false break in the drought ◐. * $P < 0.05$, ** $P < 0.01$

1 ± 0.4 , $n=8$; $U=1.5$, $P < 0.01$). Most cattle would have died of starvation and/or disease. There may have been some predation but only those attacked calves actually seen by us are indicated in Fig. 3b. Remains of cattle that had recently died were in 6 out of 48 dingo stomachs and of carrion in 18 other stomachs (Table 1). Whether dingoes had initially killed such cattle was unknown. Carcasses soon become flyblown and dingoes may feed over several days on cattle previously killed.

Dingoes ate cattle throughout most of the study period (0–41% occurrence, mean $15 \pm 4\%$, $n=12$, Fig. 3b), the trend functionally following that for carcasses (Fig. 4b). Significantly more dingoes ate carrion cattle in drought than flush periods (respective means $10 \pm 3\%$ occurrence, $n=5$; and $3 \pm 2\%$, $n=6$; $U=5$, $P < 0.05$), but overall the differences for fresh and carrion cattle, although following the same trend was not significant (respective means $25 \pm 8\%$ occurrence, $n=5$; and $8 \pm 1\%$, $n=6$; $U=10$, $P > 0.05$).

Red kangaroo. Their numbers averaged $20 \pm 6/100$ km over 21 surveys (Fig. 3c), there being many more during flush periods than drought (respective means $35 \pm 10/100$ km, $n=11$; and $3 \pm 1/100$ km, $n=8$; $U=11$, $P < 0.01$). In stomachs they averaged $17 \pm 3\%$ occurrence, $n=12$ (Fig. 3c), but in contrast to all other major prey, dietary frequencies were inverse to their abundance. Predation was most severe during drought when kangaroos were scarce (respective means $27 \pm 2\%$ occurrence, $n=5$; and $8 \pm 4\%$, $n=6$; $U=2$, $P < 0.01$). We have treated the relationships for drought and flush periods as independently functional in Fig. 4c to emphasise the difference.

Small mammals. They were prevalent during the early and late flush years of study but not during the intervening

drought (Fig. 3d). Overall a total of 267 small mammals (5 species) were trapped (mean $13 \pm 5/100$ trap-nights, $n=21$). They were mainly the feral house mouse *Mus musculus* (77%), with fewer numbers of the native sandy inland mouse *Pseudomys hermannsburgensis* (9%), long-haired rat *Rattus villosissimus* (the first record for this species in the region) (6%), brown hopping mouse *Notomys alexis* (6%), and the insectivorous marsupial, wuhl-wuhl *Antechinus spenceri* (2%). For 21 spotlight surveys a total of 605 small mammals were seen (mean $8 \pm 3/10$ km).

Whereas trapping results indicated higher population levels than transect counts earlier on, the reverse was true for the late study years (Fig. 3d). This may have been due to high vegetation in the late years which made spotlight observation difficult, and possibly to varying trappability between and within species during increasing and decreasing phases of their populations. Even so, both techniques indicated more small mammals during flush periods than drought (respective means $21 \pm 10/100$ trap-nights, $n=11$, and $4 \pm 3/100$ trap-nights, $n=9$; $U=28$, $z=1.71$, $P < 0.05$ vs $13 \pm 5/10$ km, $n=12$, and $0.04 \pm 0.04/10$ km, $n=8$; $U=13.5$, $z=2.84$, $P < 0.01$).

Overall there were 76 occurrences in stomachs (mean $19 \pm 7\%$ occurrence, $n=12$). They were the hopping mouse (37%), house mouse (32%), sandy inland mouse (11%), long-haired rat (5%), Forrest's mouse (*Pseudomys forresti*) (1%), dunnart (*Sminthopsis* sp.) (1%) and rodents of indeterminant species (13%). They formed a reasonable proportion of the diet during flush periods (mean $25 \pm 13\%$ occurrence, $n=6$, Fig. 3d), but were absent from stomachs during the early drought years. When rain briefly broke the drought in the summer of 1971/72, there was a small increase in the numbers of small mammals upon which the dingoes once more capitalised (mean $14 \pm 8\%$ occurrence, $n=5$, Fig. 3d). Predation was functional but significantly more severe during drought despite rarity (Fig. 4d).

