FAUNA
of
AUSTRALIA

54. CANIDAE

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Dingo–*Canis lupus dingo* [CSIRO Wildlife & Ecology]

Fox–*Vulpes vulpes* [CSIRO Wildlife & Ecology]

DEFINITION AND GENERAL DESCRIPTION

The family Canidae comprises the foxes, jackals, wolves and dogs. Only the Dingo (*Canis familiaris dingo*) was present in Australia when Europeans reached it, but the Dog (*Canis familiaris familiaris*), and the European Red Fox (*Vulpes vulpes*) were introduced. Canids may be solitary or social and they are carnivorous to omnivorous. Most are seasonal breeders producing a single litter each year. The skull is elongate and the dental formula is I 3/3 C 1/1 PM 4/4 M 2/3, though the number of molars may vary with the species from 1/2 to 4/5. A well-developed baculum is present.

The Dingo is a member of the group of primitive dogs and is predominantly carnivorous. Although individuals do belong to social groups, dingoes are usually seen alone. Unlike domestic dogs, dingoes are seasonal breeders (Corbett & Newsome 1975).

The Fox, a small-sized member of the family Canidae, although an opportunistic omnivore, is predominantly carnivorous, taking both live prey and carrion. It generally is regarded as a solitary species, although studies (Macdonald 1980) suggest that it can form social groups like those seen in wolves and some other canids.

HISTORY OF DISCOVERY

Although Australia is thought of as the land of marsupials, one quarter of the native mammals are eutherians. Dingoes were reported by Dampier and the Dutch explorers in the late 1600s and examples were returned to England before the end of the 18th Century by early settlers. The Dingo is a recent arrival, geologically speaking, and did not reach Tasmania, which became an island about 10 000–11 000 years ago (Mulvaney 1975). When, how and from where the Dingo arrived are uncertain. The oldest and best accredited fossil date is 3450 ± 95 ybp (Milham & Thompson 1976). There are doubts about older dates of about 8000 ybp for remains, due to problems with stratigraphic interpretation (Macintosh 1975; Mulvaney 1975; White & O'Connell 1982).

It is reasonable to assume that the Dingo came with human help. The assumption that 'the first Aboriginal and his wife and his dog and his dog's wife' came together (Jones 1921b), however, is an outmoded view in many ways, not least because the Aborigine has been here a good deal longer than 8000 years.

The date of the first introduction of European foxes to Australia is not known beyond doubt, but newspaper reports suggest that the animals could have been introduced into Victoria and New South Wales from 1845 onwards (Rolls 1969). Successful releases probably did not occur until the 1870s when several foxes were released in the Ballarat and Geelong areas of Victoria (Rolls 1969).

MORPHOLOGY AND PHYSIOLOGY

No one general text describes the canid skeleton, locomotion, general physiology, sense organs etc. Most of the information available relates to the domestic dog although this is often given in a comparative context with other mammals and vertebrates. Young (1962) examined the evolution and structure of all vertebrates and included a separate chapter on the carnivores. 'Dukes Physiology of Domestic Animals' 8th edition (Swenson 1970) provided great detail on the Dog: circulation, metabolism, water balance, skeletal muscle, reproduction and lactation etc., and the 7th edition (Dukes 1955) lists topics conveniently under 'dog' in the index. Specific anatomical details are covered by Ellenberger, Brown & Dittrich (1956). Schmidt-Neilsen (1964; 1972)

provided examples of comparative allometric studies on aspects of the environmental physiology of members of this family. Schmidt-Neilsen (1972), in particular, discusses the importance of nasal counter-currents of inhaled and exhaled air to desert animals for their water conservation. Fox (1975b) provided a compendium of what was then known of the systematics, behavioural ecology and evolution of the Caninae, species by species.

External Characteristics

The external conformation and basic skeletal characteristics of the Dingo and the Fox are similar to those for other canids, but the leg lengths of the Fox relative to the length of its spine are greater than those for most other members of the Canidae (Lloyd 1980).

The Dingo is a medium-sized dog with a head and body length of 860–980 mm and a tail length of 260–380 mm. Adults weigh 10–20 kg. The 'standard' colour is ginger with white feet, chest and tail tip, though animals of other colours including black and white are found. Experimental acclimation of animals to high and to low temperatures led to fur density that was three times higher in the dingoes in the cold than in the heat (Shield 1972). This response of the fur to cold conditions helps explain the longer fur found among the animals in the highlands of south-eastern Australia.

In southern Australia, the weight of adult foxes ranges from 3.5–7.5 kg. Total length, including tail, is 950–1150 mm. The tail is exceptionally long and accounts for some 35% of the total length so that head and body length is about 650–750 mm. The main body colour is reddish to yellowish-brown. The underparts are white or off-white and, rarely, grey or black. The white colouration of underparts extends to the chin and usually, to the upper lip. The tips and backs of the ears and the lower parts of the legs, including feet, are black or dark brown. There is a dark eye stripe. The tip of the tail is generally white, but in some animals this is much reduced or absent. Variations in basic fur colour pattern are considerable; some animals appear very light yellow and others a rufous red.

Physiology

The gut is short and simple as expected in a carnivore. Free-living dingoes consume about 7% of their weight in food per day (Green 1978). The physiology of the Dingo is not remarkably different from that of the Dog and there is no evidence of special physiological adaptations to the Australian environment. Thus, biochemically, of the 11 measurements of metabolism of the red blood cell taken by Agar & Green (1979), only one showed a significant difference (Table 54.3). While at the level of the whole animal, the conclusion was that this species has not changed its ability to tolerate extremes of temperature despite over 3000 years of isolation in Australia (Shield 1972).

The water physiology of dingoes in Australian desert regions shows no remarkable adaptation (Baverstock & Green 1975; Green & Catling 1977). They must drink. About 12% of their body weight a day is needed in summer and 7% in winter. On very hot days (>40°C), they may drink morning and evening. During lactation, water needs are even higher and would be more but for a behavioural pattern of the bitches (Baverstock & Green 1975). The mother elicits excretion from the pups by appropriate licking and then ingests the faeces and urine. This is not just an act of hygiene, for the mother recovers in this way more than 30% of the water provided in milk to the pups. Such recycling of water is found in many Australian mammals (Baverstock & Green 1975). As pups get bigger in the warmer weather, a mother is known to return and regurgitate water for pups who lick from her mouth (Newsome *et al.* 1973). The

provision of many watering points by the sheep and cattle industries has almost certainly increased the Dingo population, as has the invasion of the Rabbit (*Oryctolagus cuniculus*) which often forms the main item in the diet. Livestock that die during droughts also help dingoes survive prey shortages (Corbett & Newsome 1987).

Reproduction

Dingoes breed during winter when water needs are at their minimum. Male animals in central Australia have a testicular cycle, but not when transferred to the cooler climates of Canberra, where sperm and matings are produced even in summer (Catling 1979). The breeding season is similar in both regions, however, and determined by the females. Catling (1979) shows that the male reproductive hormone, testosterone, increases in the blood from 5.7 ± 0.6 ng ml-1 in the non-breeding season to 17.4 ± 1.8 ng ml-1 around the time of mating, probably in response to oestrus and independent of sperm production.

The female Fox is monoestrus, the period of oestrus being from 1–6 days. In southern Australia, oestrus can occur from late June through to early August (McIntosh 1963b) although Ryan (1976b) produces evidence of oestrus occurring outside this time period. In Britain, Switzerland and Sweden, there is a clear latitudinal-timing of breeding for the Fox and Lloyd (1980) believes that the probable evolutionary reason has to do with providing optimum opportunity for cub survival. There is no detailed understanding of the timing process, but it may well be determined by sensitivity to light at some phase in the endogenous rhythm of the animal as with many birds and mammals.

Both sexes are usually capable of breeding—at about 10 months of age—in the season following that of their birth. The reproductive system and process follow the general pattern for the Canidae. The only notable difference is that in foxes, sperm penetration cannot take place until the secondary oocyte spindle stage has been reached (Pearson & Enders 1943). McIntosh (1963b) and Ryan (1976b) have both reported a maximum of spermatogenic activity for males in winter and little or no spermatogenic activity in summer.

There is evidence that the Fox is monogamous and that pairs remain together for as long as both members remain alive. The gestation period is 52–53 days and pseudo-pregnancy in unmated or sterile vixens lasts for about 40 days. Weight of embryos at birth is about 70–100 g and the growth rate of embryos follows the general curve described by the formula of Huggett & Widdas (1951) for placental mammals.

Research in the Northern Hemisphere suggests that a proportion of adult vixens in any given population may be non-productive (Englund 1970; Lloyd 1975) and, in Australia, McIntosh (1963b) and Ryan (1976b) produce some evidence of barren females. Nonetheless, the real extent of barrenness in adult vixens from various habitats in Australia is unknown.

Embryology and Development

Litter sizes in dingoes are normally three to five, but can be as low as one or as many as eight. Growth and development follow the same pattern as is seen in domestic dogs. The sex ratio is even. Young dingoes are capable of breeding during the next annual breeding season, but social constraints within the group may delay breeding for at least another year. As with many species, many young do not survive, but some animals live to an estimated age of 10–12 years in the wild.

Mean litter size for foxes in southern Australia has been estimated at 4.3 by McIntosh (1963b) and 3.7 by Ryan (1976b). Subsequent investigations, however, suggest that litter sizes may vary from year to year and place to place (B.J. Coman unpublished data). Similar variations have been reported for this species in the Northern Hemisphere by Lloyd (1980).

Cubs are born and raised in a den which, in Australia, is commonly an enlarged rabbit burrow previously excavated by the vixen. Other den sites include hollow logs and rock piles. At birth, cubs are covered with short grey fur which changes to dark brown within a few weeks. The eyes and ears open at 12–14 days. Cubs begin eating solid food at about 4 weeks of age and, shortly thereafter, they begin to emerge from the den. The young animals gradually explore the immediate environs of the den and enlarge their range until, at 8–10 weeks of age, they effectively abandon the natal den and rely solely on surface cover. Nonetheless, the natal den or, indeed, any available rabbit warren or hollow log may still be used by large juveniles as a form of daytime cover. Very often, cubs at the 'exploratory' stage will occupy two or more discrete dens, usually within a few hundred metres of each other. This occurs when some members of the litter from the original natal den take up residence in nearby rabbit warrens or other available 'den' sites.

The population biology of foxes in Australian habitats has not been reported in any detail although aspects such as age structure and sex ratios have been mentioned in the literature. On the basis of eye lens weight, Ryan (1976b) estimates that some 50–80% of a sample of animals shot in spring and summer were juveniles. The upper estimate is uncommonly high and current studies, using more accurate techniques of ageing, suggest that for foxes shot during the April-August fur season in Victoria, at least 54% of all animals are less than 1 year old and 71% are less than 2 years old (B.J.Coman unpublished data). Few animals survive beyond 4 years.

NATURAL HISTORY

Ecology

Mammals comprise the main diet of dingoes, but the actual species and amounts of various size classes of prey depend on locality and abundances (Table 54.1). Mostly medium- and large-sized prey are utilised. For example, in central Australia where large native mammals are uncommon, medium-sized mammals (mostly the Rabbit) predominate in the diet (Corbett & Newsome 1987). The opposite is the case for inland Western Australia where Red Kangaroos (*Macropus rufus*) and the Common Wallaroo (*M. robustus)* are quite abundant, but the medium sized rabbit is uncommon (Whitehouse 1976). Small mammals are usually unimportant to the diet, but may be taken when in plague numbers (Corbett & Newsome 1975; 1987) (Table 54.1, central Australia). Certain species, for example, possums and wallabies in eastern Australia, are important to the diet of the Dingo (Coman 1973a; Newsome, Catling & Corbett 1983b; Robertshaw & Harden 1985a; 1985b) – there are no wallabies of similar size in inland Australia.

An extra factor involved in prey selection for the Dingo is pack size. For example, the larger dingo packs found in the Snowy Mountains occasionally catch one of the wild Horses found there (Newsome *et al*. 1983b). Where horses are eaten, so are other large prey (wombats and kangaroos) regardless of their abundance. Large packs may be a response to the presence of horses. Even though caught infrequently, the profit in terms of food per dingo is worthwhile. In a study of Spotted Hyaena (*Crocuta crocuta*), Kruuk (1972) found that for

Table 54.1 Regional diets of the Dingo (% occurrence). 1. Robertshaw & Harden (1985b); 2. Newsome *et al*. (1983a); 3. Newsome *et al*. (1983b); 4. Whitehouse (1977); 5. L.K. Corbett & A.E. Newsome unpublished data; a. *Perameles* and *Isoodon* for Temperate and *Macrotis* for Arid; b. *Potorous* and *Thylogale* for Temperate and *Lagorchestes*, Nail-tail Wallaby and Rock Wallaby for Arid; c. Grey in Temperate, Red and Euro in Arid; d. Swamp Wallaby and *Macropus* in Temperate.

PREY	TEMPERATE ZONE				ARID ZONE	
	New England [1]	Nadgee Nature Reserve [2]	Kosciusko National Park [2]	Gippsland [3]	Western Australia [4]	Central. Australia [5]
SMALL SIZE MAMMALS						
Marsupial mice	4.5	3.7	4.1	0.3	1.4	0.7
Rodents	14.1	16.1	4.4	1.4	2.1	25.4
	(18.6)	(19.8)	(8.5)	(1.7)	(3.5)	(26.1)
MEDIUM SIZE MAMMALS						
Echidnas	3.9	0	-	7.0	1.4	0.3
Bandicoots [a].	6.0	3.5	-	0.6	0.7	0.1
Possums	14.6	18.3	16.6	11.6	-	-
Smaller Wallabies [b].	5.8	0.9	-	0.5	2.1	1.5
Rabbits	5.3	10.2	17.8	7.8	5.5	37.7
Feral foxes	0	0	0.1	1.6	0	0.1
Feral cats	0	0	0	0.3	0.7	1.8
	(35.6)	(32.9)	(34.5)	(29.4)	(10.4)	(41.5)
LARGE SIZE MAMMALS						
Kangaroos [c].	0.2	5.0	2.9	5.9	66.9	10.2
Wombats	-	2.1	51.3	12.9	-	-
Larger Wallabies [d].	47.8	41.1	19.4	50.8	-	-
Feral pigs	-	-	-	4.0	-	-
Feral goats	-	-	-	-	2.1	-
Feral donkeys	-	-	-	-	-	0.3
Feral horses	-	-	1.3	0.3	-	1.7
Sheep	0	-	-	4.8	-	-
Cattle	0	-	-	2.4	0.7	1.7
	(48.0)	(48.2)	(74.9)	(81.1)	(69.7)	(13.9)
OTHER						
Birds		14.3	0	2.4	15.3	11.6
Reptiles		-	0	1.9	5.6	14.1
Fish	3.9	-	-	0.3	-	-
Cattle	(inclusive)	-	0	2.7	-	21.3
Insects		-	0	4.4	5.5	4.0
	(3.9)	(14.3)	(0)	(11.7)	(26.4)	(51.0)
SAMPLE SIZE	1726	1102	314	372	160	1464
	(faeces)	(faeces)	(faeces)	(stomach)	(stomach)	(stomach)

every doubling in weight of a prey killed, three times the number of hyaena were fed. Indeed, the hyaenas organise large packs to travel some distance to hunt the scarce zebra (*Equus burchelli*).

The issue of the killing of livestock by the Dingo is not a straightforward matter (Thompson 1984). Nonetheless, the distribution of this species essentially determines whether sheep or cattle are run throughout Australia, although parts of Western Australia are exceptions. Dingoes certainly do kill stock, calves and sheep, but it may not be the killing that is the worst of it, rather the maiming and forced mismothering due to separations of cow and calf or the 'herding' of sheep in paddocks. Of 421 dingo stomachs collected in south-eastern Australia (Table 54.1), only 10 contained remains of sheep that were not carrion (Newsome *et al*. 1983a). Seven other dingoes contained carrion, but two of them were obtained from dead sheep used as lures by 'doggers' trapping for dingoes in the forest. Three of nine animals containing cattle remains also had eaten from lures. Against these low scores, 4% of dingoes had eaten feral pigs and 8% rabbits, both known pests, and 70% had eaten wombats, wallabies and kangaroos which utilise pastures grazed by sheep and cattle. The balance is not easy to strike (see Coman 1985; Oliver 1980). Stock losses have been impossible to gauge accurately; what is clear is that native herbivores and rabbits are overwhelmingly preferred as food by dingoes. Whether killing of calves is economically wasteful during drought is also debatable (Newsome *et al*. 1973); much depends on the length of the drought, and a breeding cow whose calf is killed by dingoes will have a better chance of surviving a long drought.

The diet of the Fox has been well studied both in southern Australia (Brunner, Lloyd & Coman 1975; Coman 1973a; McIntosh 1963a; Ryan & Croft 1974) and overseas (see Lloyd 1980). These studies indicate that this species is an opportunistic feeder, taking a wide range of animal and vegetable foods. Nonetheless, the fox is primarily a carnivore, preying on smaller mammals or feeding from the carcasses of larger ones. There are marked seasonal and habitat differences in diet (Table 54.2). In areas of agricultural or pastoral land in Australia, sheep (as carrion), rabbits and mice are the most important mammalian foods eaten. In alpine forest country, however, smaller native mammals are consumed in larger quantities and appear to substitute for the lack of sheep and house mice in these situations. Insects, fruit and herbage often feature prominently in the diet, but in terms of volume they are generally insignificant. Exceptions may occur at times when blackberries or other wild fruits are available or when there is a massive emergence of certain insect species (Coman 1973a). Foxes have been shown to be important predators of rabbits in inland Australia (Wood 1980). Together with feral domestic Cats (Felis catus), they can continue to suppress populations of rabbits reduced by drought for 2–3 years (Newsome, Parer & Catling (1989). There is also ample evidence that predation by foxes (Fig. 54.1) on native animals is a major threat to native ground-dwelling mammals and nesting birds, many of which are endangered or vulnerable

In terms of habitat requirement, the Fox is perhaps one of the most unspecialised wild canid. The huge geographical range of the animal, both in Australia and overseas, is evidence of its adaptability. In Australia, as elsewhere, foxes are found in habitats ranging from city parks and urban wasteland through heavy forests and into desert country.