Lizards. They were seen at all times but snakes were seldom seen. A total of 113 small lizards were dug out from quadrats (mean 4 ± 1 ha, $n=16$). They were the central netted dragon *Amphibolurus nuchalis* (89%), skinks (*Ctenotus* spp. 7%, *Ablepharus greyi* 1%), knob-tailed barking gekko *Nephurus asper* (2%), and legless lizard *Lialis* sp. (2%). There were more small lizards in flush periods than drought (respective means 5 ± 1 ha, $n=6$; and $2 \pm 1/ha$, $n=8$; $U=9$, $P < 0.05$) despite the increase in numbers of small lizards to a peak after the false break in the drought (Fig. 3e). There was no significant difference in the observed numbers of large lizards (sand monitor *Varanus gouldii*, bearded dragon *Amphibolurus vitticeps*) between flush periods and drought (respective means $0.08 \pm 0.05/day$, $n=9$; and $0.40 \pm 0.03/day$, $n=8$; $U=32$, $P > 0.05$).

There were 34 lizards in dingo stomachs of which 82% were the small central netted dragon (Table 1). Small lizards comprised 0–43% occurrence of the dingo's diet (mean $11 \pm 5\%$, $n=12$), and most were eaten following the false break in the drought (Fig. 3e). Figure 4e indicates that lizards were not important to the diet during flush periods (mean $2 \pm 1\%$ occurrence, $n=6$) despite their abundance but were so during drought ($21 \pm 9\%$, $n=5$) when abundance was lower.

Birds, insects and others. Few birds were eaten (0–9% occurrence, mean $3 \pm 1\%$, $n=12$) despite differences in abun-

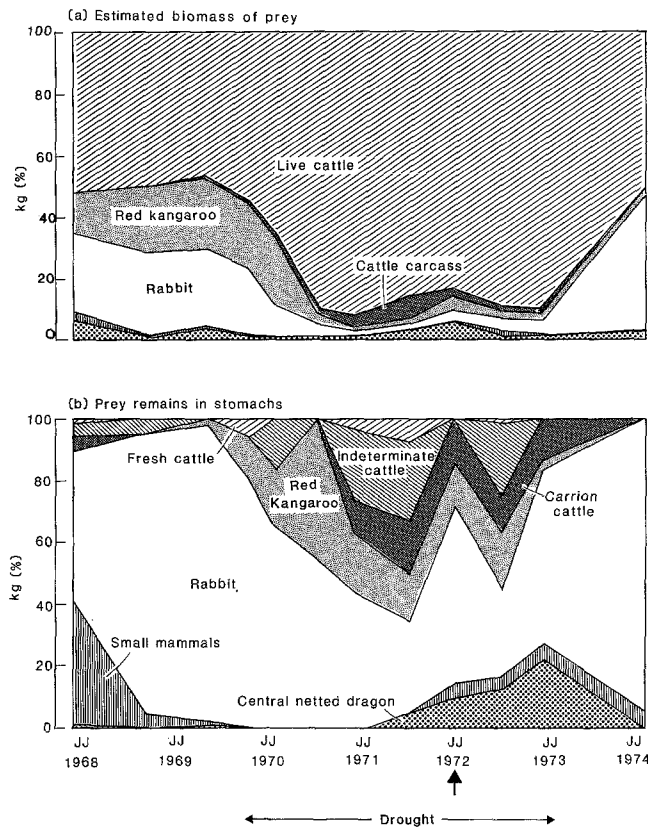


Fig. 5a, b. The relative biomass of prey **a** compared with the relative weight of prey in dingo stomachs **b**. The listed prey accounted for 96% of the total weight of food in stomachs (37 kg). The arrow indicates samples collected during the false break in the drought

dance as indicated by the zebra finch (Fig. 3f). Most were small passerines (Table 1). No attempt was made to estimate an index of abundance for insects. They were also unimportant being in only 4 dingo stomachs (undetermined species of beetle and grasshopper, Table 1). Another 2 stomachs contained mammal remains and berries respectively (both undetermined sp.).

Diet relative to prey biomass (Fig. 5)

The conversion of both diet and prey abundance to biomass illustrates clearly the importance of rabbits at all times, the high preference for small mammals when available and conversely for red kangaroos when rare during drought. Comparisons also indicate the selective value of lizards at some times and not others, and the great bulk of cattle though utilised little and mostly as carrion during drought. In comparison with large prey, the medium-sized and small prey together comprised the bulk of the dingo's diet (overall mean $70 \pm 7\%$, $n=12$, $U=19$, $P<0.001$; flush periods $87 \pm 6\%$, $n=6$, $U=0$, $P=0.001$; drought $50 \pm 8\%$, $n=5$, $U=10$, $P>0.05$) despite their low proportion of the biomass at all times (overall $17 \pm 4\%$, $n=12$, $U=0$, $P<0.001$; flush periods $29 \pm 5\%$, $n=6$, $P=0.001$; drought $5 \pm 1\%$, $n=5$, $U=0$, $P<0.01$).

Diet by age-class and sex of dingoes

There were no significant differences in the major categories of diet for 324 dingoes classified as mature (>18 months

old) or younger ($X^2_5 = 6.00$, $P>0.05$) or between sexes ($X^2_5 = 2.03$, $P>0.05$).

Discussion

Diet in relation to prey availability

Dingoes ate a wide variety of food (26 species), but mammals predominated (12 species, 97% occurrence). The species eaten most was the medium-sized rabbit (56%) which contrasts with studies elsewhere in Australia where large macropodid prey were recorded most frequently (Coman 1972; Corbett 1974; Whitehouse 1977; Shepherd 1981; Newsome et al. 1983a, b; Robertshaw and Harden 1985).

The rabbit comprised the bulk of the dingo's diet even during drought. Its importance was illustrated again during the false break in the drought. There was a sudden increase in the frequency of rabbit in the diet from 41% to a peak of 65% occurrence (Figs. 3a, 5b), but rabbit numbers did not appear to increase in response to that rain. This suggested that rabbits bred, but dingoes inhibited population growth, probably by eating most of the young as soon as they emerged from breeding burrows as recorded elsewhere for foxes *Vulpes vulpes* (Wood 1980) and feral cats *Felis catus* (Parer 1977). The capacity for predation to suppress growth of prey populations has been suggested for dingoes on rodents (Newsome and Corbett 1975) and demonstrated recently for rabbits by experimental removal of foxes and cats (A Newsome, I Parer and P Catling unpublished). Continued rain in the second flush period allowed rabbit numbers to increase again, despite heavy predation by dingoes (Fig. 3a).

Prey numbers varied greatly in response to the climate. For most prey the dingo's dietary responses were essentially functional with predation most severe during drought. However the frequency of prey remains in dingo stomachs were not always directly related to estimated biomass of prey. That result may be due to the extrapolations involved in estimating biomass, but it also suggests that dingoes preferred particular prey to others. Overall the dingo's dietary preferences in relation to prey biomass can be classified into 3 broad categories (Fig. 5): those prey sought all the time, but subject to large fluctuations in biomass during flush periods (rabbit, small mammals) or drought (dead cattle); those eaten inversely to absolute abundance, but only ever present in relatively small amounts (red kangaroo); and those eaten infrequently, but present either in large amounts (live cattle) or small amounts (lizards and probably birds).