Basically, the Fox is a surface dweller, but requires secure cover, usually below ground, for rearing cubs. Outside the breeding season, the animal also requires some form of cover for 'laying up' during the day. Thickets of bush or scrub, areas of high grass, rock piles, hollow logs and leaning trees are all utilised for
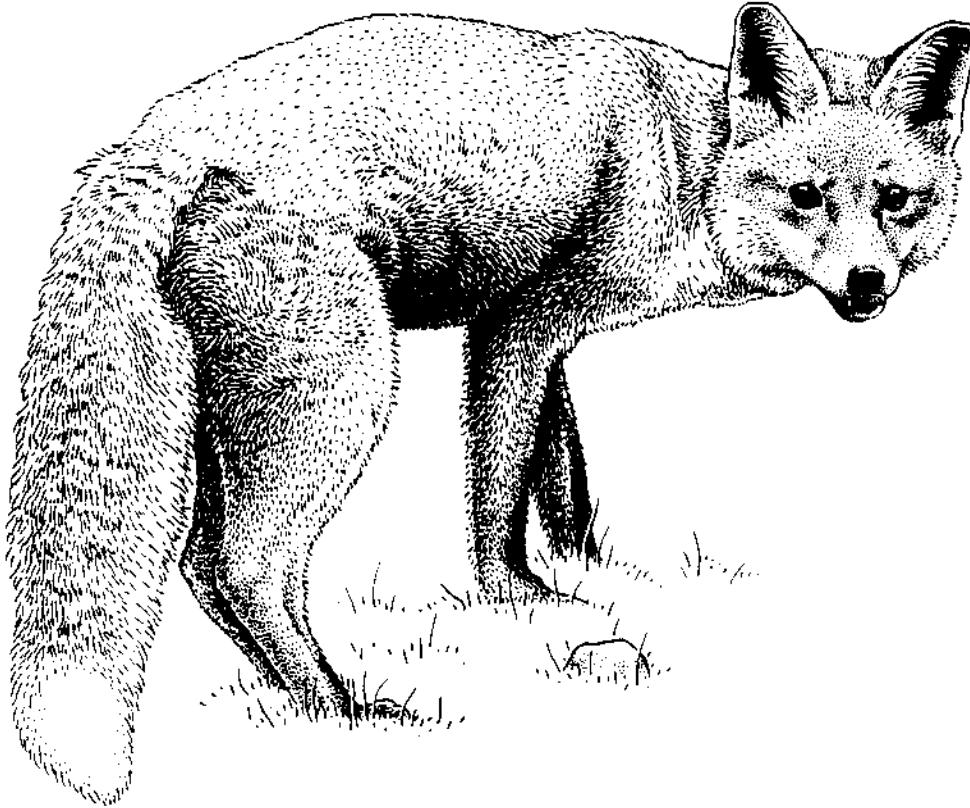
Figure 54.1. Removal of the threat to native wildlife by eradication of foxes on mainland Australia is not presently feasible. However, threat abatement, including development and implementation of effective control programs provides a means of minimising the threat. The plan for foxes places emphasis includes minimising predation on wildlife in areas of high conservation priority by controlling fox numbers. The plan may be viewed (Environment Australia 1999b) may be viewed at **http://www.biodiversity.environment.gov.au/plants/threaten/plans/ threat_abatement_plans/land_degradation_by_foxes/index.htm**. (© Environment Australia). [K. McInnes]

Table 54.2 The percentage occurrence of various food items in the diet of foxes taken from farmlands and heavy forest. (Adapted from the data of Coman 1973a and Brunner *et al*. 1975)

SPECIES EATEN	PERCENTAGE Farmlands	OCCURRENCE Heavy forest
Rabbit	39	19
Sheep	31	neg.
Mice	26	3
Native mammals	11	48
Birds	20	17
Insects	36	43
Vegetable matter	57	37
Other	19	37

daytime concealment. Adolescent animals often continue to use the natal den or neighbouring rabbit burrows for daytime concealment. When severely harassed, adult animals too will often 'go to earth'.

Population densities of foxes have not been determined accurately in Australia. In prime habitat with ample food and cover, the minimum winter density is of the order of three foxes per 2 km^2 (B.J. Coman unpublished data). In summer and early autumn of each year, this figure is much higher as young animals appear in the population. These density estimates are similar to those reported in the United Kingdom (Lloyd 1980) and exceed those reported in many parts of Europe (Lloyd *et al*. 1976).

Aspects of interspecific and intraspecific competition for the Fox and Dingo in Australia are not known. The ranges of foxes, dingoes and feral cats, however, overlap in many areas and there is no clear evidence of serious competition; but for unknown reasons, where dingoes are common, foxes are not, and vice versa across a number of habitats (A.E. Newsome, P.C. Catling & L.K. Corbett unpublished data). The position regarding competition between the Fox and marsupial carnivores is unknown, but the presence of larger dasyurids in higher population densities in Tasmania (fox and dingo free) than in mainland Australia could be taken as indirect evidence of competition on the mainland.

Disease: Dingoes harbour the same parasites as domestic Dogs and suffer from the same diseases. Some of these diseases and parasites may debilitate this species and even provide a degree of biological control. For example, an outbreak of the viral disease, distemper, decimated populations across the Barkly Tableland, N.T. in 1969-70, killing up to 90% of animals (Newsome *et al*. 1973). In captivity in central Australia, dingoes inoculated against distemper regularly died from canine hepatitis until also immunised against this disease (L.K. Corbett unpublished data).

There are a few diseases and parasites which may cause problems to dingoes in the wetter south-eastern parts of Australia (Newsome *et al*. unpublished). One parasite, *Oslerus* (formerly *Filaroides*) *osleri*, recorded only rarely before in Australia, proved to be common in dingoes (Dunsmore & Burt 1972; Dunsmore & Spratt 1979; Newsome *et al*. 1973). This nematode forms cysts in the bronchae, partially blocking them. In domestic dog pups, the cysts can cause death. An external parasite, the bandicoot tick, *Ixodes holocyclus,* can cause tick fever or tick staggers, known to be fatal in domestic dogs.

Mange is caused by minute mites which infect hair follicles causing baldness in the affected area. General mange (and total baldness) is caused by *Sarcoptes scabei*. There is a localised mange of the upper snout called demodectic mange caused by another mite, *Demodex canis*, which can be very troublesome in captive Dingoes. The ear canker mite, *Otodectes cynotis*, may also occur on the Dingo.

An array of intestinal parasites is present in dingoes from south-eastern Australia (Table 54.3; Newsome *et al*. unpublished). One of these, the tapeworm *Echinococcus granulosu*s (hydatids), is of human concern and is found in dingoes and dogs. Its intermediate host is a herbivore, usually sheep, and kangaroos and wallabies, prior to parasitising Dogs and Dingoes respectively; there is a domestic and a wild (or sylvatic) cycle for the parasite with differing strains of *E. granulosus*, respectively (Gemmel 1959; Coman 1972; Arundel 1979; Thompson 1979; Kumaratilake & Thompson 1984; Thompson & Kumaratilake 1985). In an intermediate host the parasite forms the hydatid cyst which contains myriads of scolices, the 'hydatid sand'. The cyst is usually in the lungs or liver and can grow quite large, enfeebling the host. If eaten by a Dog or a Dingo, each scolex can develop into a tapeworm, so continuing the cycle.

Human beings can be affected as intermediate hosts. Ingestion of the tapeworm's eggs results from handling infected *Canis*. Hydatid cysts form in the lungs, liver and brain, causing medical problems.

Table 54.3 Infection rates of helminths in Dingoes and related canids in south-eastern Australia (%)*; (n = sample size); *from Newsome *et al*. (ms).

LOCALITY	ECHINOCOCCUS GRANULOSUS	OTHER INTESTINAL CESTODES	INTESTINAL NEMATODES
Southeast N.S.W. (n = 53)	90.4	75.5	62.7
Forested Ranges (n = 282)	80.1	47.2	60.3
Subalpine & Alpine(n = 233)	74.2	52.6	71.1 (62)
Means	78.6	51.7	63.8

Up to 90% of dingoes in south-eastern Australia are heavily infected with *Echinococcus granulosus* tapeworms (Table 54.3) (Newsome *et al*. unpublished). Infection rates of *E. granulosus* are similar in dingoes, feral dogs and hybrids; animals aged 1–4 years have the heaviest infections.

The other intestinal cestodes found are *Taenia pisiformis* (also found in central Australia because the intermediate host is the Rabbit), *T. serialis*, *T. hydatigena*, *Spirometra erinaceae*, *Uncinaria stenocephala* and *Dipylidium caninum*. The following nematodes are found: *Toxocara canis*, *Ancyclostoma caninum*, *Trichuris vulpis* and *Cyathospirura dasyuridis* (Coman 1972). Note that many of the intestinal helminths are in foxes as well (see below).

Newsome *et al*. (unpublished) also reported the heartworm, *Dirofilaria immitis*, in one dingo from south-eastern New South Wales and an unknown acanthocephalan from an animal in central Australia (A.E. Newsome unpublished data). One further unusual parasite inhabits the nasal sinus of dingoes and other canids and must cause discomfort. The adult of a pentastomid arthropod, *Linguatula serrata*, is quite sizeable, 20–40 mm long, and has hooks on the head to anchor it.

Demodectic mange is both widespread and common in Australian foxes and there is presumptive evidence of serious summer/autumn outbreaks in some years. There is little doubt that animals can succumb to the disease as severely affected animals showing extreme loss of hair are commonly emaciated. Other ectoparasites are usually innocuous. Fleas, particularly *Ctenocephalides canis*, are common and lice (species of *Heterodoxus* and probably *Trichodectes* and *Linognathus*) less so. Species of ticks probably occur on foxes in Australia, but there is no published record.

The gastrointestinal helminth parasites of Australian foxes have been well studied, largely because of an earlier presumed involvement of some species in the spread of ovine cysticercosis. In fact, *Taenia ovis* and *Taenia hydatigena*, the two common causes of cysticercosis in sheep, are either rare or absent in Australian foxes (Coman 1973b; Ryan 1976a) and the hydatid tapeworm, *Echinococcus granulosus,* has been found only on two occasions (R.C.A. Thompson personal communication 1985). The common tapeworms in Australian foxes are *Taenia pisiformis*, *Taenia serialis* (both with intermediate stages in rabbits) and *Dipylidium caninum*. The pseudophyllid, *Spirometra erinace*i, is also very common. Perhaps the most prevalent helminth parasite of the Fox in Australia is the roundworm *Toxocara canis*, although hookworms (*Uncinaria stenocephala* or *Ancyclostoma caninum*) are also ubiquitous. Other fox nematodes reported from Australia include *Cyathospirura dasyuridis*, *Trichuris vulpis* and *Oslerus osleri*. The prevalence of lungworms is unknown.

In general terms, few if any of the helminth parasites could be regarded as serious pathogens of the Fox. Since heavy infections of roundworms and hookworms can cause severe problems for the young of domestic dogs, these same parasites may be of significance in the survival of cubs. In Australia, there is no evidence to suggest that the Fox is involved in the persistence or spread of any disease which has a major economic or public health significance. Nonetheless, animals do harbour a wide range of diseases and parasites which may or may not exert some pathogenic effect upon their hosts. The extent and significance of common canine viral diseases such as distemper, hepatitis and canine parvovirus are unknown.

Dispersal and Home Range: Wherever rabbits are common in inland Australia beyond the Dingo Barrier Fence, dingoes are most abundant. There is a direct relationship between dingo numbers and food in central Australia. Animals are twice as abundant in the better watered valleys among the ranges, where the food supply is best, than in the rugged ranges themselves or in the desert (Table 54.4) (Newsome *et al*. 1973). Packs of two to five Dingoes in south-eastern Australia range over areas of about 5–15 km^2 (A.E. Newsome & P.C. Catling unpublished data).