Newsome et al. (1983b) defined prey as staples, supplementary, opportune and scavenged. Staple prey were those which dingoes could rely upon over time. Rabbits therefore were both the staple and preferred prey at Erldunda since they were eaten most consistently and most commonly. By contrast, in south-eastern Australia where the prey staples were also medium-sized mammals (rabbit, ringtail possum *Pseudocheirus peregrinus*), such prey did not comprise the majority of the diet. The large mammals did so. In that study, prey numbers changed markedly in response to a severe wildfire, just as for drought in this study. Some other studies of the dingo's diet elsewhere in Australia (Coman 1972; Corbett 1974; Whitehouse 1977; Shepherd 1981) did not estimate prey abundances and were of brief duration.

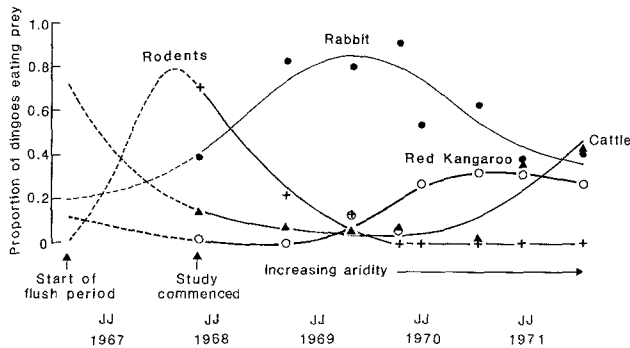


Fig. 6. Sequential predation on prey of increasing size in relation to increasing aridity. Broken lines indicate the probable emphases in predation back to the break of an 8 year drought prior to this study

Their inference that large macropodids are the staple prey of dingoes may therefore be suspect.

No other prey than rabbits comprised a consistent portion of the diet throughout the study period, so they may be defined as supplementary prey. Among them dingoes appeared to show a preference for small mammals and lizards since they constituted a relatively large part of dingo diet in relation to their small contribution to the total biomass during flush periods and the false break in the drought (Fig. 5). During drought when small and medium-sized prey were scarce, kangaroos were preferred to cattle since they were eaten in larger proportions relative to biomass (Fig. 5).

Sequential utilization of prey of increasing size (Fig. 6)

When great rains broke a severe and widespread drought at the start of this study, rodents erupted over widespread areas (Newsome and Corbett 1975) and dingoes concentrated on them for about a year (Fig. 6). The rabbits responded next and they predominated in the dingo's diet for 3 years. As rabbits declined in numbers during another drought, predation increased on the next largest species, the red kangaroo, even though it was uncommon. They are, however, forced to congregate around remaining food supplies during drought (Newsome 1965) and probably around waters and thus may have been more vulnerable to predation. With the prolonged drought the above-mentioned prey remained scarce, but cattle began to die and carrion became increasingly important in the diet.

Clearly there was sequential emphasis upon vertebrate prey of increasing body size as aridity increased. There are 2 important implications. First, the introduced and abundant rabbit and cattle now provide a major food resource for dingoes in central Australia whose numbers may therefore be much higher today than originally. In pre-European times, the abundance of probably all native prey species would have become very low during drought so that, with few permanent waters as well, dingoes would have starved or died of thirst. Second, since rabbits, cattle carrion and cattle waters buffer dingoes across droughts, predation upon red kangaroos (and other less numerous native prey) may be more severe than in previous times, and may prevent natural population increases at times as indicated above for the rabbit. The implications for red kangaroos are less clear, but their populations remained low following the drought (about 15% of their pre-drought level, Fig. 3c).

Table 2. Prey rank order^a in dingo stomachs

Prey	First flush		Second flush ^b		Drought ^c	
	%	Rank	%	Rank	%	Rank
Rabbit	69.0	1	90.0	1	43.2	1
Small mammals	25.6	2	20.0	2	13.8	5
Red kangaroo	9.2	3	0		27.1	2
Cattle (live and dead)	8.0	4	10.0	3	24.6	3
Birds	3.3	5	0		2.6	7
Lizards	2.1	6	0		20.7	4
Feral cat	1.3	7	0		1.8	8
Insects	0		0		3.5	6

^a Decreasing mean frequency of occurrence

^b Study terminated within the second flush period

^c Excludes data for the false break in the drought

At another site north-east of Alice Springs, red kangaroos had declined from being common in 1960 to very rare by 1968 after the long drought (Newsome 1975) and had not recovered, even by 1976. Dingoes had become increasingly common as rabbits became abundant (L Best unpublished) indicating that dingoes may mediate competition between rabbits, cattle and kangaroos to the detriment of the native herbivore, as suggested from indirect evidence by Caughley et al. (1980). Predation may be heaviest upon juvenile red kangaroos (80 of 83 kills, Shepherd 1981).

Do dingoes select the optimal diet?

Models of optimal diet (e.g. MacArthur and Pianka 1966; Schoener 1971; Rapport 1971; Pulliam 1974; Werner and Hall 1974; Charnov 1976) assume that the most valuable prey must provide high energy (calories, weight), be captured quickly (low search time) and easily (low handling time), and that the predators' environment be 'fine grained' (spatially homogeneous with constant food resources), and that predators make 'optimal decisions'. That is, predators are expected to behave as though they rank prey in order of value and estimate the nett rate of food intake from different diets. How the major predictions of optimal diet theory (see reviews in Pyke et al. 1977; Krebs 1978; Pyke 1984) relate to dingoes in central Australia are discussed below:

Prediction 1. When all prey are sufficiently abundant, a predator should select only the most valuable type(s) of prey. Although dingoes ate the same range of prey (except insects) throughout flush and drought periods (contra prediction 1), the rank orders were not significantly different ($r_s = 0.70$, $P < 0.05$, Table 2). Rabbits, the staple prey, were always ranked first regardless of abundance and climatic period and were eaten most in the second flush period with many lower ranked prey excluded from the diet. Rabbits are readily captured by free-living dingoes (Corbett and Newsome 1975) which consume about 7% of their body weight per day, which is about 1 kg of food and approximately the weight of a rabbit (Green and Catling 1977). These data support prediction 1 and suggest that rabbits are the most valuable food for a dingo.

However, during the first flush period, changes in the dingo's consumption of rabbits and rodents in relation to whichever species was most common (Fig. 3) conforms with

Table 3. Changes in the number of prey species in 285 dingo stomachs per sample

Sample no.	First flush period					Drought						Second Flush
	1	2	3	4	5	6	7	8	9	10	11	12
Total no./sample	12	9	6	3	5	5	5	6	8	12	8	3
No. deleted from previous sample		5	5	3	0	2	2	2	2	2	7	5
No. added to previous sample		2	2	0	2	2	2	3	4	6	3	0
No. new species ^a		2	0	0	2	1	1	1	1	5	1	0

^a Prey recorded in the diet for the first time

Murdoch's (1969) concept of prey switching and is contra optimal foraging theory since switching occurred within the same habitat.

Prediction 2. Inclusion of a prey in the optimal diet is independent of its own abundance, and depends only on the absolute abundances of prey of higher value. During flush periods when most prey were abundant, there was no evidence that dingoes specialised on prey of relatively low value. During the drought when all small and medium-sized prey were scarce, rabbits continued to predominate in the diet but as they became increasingly scarce, significantly more dingoes ate red kangaroos despite their rarity (Fig. 3a, c, Table 2). These data support prediction 2.

Prediction 3. As prey abundance declines, the diversity of prey in the diet should increase with prey added in order of value (i.e. predators will generalise). Conversely, an increase in overall prey abundance will lead to greater specialisation on prey of high value. The mean number of species eaten per sample during drought (7.3 ± 1.1) was the same as in the first flush period (7.0 ± 1.2) which contradicts prediction 3. However 10 'new' species were added to the diet during the drought (Table 3). They were all single occurrences, mostly small prey, and probably of low value. Conversely, dingoes increasingly specialised on rabbits as they became abundant during the second flush period (Fig. 3a, Tables 2, 3) despite increases in the abundances of other prey (Fig. 3). These data support prediction 3.