Table 54.4 Indices of Dingo abundance and the food supply across habitats in central Australia. (After Newsome *et al*. 1973)

HABITAT	MEAN NO. OF DINGOES WATERING	MEAN INDEX OF FOOD ABUNDANCE
Wide valleys among mountain ranges	4.8	2.1
Open plains flanking the ranges	4.0	1.6
Rugged ranges	2.7	1.2
Desert	2.4	1.2

There is little or no evidence that Dingoes travel up to 75 km and back to attack stock as is reported anecdotally nor that they migrate 200 km from ranges to the coast to breed in the winter, returning in the summer in south-eastern Australia. Rather, dingoes that have been caught, radio-collared and released are remarkably localised in movements, with 75% of resightings within 6 km of the release point (Newsome *et al*. 1973). The largest movement observed was 34 km along a valley.

Dispersal in fox populations has been well studied in other countries, largely because of its significance in the spread of rabies. These studies indicate that dispersal generally occurs when cubs are 6–9 months old and that these juveniles disperse quite randomly. Mean dispersal distances have been quite variable but generally less than 20–30 km. Nonetheless exceptional movements of over 100 km have been recorded. Most of the longer movements have involved males rather than females (Storm *et al*. 1976; Lloyd 1980;). Current studies in Victoria indicate a similar dispersal picture for foxes in southern Australia (B.J. Coman unpublished data) with dispersal taking place in autumn when the cubs are 7–9 months old.

Overseas studies indicate that foxes establish and maintain home ranges, the size of these being variable, but generally in the range from 400–1600 ha (Lloyd 1980). Local studies suggest that home ranges are similar here (B.J. Coman unpublished data). Territoriality is indicated by scent marking with faeces and urine and by aggressive interactions. Recent studies from the United Kingdom (Macdonald 1980) suggested that not all territories comprise of one breeding pair only. In some habitats, foxes live in social groups comprising one adult

male and several adult vixens. This has important ramifications for, as Macdonald (1980) has pointed out, it can lead to reproductive suppression. This would explain the widely different figures for proportions of barren vixens in populations studied in different regions. Lloyd (1980) has also described a primary unit of dispersion consisting of two males and two females.

Behaviour

Opportunism and flexibility form the basis of hunting behaviour in dingoes. As indicated above, sociality allows this species to hunt larger prey. Dingoes also hunt alone for small and medium-sized prey and will even survive on insects if they must. They will attack from ambush or by chasing. In north-western Australia, Common Wallaroos are taken from ambush when coming into dark or isolated waterholes, or when following their well-made trails in the hills. There are reports of Dingoes simply staying on the track of individual kangaroos until they are exhausted. A case of two animals being at least 20 minutes behind a Red-necked Wallaby (*M. rufogriseus)* has been reported (Newsome *et al.* 1983b). The wallaby burst out of the scrub and plunged into a lake where it remained exhausted for several hours (M. Burt personal communication). The dingoes emerged on the wallaby's track about 20 minutes later. They remained at the edge of the water for a few minutes looking out at the animal before departing. To swim out to attack the wallaby would have risked drowning. Kangaroos will defend themselves by holding dogs under until they drown.

Like many mammals, the Dingo does not place faeces and urine at random; they are placed as 'messages'. Scent marking appears to convey the boundaries of territories and the presence of particular animals. Stream crossings, crossroads and watering points are most frequently marked (A.E. Newsome & P.C. Catling unpublished data). Such resources are time-shared and are likely to be nodes for the social organisation for this species.

One claimed characteristic of the Dingo is that it does not bark. That is not so. The Dingo does not bark in the normal course of events as domestic dogs do, but only if extremely alarmed. Presumably, the domestic dog has been selected by man to give the alarm. Howling is for dingoes their means of communication with one another over a distance. It is a social matter and is more common during the mating season than at any other time (Fig. 54.2; Corbett & Newsome 1975). There is a sharp rise in howling as breeding comes on and a sharp fall thereafter. Group howling follows the same pattern except for a rise in summer as pups become independent of their parents and howl together. Howling probably serves to unite separated members of a group, to unify a group socially and to broadcast a pack's presence to other groups, much as in wolves.

Foxes in Australia, as elsewhere, are largely nocturnal hunters, but activity of radio-tagged animals give some suggestion of a crepuscular pattern (B.J. Coman unpublished data) and long periods of rest at night are not uncommon. Hunting behaviour has been studied in some detail in the Northern Hemisphere (see Lloyd 1980) and it seems that, although vision may be important in locating food during daylight hours, at night the senses of smell and hearing are of paramount importance. Both stalking and assiduous pursuit have been observed in the case of animals taking smaller-sized prey and, again according to Lloyd (1980), the methods of hunting vary greatly. Food caching is common and has been studied in some detail (Macdonald 1976), usually with captive animals. The burying of surplus food must be advantageous to the animal, but there have been remarkably few observations of wild foxes recovering cached food.

There is extensive vocal communication in foxes and Tembrock (1963) and others have recorded a wide range of sounds. Many are clearly associated with particular situations such as greeting, threatening, 'care-call' of cubs and warning calls.
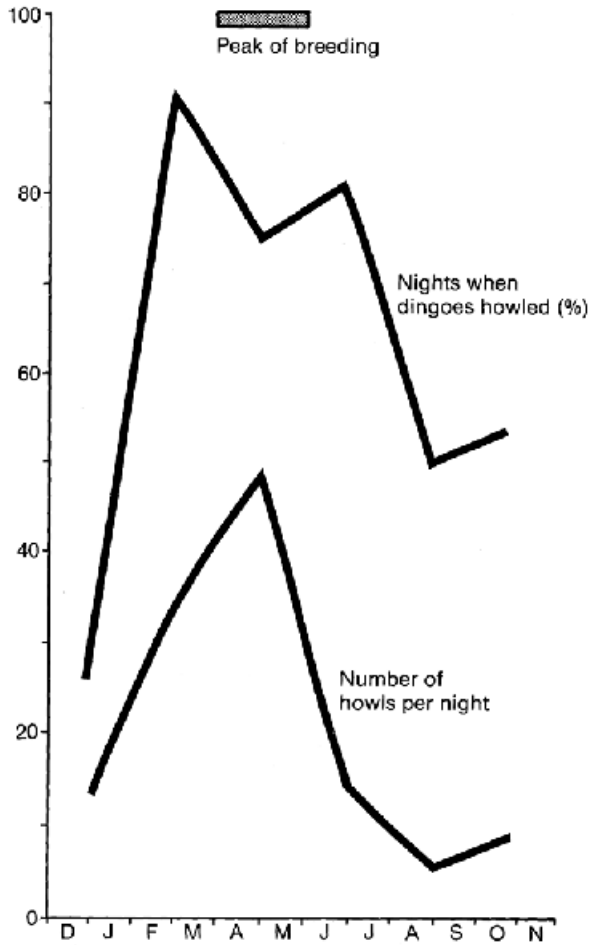
Figure 54.2 Association of howling with the peak of the breeding season in dingoes. (After Corbett & Newsome 1975)

Economic Significance

The role of dingoes in stock losses was considered above. A significance aspect of the ecology of the wild Canidae is related, however, to their role as top predators in Australian ecosystems. As such, they may play an important part in the regulation of numbers of several economically important prey species (see Newsome & Corbett 1975; Caughley *et al.* 1980; Corbett & Newsome 1987; Fig. 54.3).

Thus after the collapse of a rabbit plague in semi-arid central New South Wales, foxes and cats sometimes outnumbered the rabbits which are their main prey. Rabbits remained scarce throughout the next year despite quite reasonable rainfall. When foxes and cats were shot persistently on 70 km^2 of prime rabbit habitat, the response was startling (Fig. 54.3). In 3 months, the rabbit population had grown by up to a factor of four while on the unshot control area rabbit numbers did not on average change significantly (Newsome *et al.* 1989).

Following extensive control programmes for dingoes in Queensland and tropical parts of the Northern Territory in the early 1970s, there were reports of increased numbers of feral pigs, seen as a direct result of dingo control by some graziers and officially so in the Northern Territory. Also, an analysis of bounty payments for pigs and dingoes between 1945-1976 in Queensland has supported the suggestion of a direct link between dingo predation and the numbers of pigs (Wordall 1983). On the New England Tablelands, increases in the numbers of wallabies to pest proportions were reported following aerial baiting campaigns for dingoes.
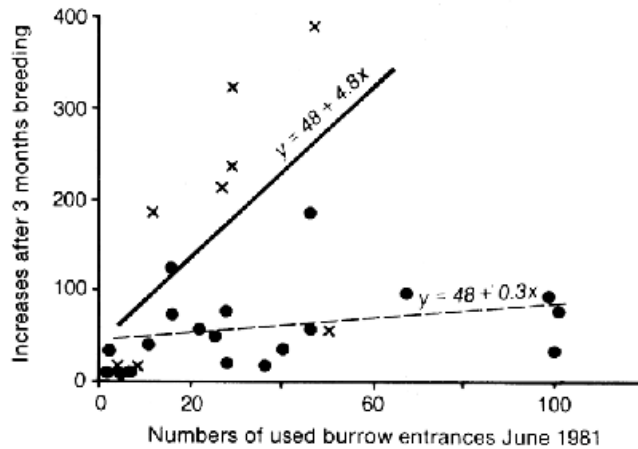
Figure 54.3 The four-fold increase of rabbit numbers in populations where foxes and feral cats were persistently shot (X) during a breeding season compared with almost no increase on average in numbers in populations where predators were untouched (O). (After Newsome, Parer & Catling 1989)

There are overseas examples of predators controlling multiple prey populations, and others where cyclic interactions between predator and prey (lynx and snowshoe hares in the North American Arctic) are being studied. In Australia, predation may have its greatest impact when interacting with the episodic environmental events like drought and wildfire that so characterise our environment.