Prediction 4. Predators should not exhibit partial preferences (i.e. prey are completely included in the optimal diet or completely excluded). Except for rabbits, most of the 26 prey species eaten (Table 1) were deleted and/or added to the diet at least once throughout the study (Table 3). Such variable consumption of prey types contradicts prediction 4 (see Newsome et al. 1983b also).

Overall, the dingo's foraging behaviour was mostly in qualitative agreement with the predictions of classical diet models of optimal foraging theory. However, support or rejection of predictions was not unequivocal. The reasons for disparities between observed and expected results almost certainly related to the dingo's high preference for one particular prey (rabbits) and to the heterogeneity ('coarse grain') of the arid Australian environment in time and space. Thus many assumptions of optimal foraging models were not met as follows.

At all times the abundances of rabbits was paramount in deciding the dingo's food choice, rather than the abundances of other prey. This departure from predictions has also been found in some other studies (Jaeger et al. 1981;

Turner 1982; Visser 1982). The relative abundances of prey populations were not constant since they irrupted and fluctuated independently of each other and some became depleted. Further, dingoes often encountered different prey types simultaneously which partly explains the partial preferences observed in this study. In addition, other factors affecting fitness (sociality and access to resources, see below) not only further explains partial preferences, but belies the assumption that dietary choice does not influence an animal's ability to perform other tasks. Also differences in the catchability within and between prey species of different size and age probably does influence dietary intake and hence predator fitness. This constraint negates the assumption that fitness may always be realistically expressed as food or energy gain as concluded by at least 15 other studies (e.g. Zimmerman 1979; Houston et al. 1980; Waddington et al. 1981; Real et al. 1982).

Similar conclusions that classical optimal foraging models may not consistently predict predator behaviour in complex and fluctuating natural multifood systems, additional disparities, and modifications of theory have been derived empirically by other authors (McCleery 1977; Milinski and Heller 1978; Heller 1980; Lacher et al. 1982; Sih 1982; Milinski 1982; Richards 1983) or from literature reviews (Schluter 1981; Palmer 1981; Abrams 1982; Winterhalder 1983; Lucas 1983).

Prey selection by dingoes

If dingoes do not forage according to optimal foraging models at all times, what determines prey selection? The key issues involve prey choice in flush periods *vs* drought, probably prey availability *vs* abundance, and, of particular importance here, the flexible nature of dingo society.

The choice during flush periods is wide as live prey are abundant. At such times dingoes prefer to eat the smaller prey (rabbits and rodents) presumably not only because they are abundant and widespread (i.e. search time is low), but also because they are easily captured (low handling time). That is, nett energy gain per feeding time appears to be maximized. As the relative abundance of rabbits and rodents vary, dingoes consume a disproportionate amount of the most common of them (prey switching, Murdoch 1969). Although common, few other small prey (birds, lizards) are eaten, presumably because they are harder to catch. Since hunting time is low in flush periods ('time minimizers', Schoener 1971) and home range size reduced (L. Best unpublished), time is thus gained for other social activities. For dingoes, social activities appear to be important around watering points in arid areas because these

shared, dispersed, point resources may be controlled by a dominant group of dingoes (Corbett unpublished work).