In a study of the population recovery of several species following wildfire in coastal south-eastern Australia, no post-fire increase was found in the numbers of large mammals for 3 years due to predation by dingoes (Newsome *et al.* 1983b). In the fourth year, dramatically, predation upon large mammals fell by almost a half, and fell in the next year by over a half again (Fig. 54.4). The advent of large numbers of waterbirds (25 000 coots and 1000 swans) apparently took the pressure off the large mammals. Only then did their populations recover from the combined effects of wildfire and predation.

Rabbits are the mainstay of the diet of the dingo, fox and the feral cat. The rabbit's occasional eruptions provide large amounts of food. Some of the non-eruptive native species (but not the eruptive) are now extinct or rare. Their small numbers may simply have been mopped up as a side issue to the main predator/prey interactions induced by rabbits. Of course, the rabbits themselves may have directly altered the habitats to the detriment of native species as well. And, as mentioned above, dingoes and foxes are buffered from starvation in drought by carrion sheep and cattle and from thirst by artificial watering points. Nonetheless, if we wish to control these canids (and probably cats), we should control rabbits.

Poisoning campaigns for dingoes mostly use 1080 (sodium fluoroacetate) in fresh meat baits, either dropped from the air or placed by hand on the ground. Strychnine is just as effective a poison as a comparative trial conducted in central Australia during drought showed (Best *et al.* 1974). The timing and kind of bait were shown to be important in an earlier study of the effect of an extensive animal bait campaign which was ineffective on populations of dingoes (Newsome, Corbett & Stephens 1972).

In Australia, foxes have been considered as serious predators of young lambs, but investigations on the causes of lamb mortality in southern Australia (Rowley 1970) do not support this view. In general, the biggest single factor in lamb loss
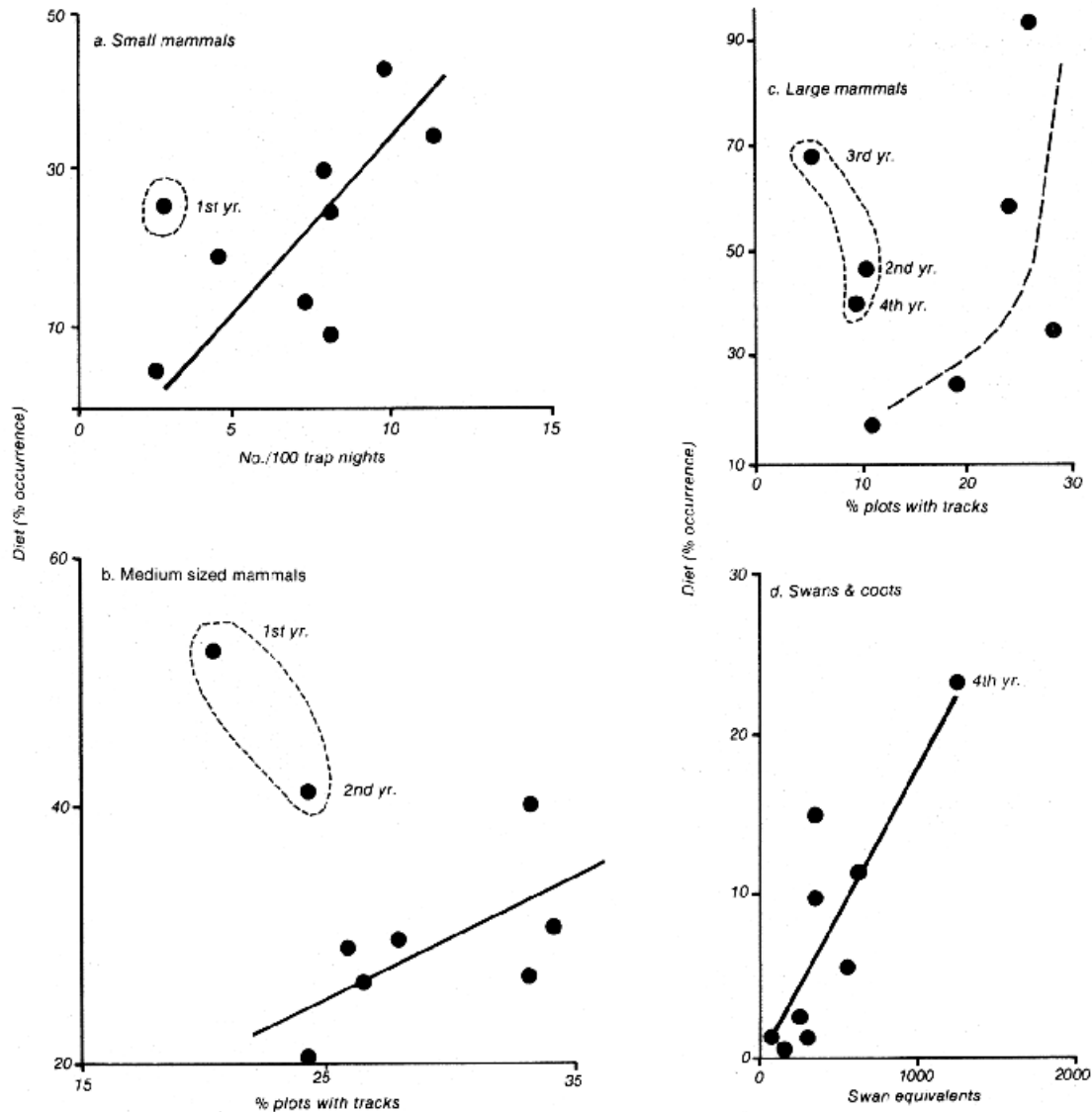
Figure 54.4 The generally direct relationships between the diet and the abundance of various kinds of prey of dingoes in south-eastern Australia, except for the evidence of severe predation on small to large mammals in the 1st and 2nd years post-fire, respectively. See discussion in text. (After Newsome *et al.* 1983b)

appears to be starvation; less than 3% of all lamb losses were directly attributed to predators. Unfortunately, most of the major causes of lamb loss are inconspicuous whereas damage caused by predators is readily observed. Again, few sheep owners make a distinction between those lambs that were healthy when killed and those that were moribund or already dead from other causes when attacked and eaten.

Nonetheless, some studies on individual flocks have revealed heavy losses to foxes and other predators (see Rowley 1970). Most of these, however, were attributed to circumstances peculiar to a single flock or to a small local area. Some of the predisposing causes include the unusually small size of lambs, physiological stress and absence of suitable cover for lambing. Recent studies, however, have shown that fox control around the time of lambing has improved lamb-marking by up to 25% in western New South Wales (Lugton 1987).

Predation by foxes on domestic poultry, particularly in smaller, unconfined flocks on mixed farms, is widespread in Australia, but the extent of losses is not high. Much of the predation can be attributed to poor management for, in the larger commercial poultry operations, predation is very rare.

As mentioned earlier, the Fox in Australia is not implicated in the persistence or spread of any economically important diseases. This position could be drastically altered in the event of the accidental introduction of rabies to Australia. In Europe, the Fox is the main vector of rabies (Lloyd 1980) and, in view of what is known of the density and distribution of animals in Australia, they must be regarded as the most important of the potential wild hosts of the disease in this country.

On the positive side, Australia has had for the past decade a flourishing export market in fox furs estimated conservatively at $4–6 million annually. Each year some 300 000 skins are traded on the Melbourne and Sydney markets. This level of harvesting has apparently had little effect on population densities as the export figures have remained reasonably constant over the last decade.

Until comparatively recent times, many States operated a bounty payment system on scalps of foxes. This proved to be completely ineffectual in reducing numbers (Whitehouse 1976). In fact, there is no clear evidence in Australia that man-imposed control has drastically altered fox numbers in the long term. Food supply and disease, particularly mange, are much more likely to operate as factors limiting population size. Where man-imposed control of fox populations is required (such as in the case of a rabies outbreak), the technique of choice would appear to be the use of buried lethal baits. Current trials (B.J. Coman & H. Brunner, unpubl. data) suggest that high kills of this species might be obtained by a systematic and well-planned poisoning campaign using buried meat baits containing 1080 (sodium fluoroacetate).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The distributions of dingoes and foxes in Australia are shown in Fig. 54.5. Both species are absent from Tasmania and foxes are not found, for unknown reasons, in the extreme north of the continent.

The Dingo was found throughout mainland Australia at the time of European settlement. Though its range has been reduced and there has been hybridisation with the feral dog (see below), it still occurs in many areas. As mentioned above, the presence or absence of dingoes essentially decides whether cattle or sheep are run on inland pastures or in the forested regions of south-eastern Australia. Put simply, dingoes and sheep are incompatible, so much so that a giant barrier fence 9660 km long separates sheep lands from cattle runs, the longest fence in the world (Fig. 54.5). The Dingo Barrier Fence is maintained by graziers and dingo trappers or 'doggers', whose houses are placed every 100 km or so along it in New South Wales. Every panel of this 3 m fencing is checked every 2 days and holes repaired.

Following their introduction into Victoria in the 1860s and 1870s, foxes appeared to spread slowly at first, but by 1900, they had occupied all of Victoria and most of New South Wales (Rolls 1969). The species was first reported in Western Australia near Eucla in 1911-12 and 100 miles west of the South Australia border in 1915. By 1931, animals in Western Australia were in every district except Marble Bar and the Kimberley (Gooding 1955). Colonisation in the west may still be continuing as, in more recent times, foxes have been reported in the west and east Kimberley. The spread of this species into
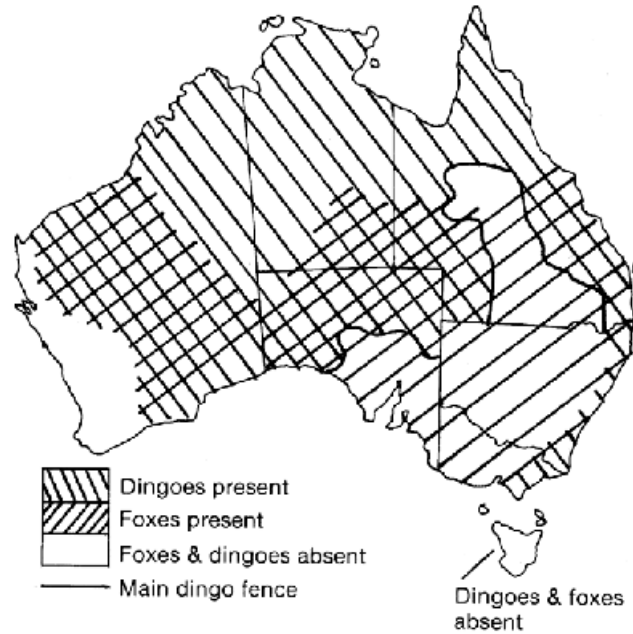
Figure 54.5 Map of Australia showing the approximate distribution of dingoes and foxes and the location of the main dingo fences in Australia. A few dingoes may be present inside the main dingo fence at any time. (After Coman 1985)

Queensland followed a similar time sequence with reports of animals in southern Queensland as early as 1911. In 1920, an individual animal was seen at Longreach and, according to Rolls (1969), their recent northern limit is around Julia Creek, several hundred kilometres north-west of Longreach. The northern limit for foxes, however, appears to vary according to seasonal conditions (Murray & Snowdon 1976).

Phylogenetic Relationships

The Dingo and the European Red Fox belong to the family Canidae, subfamily Caninae, as do the wolves, coyotes, jackals and foxes of the genera *Alopex*, *Fennecus*, *Urocyon*, *Nyctereutes*, *Dusicyon*, *Cerdocyon*, *Atelocynus* and *Chrysocyon*. Wolves and the coyotes inhabit northern America and the jackals, Africa and the Middle East across to India. The foxes, 26 species, inhabit variously almost all parts of the world including the Arctic. Taxonomically, all of the above form a unit due to the common dental formula. Individual shapes of teeth vary allometrically with genera and species, as do shapes, sizes and proportions of the bones of the skull and, especially, the postcranial skeleton. The carnassials, or shearing teeth, are the fourth premolar on the upper jaw and the first molar on the lower jaw.

Essentially, the Dingo belongs to a group of primitive dogs which inhabit equatorial lands like New Guinea, Malaysia and Thailand. Indeed, a recent study has shown such a close relationship between primitive dogs in Thailand and Australian Dingo that the former have been called Thai Dingoes (Corbett 1985). One of the best known primitive dogs is the Basenji from the Congo, which is kept in domesticity. What is a primitive dog? Its main characteristic is breeding seasonally once a year like related species, the Wolf (*Canis lupus*), Coyote (*C. latrans*) and Jackal (*C. adustus*). Domestic dogs breed at any time and usually twice a year.

The relationships of the Canidae, and especially the subfamily Caninae, have been examined by Clutton-Brock, Corbett & Hills (1976). They used measurements of teeth, skull bones, gross body characteristics (ear, tail, body,
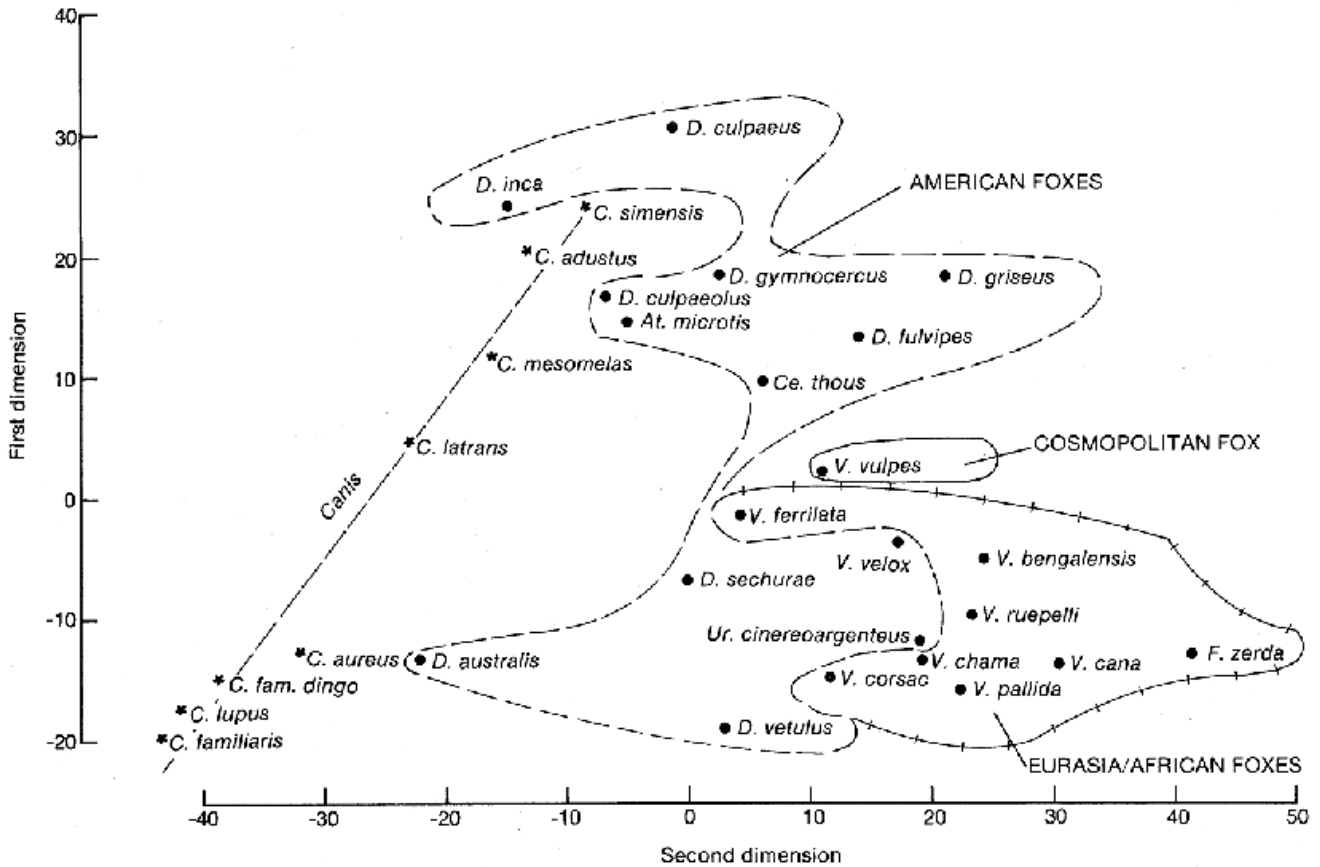
Figure 54.6 The relationships of the Caninae based on principle coordinate analysis of skull and teeth characters. Note that all *Canis* species are denoted by an asterisk and a connecting dashed line drawn by eye. Old World and New World foxes are demarcated and *Vulpes vulpes* is singled out; C. = *Canis*; V. = *Vulpes*; D. = *Dusicyon*; Ce. = *Cerdocyon*; At. = *Atelocynus*; F. = *Fennecus*; Ur. = *Urocyon*. (After Clutton-Brock *et al*. 1976)

limbs), coat colours as well as ecological and behavioural qualities (diet, feeding, social behaviour) to indicate similarities. Figure 54.6 shows the relationships of the Caninae based on principle coordinate analysis (Gower 1966) of the skull and tooth characters (Clutton-Brock *et al*. 1976). The axes are dimensionless, but results show the linearity in the relationship between dogs, dingoes, jackals, coyotes and wolves and their taxonomic distance from the array of foxes.

Another examination of selected canids is presented in Fig. 54.7, based on canonical analysis of 16 selected skull and tooth measurements of wolf, coyote and domestic dog from North America (Lawrence & Bossert 1967, 1975) and of dingoes and similarly sized domestic dogs from Australia (Newsome, Corbett & Carpenter 1980). The wolf, dingo and coyote lie in the same relationship as in Fig. 54.6; but the positions of the three samples of domestic dog are different and probably reflect the dog breeds selected for study. Based on skull and teeth characters, dingoes and dingo-like domestic dogs from Australia (mostly blue heelers and kelpies) appear closely related (Fig. 54.7) and yet their differences were sufficient to distinguish dingoes, dogs and dingo/domestic dog hybrids. Figure 54.8 summarises a comparison of skull measurements of samples of 'dingoes' from Gippsland and central Australia (Newsome & Corbett 1982). Many of the former resemble hybrids born in captivity and some were domestic dogs outright. Larger samples of dingoes indicate that stocks are pure in the main in remote regions like the Northern Territory, but not in south-eastern Australia (Newsome & Corbett 1985) (Table 54.5)

Table 54.5 Hybridisation between dogs and dingoes in remote (north) and settled (south) regions of Australia. The specimens have been classified from skulls, *a town dog.

REGION	LATITUDE (°S)	DINGO (%)	HYBRIDS (%)	DOGS (%)	SAMPLE SIZE
Submonsoonal Northern Territory	16-23	97.2	2.5	0.3*	316
Central Australia	22-25	96.8	3.4	0	-
Simpson Desert	23-26	100	0	0	242
SE New South Wales	34-37	22.6	56.6	20.8	53
Gippsland & Alpine Victoria	36-38	60.2	30.5	9.3	354

Coat colour frequencies of the Dingo for those two regions are shown in Table 54.6 (Newsome & Corbett 1985). The 'standard' colour of ginger (of varying hues) with white feet, chest and tail tip predominates in remote regions. The other generally accepted pattern of black coat with tan feet and white extremities ('black and tans') is uncommon there, but not in south-eastern regions where hybridisation is so prevalent. It is an odd fact, but reports in the journals of the early explorers on dingoes, or the Australian native dog as it was called then, were of the standard ginger colouration, black, black and white and white animals. Black and tan was never recorded (Newsome & Corbett 1985). If the reports were accurate and other colours not overlooked, then the high level of black and tans in the current populations of dingoes in south-eastern regions today may indicate that such coat patterns have arisen as a result of hybridisation. Patchy, multi-coloured or brindled coats do indicate hybrids, but all hybrids are not so variable (Table 54.5). In dingo/dog crosses in captivity, the ginger coat proved dominant, as it did to black and tans and to the rare pure white (not albino); both of these latter colourations breed true as recessives (Newsome & Corbett 1985).