During drought most native prey become rare and the dingo is faced with a limited choice of accessible prey if not with outright starvation. Dispersal from areas of food shortage is rarely an option, because droughts are widespread and dingoes are tied to localised home ranges (Newsome et al. 1973; L Best unpublished work). Searching time for preferred prey should increase as prey numbers decline and the proportion of successful hunts should fall. Dingoes appear therefore to be forced to change their hunting strategies and concentrate more on large prey ('energy maximizers', Schoener 1971) despite the high handling costs. Again the importance of dingo sociality is highlighted since packs are necessary to capture red kangaroos and live cattle. Other examples are hyaena *Crocuta crocuta* (Kruuk 1972), lion *Panthera leo* (Schaller 1972), hunting dog *Lycan pictus* (Estes and Goddard 1967). But such hunting by the dingo, as indicated by the diet, appears to be uncommon, or else the proportion of successful hunts is very low. Eventually many cattle die and provide accessible food; but other costs may be involved in exploiting carcasses. A tightly-knit social group may sometimes be necessary to withstand competition from other dingo groups, and all the individual group members may not be guaranteed an adequate food share because of the dominance hierarchy within packs (Corbett unpublished). This could also introduce problems in sampling dietary intake (via stomach contents) since the diets of high and low ranking dingoes may be different.

Prey switching by dingoes: a model of diet relative to prey availability

The changing emphasis in predation from small to large prey as drought developed (Fig. 6) provides an important extension to Murdoch's (1969) concept of switching (see Murdoch and Oaten 1975 also). Dingoes selected in turn the most available prey, irrespective of habitat, preference or body size, and largely independent of absolute abundance or biomass (Fig. 7). Despite the smaller biomass, the fluctuating abundance of small and medium-sized prey always determined the relative availabilities of both themselves and other larger prey and hence their consumption. This concept of 'alternation of predation' on the most available prey is presented as a general model (Fig. 7) to incorporate relationships of diet, prey size and climatic regimes. The model is based on actual data points and indicates that dingoes will select small and medium-sized prey (mainly mammals) during flush periods, and large prey (also mainly mammals) during drought. Whenever small to medium-sized prey 'reappear' (however briefly) following periods of scarcity, dingoes will immediately switch to them.

The inherent tenet of this model is that dingoes adopt a feeding strategy to gain at least a threshold aliquot of energy or nutrient. This concept has been previously suggested e.g. Simon's (1955, 1956) model of 'rational choice' (also see discussion in McCleery 1978; Janetos and Cole 1981; Myers 1983). In the capricious environment of arid Australia where prey availability fluctuates greatly and prey are often encountered simultaneously, constraints are imposed on the dingo to always select the most valuable prey. The dingo must be risk-prone (Caraco 1980; Caraco et al.

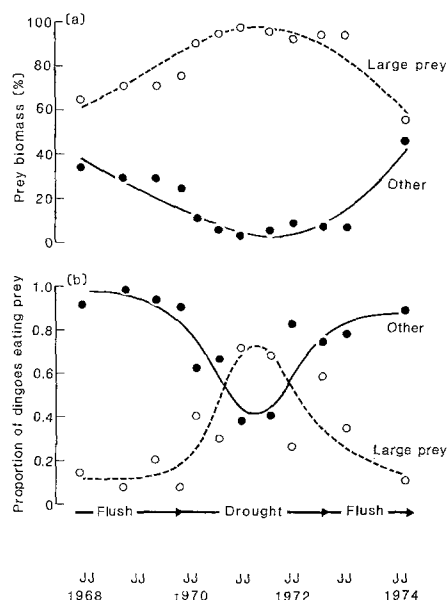


Fig. 7a, b. The model of alternation of dingo predation depending upon climatic fluctuations. **a** Changes in relative prey biomass. **b** Changes in predation in relation to prey body size. Large prey are kangaroos and cattle. Others are all small and medium-sized prey. Curves were fitted by eye through data points

1980) and seek a trade-off between foraging and other ecological requirements affecting fitness including maintenance of social bonds, defence of resources and avoidance of physiological stress. The foraging behaviour of dingoes therefore can be consistent with predictions of all models (optimal, sub-optimal, non-optimal and their various extensions) depending on environmental circumstances. It may be that all foraging behaviours are part of a continuum of strategy sets involving just one model simply embodying foraging theory.

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