Hybridised populations of dingoes are probably the norm where they occur in proximity to European settlement, such as throughout the Australian Great Dividing Range (except perhaps in the remote northern regions of Cape York). Similar hybridisation now provides mixed population of wolves, coyotes and domestic dogs in the New England region of the United States (McCarley 1962; Lawrence & Bossert 1967; 1975)..

Table 54.6 Variety in coat colour in south-eastern Australia (expressed as a percentage of the sample population). (After Newsome & Corbett 1985)

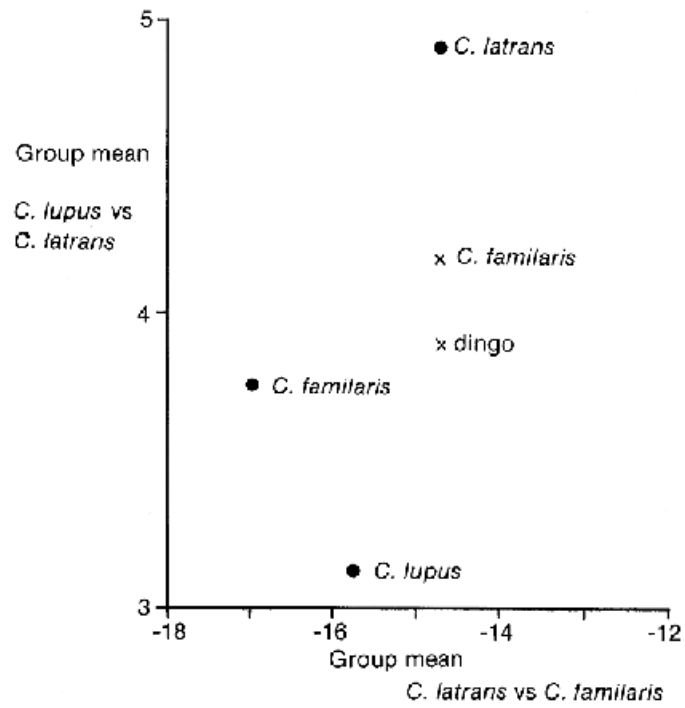| CLASSIFICATION	GINGER	BLACK AND TAN	WHITE	PATCHY GINGER	BRINDLE	OTHER	SAMPLE SIZE
Dingoes	46.5	19.4	0.5	2.8	9.0	21.8	211
Hybrids	48.9	19.2	0	3.0	7.4	21.5	135
Dogs	33.3	16.7	0	0	7.1	42.9	42
Means	45.9	19.1	0.2	2.6	8.2	24.0	388

Figure 54.7 The relationships of various canids based on canonical analysis of skull and teeth characters. Circles represent original data of Lawrence & Bossert (1967) and crosses represent data from Newsome *et al.* (1980). See text for full discussion. (After Newsome *et al.* 1980)
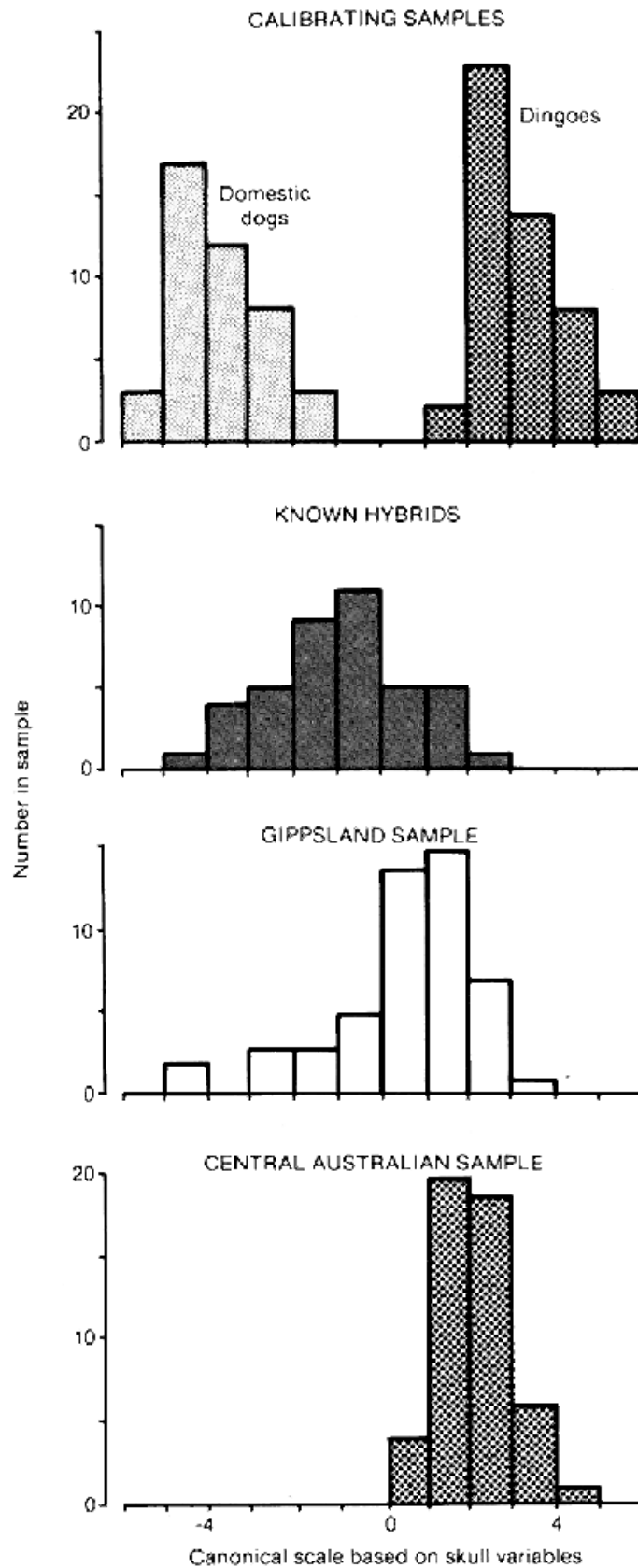
Figure 54.8 Comparison of dingoes, domestic dogs and hybrids using eight skull measurements showing the similarity of the Gippsland sample to known hybrids and the central Australian sample to 'dingoes'. See text for full discussion. (After Newsome & Corbett 1982)

LITERATURE CITED

Agar, N.S. & Green, B. (1979). Comparative red cell metabolism in the domestic dog and the dingo. *Research in Veterinary Science* 27: 262-263

Arundel, J.H. (1979). Hydatid disease of animals in Australia. *Australian Veterinary Journal* 55: 126-130

Baverstock, P. & Green, B. (1975). Water recycling in lactation. *Science* 187: 657-658

Best, L.W., Corbett, L.K., Stephens, D.R. & Newsome, A.E. (1974). Baiting trials for dingoes in central Australia, with poison '1080', encapsulated strychnine, and strychnine suspended in methyl cellulose. *CSIRO Division of Wildlife Research Technical Paper* No. 30 7 pp.

Brunner, H., Lloyd, J.W. & Coman, B.J. (1975). Fox scat analysis in a forest park in south-eastern Australia. *Australian Wildlife Research* 2: 147–154

Catling, P.C. (1979). Seasonal variations in plasma testosterone and testis in captive male dingoes. *Australian Journal of Zoology* 27: 939-944

Caughley, G., Grigg, G.C., Caughley, J. & Hill, G.J.E. (1980). Does dingo predation control the densities of kangaroos and emus? *Australian Wildlife Research* 7: 1-12

Clutton-Brock, J., Corbet, G.B. & Hills, M. (1976). A review of the family Canidae, with a classification by numerical methods. *Bulletin of the British Museum Natural History (Zoology)* 29: 1-199

Coman, B.J. (1972). Helminth parasites of the dingo and feral dog in Victoria with some notes on the diet of the host. *Australian Veterinary Journal* 48: 456-461

Coman, B.J. (1973a). The diet of red foxes, *Vulpes vulpes* L., in Victoria. *Australian Journal of Zoology* 21: 391-401

Coman, B.J. (1973b). Helminth parasites of the fox (*Vulpes vulpes*) in Victoria. *Australian Veterinary Journal* 49: 378-384

Coman, B.J. (1985). Australian predators of livestock. Pp. 411-425 *in* Gaatar, S.M., Howard, W.E. & Marsh, R.E. (eds) *Parasites, Pests and Predators*. Elsevier : Amsterdam

Corbett, L.K. (1985). Morphological comparisons of Australian and Thai dingoes: a reappraisal of dingo status, distribution and ancestry. *Proceedings of the Ecological Society of Australia* 13: 277-291

Corbett, L.K. & Newsome, A.E. (1975). Dingo society and its maintenance: a preliminary analysis. Pp. 369-379 *in* Fox, M.W. (ed.) *The Wild Canids: Their Systematics, Behavioural Ecology and Evolution*. Van Nostrand Reinhold : New York

Corbett, L.K. & Newsome, A.E. (1987). The feeding ecology of the dingo. III. Dietary relationships with widely fluctuating prey populations in arid Australia: an hypothesis of alternation of predation. *Oecologia* 74: 215-227

Dukes, H.H. (1955). *The Physiology of Domestic Animals*. Cornell University Press : Ithaca 1920 pp.

Dunsmore, J.D. & Burt, R.J. (1972). *Filaroides osleri* in dingoes in southeastern Australia. *Australian Veterinary Journal* 48: 548-551

Dunsmore, J.D. & Spratt, R.J. (1979). The life history of *Filaroides osleri* in wild and domestic canids in Australia. *Veterinary Parasitology* 5: 275-286

Ellenberger, W., Baum, H. & Dittrich, H. (1956). *An Atlas of Animal Anatomy.* Dover Publications : New York 2nd edn 153 pp.

Englund, J. (1970). Some aspects of reproduction and mortality rates in Swedish foxes. *Viltrevy* 8: 1-82

Environment Australia (1999b). Threat abatement plan for predation by the European Red Fox. National Feral Animal Control Program, Biodiversity Group, Environment Australia : Canberra iv 33 pp.

Fox, M.W. (ed.) (1975b). *The Wild Canids: Their Systematics, Behavioural Ecology & Evolution*. van Nostrand Reinhold : New York 508 pp.

Gemmell, M.A. (1959). Hydatid disease in Australia. IV Observations on the incidence of *Echinococcus granulosus* on stations and farms in endemic regions of New South Wales. *Australian Veterinary Journal* 35: 396-402

Gooding, C.D. (1955). The vermin bonus system in Western Australia. *Journal of Agriculture of Western Australia* 4: 433-439

Gower, J.C. (1966). Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrica* 53: 325-338

Green, B. (1978). Estimation of food consumption in the dingo (*Canis familiaris dingo*) by means of Na22 turnover. *Ecology* 59: 207-210

Green, B. & Catling, P. (1977). The biology of the dingo. Pp. 51-60 *in* Messel, H. & Butler, S.T. (eds) *Australian Animals and their Environment*. Shakespeare Head Press Sydney

Huggett, A.S. & Widdas, W.F. (1951). The relationship between mammalian foetal weight and conception age. *Journal of Physiology* 114: 306-317

Jones, F. Wood (1921b). The status of the dingo. *Transactions and Proceedings of the Royal Society of South Australia* 45: 254 -263

Kruuk, H. (1972). *The Spotted Hyaena: A Study of Predation and Social Behaviour*. University of Chicago Press : Chicago 335 pp.

Kumaratilake, L.M. & Thompson, R.C.A. (1984). Morphological characterisation of Australian strains of *Echinococcus granulosus*. *International Journal of Parasitology* 14: 467–477

Lawrence, B. & Bossert, W.H. (1967). Multiple character analysis of *Canis lupus*, *latrans* and *familiaris*, with a discussion of the relationships of *Canis niger*. *American Zoologist* 7: 223-232

Lawrence, B. & Bossert, W.H. (1975). Relationships of North American *Canis* shown by multiple character analysis of selected populations. Pp. 73-76 *in* Fox, M.W. (ed.) *The Wild Canids: Their Systematics, Behavioural Ecology and Evolution*. van Nostrand Reinhold : New York

Lloyd, H.G. (1975). The red fox in Britain. Pp. 207-215 *in* Fox, M.W. (ed.) *The Wild Canids: Their Systematics, Behavioural Ecology and Evolution*. van Nostrand Reinhold : New York

Lloyd, H.G. (1980). *The Red Fox*. B.T. Batsford : London 320 pp.

Lloyd, H.G., Jensen, B., van Haaften, J.L., Neiwold, F.J.J., Wandeler, A., Bogel, K. & Arata, A.A. (1976). Annual turnover of fox populations in Europe. *Zentralblatt für Veterinärmedizin* 23: 580-589

Lugton, I. (1987). Fox predation and lamb losses. *Agtalk* (Dept. Agriculture N.S.W.) [oral presentation]

MacDonald, D.W. (1976). Food caching by red foxes and some other carnivores. *Zeitschrift für Tierpsychologie* 42: 170-185

MacDonald, D.W. (1980). Social factors affecting reproduction amongst red foxes, *Vulpes vulpes*. Pp. 107-122 *in* Zimen, E. (ed.) *The Red Fox. Symposium on Behaviour and Ecology*. Junk : The Hague

MacIntosh, N.W.G. (1975). The origin of the dingo: an enigma. Pp. 87-106 *in* Fox, M.W. (ed.) *The Wild Canids: Their Systematies, Behavioural Ecology and Evolution*. van Nostrand Reinhold : New York

McCarley, H. (1962). The taxomic status of wild *Canis* (Canidae) in South Central United States. *Southwestern Naturalist* 7: 22-35

McIntosh, D.L. (1963a). Food of the fox in the Canberra district. *CSIRO Wildlife Research* 8: 1–20

McIntosh, D.L. (1963b). Reproduction and growth of the fox in the Canberra district. *CSIRO Wildlife Research* 8: 132-141

Milham, P. & Thompson, P. (1976). Relative antiquity of human occupation and extinct fauna at Madura Cave, south-eastern Western Australia. *Mankind* 10: 175-180

Mulvaney, D.J. (1975). *The Prehistory of Australia*. Penguin : Ringwood revised edn 276 pp.

Murray, M.D. & Snowdon, W.A. (1976). The role of wild animals in the spread of exotic diseases in Australia. *Australian Veterinary Journal* 52: 547-554

Newsome, A.E. & Corbett, L.K. (1975). Outbreaks of rodents in semi-arid and arid Australia: causes, preventions & evolutionary considerations. Pp. 117-153 *in* Prakash, I. & Ghosh, P.K. (eds) *Rodents In Desert Environments*. Junk : The Hague

Newsome, A.E. & Corbett, L.K. (1982). The identity of the dingo. II. Hybridisation with domestic dogs in captivity and in the wild. *Australian Journal of Zoology* 30: 365-374

Newsome, A.E. & Corbett, L.K. (1985). The identity of the dingo. III. The incidence of dingoes, dogs & hybrids & their coat colours in remote and settled regions of Australia. *Australian Journal of Zoology* 33: 363-375

Newsome, A.E. & Corbett, L.K. & Carpenter, S.M. (1980). The identity of the dingo. I. Morphological discriminants of dingo and dog skulls. *Australian Journal of Zoology* 28: 615-625

Newsome, A.E., Catling, P.C., Burt, R.J. & Corbett, L.K. (unpublished). *Echinococcus granulosus* and other parasites of wild canids in southeastern Australia.

Newsome, A.E., Catling, P.C. & Corbett, L.K. (1983b). The feeding of the dingo *Canis familiaris dingo* 2. Dietary and numerical relationships with fluctuating prey populations in southeastern Australia. *Australian Journal of Ecology* 8: 345-366

Newsome, A.E., Corbett, L.K. & Stephens, D.R. (1972). Assessment of an aerial baiting trial campaign against dingoes in central Australia. *CSIRO Division Wildlife Technical Paper* No. 24 11 pp.

Newsome, A.E., Corbett, L.K., Best, L.W. & Green, B. (1973). The Dingo. *Australian Meat Research Committee Review* No. 14 pp. 1-11

Newsome, A.E., Corbett, L.K., Catling, P.C. & Burt, R.J. (1983a). The feeding ecology of the dingo. I. Stomach contents from trapping in south-eastern Australia, and the non-target wildlife also caught in dingo traps. *Australian Wildlife Research* 10: 477–486

Newsome, A.E., Parer, I. & Catling, P.C. (1989). Prolonged prey suppression by carnivores - predator-prey removal experiments. *Oecologia* 78: 458-467.

Oliver, A.J. (1980). *Dingo Research*. Agriculture Protection Board of Western Australia : Perth 12 pp.

Pearson, O.P. & Enders, R.K. (1943). Ovulation, maturation and fertilization in the fox. *Anatomical Record* 85: 69-83

Robertshaw, J.D. & Harden, R.H. (1985a). The ecology of the dingo in northeastern New South Wales. II. Diet. *Australian Wildlife Research* 12: 39-48

Robertshaw, J.D. & Harden, R.H. (1985b). The ecology of the dingo in northeastern New South Wales. III. Analysis of macropod bone fragments found in dingo scats. *Australian Wildlife Research* 12: 163-171

Rolls, E. (1969). *They All Ran Wild. The Story of Pests on the Land in Australia.* Angus & Robertson : Sydney 444 pp.

Rowley, I.C. (1970). Lamb predation in Australia : Incidence, predisposing conditions and the identification of wounds. *CSIRO Wildlife Research* 15: 79-123

Ryan, G.E. (1976a). Helminth parasites of the fox (*Vulpes vulpes*) in New South Wales. *Australian Veterinary Journal* 52: 126-131

Ryan, G.E. (1976b). Observations on the reproduction and age structure of the fox *Vulpes vulpes* L. in New South Wales. *Australian Wildlife Research* 3: 11-20

Ryan, G.E. & Croft, J.D. (1974). Observations on the food of the fox, *Vulpes vulpes* (L.), in Kinchega National Park, Menindee, N.S.W. *Australian Wildlife Research* 1: 89-94

Schmidt-Nielsen, K. (1964). *Desert Animals: Physiological Problems of Heat and Water.* Clarendon Press : Oxford 277 pp. [60]

Schmidt-Nielsen, K. (1972). *How Animals Work.* Cambridge University Press : Cambridge 114 pp.

Shield, J. (1972). Acclimation and energy metabolism of the dingo, *Canis dingo* and the coyote, *Canis latrans*. *Journal of Zoology , London* 168: 483-501

Storm, G.L., Andrews, R.D., Phillips, R.L., Bishop, R.A., Siniff, D.B. & Tester, J.R. (1976). Morphology, reproduction, dispersal and mortality of midwestern red fox populations. *Wildlife Monographs* 49: 1-82

Swenson, M.J. (ed.) (1970). *Dukes Physiology of Domestic Animals*. 8th edn Cornell University Press : Ithaca 1543 pp.

Tembrock, G. (1963). Acoustic behaviour of mammals. Pp. 751-788 *in* Busnel, R.G. (ed.) *Acoustic Behaviour of Animals*. Elsevier : Amsterdam

Thompson, P.C. (1984). Dingoes and sheep in pastoral areas. *Journal of Agriculture of Western Australia* 25: 27-33

Thompson, R.C.A. (1979). Biology and speciation of *Echinoccocus granulosus*. *Australian Veterinary Journal* 55: 93-98

Thompson, R.C.A. & Kumaratilake, L.M. (1985). Comparative developement of Australian strains of *Echinococus granulosus* in dingoes (*Canis familiaris dingo*) and domestic dogs (*C. f. familiaris*) with further evidence for the original of the Australian sylvatic strain. *International Journal of Parasitology* 15: 535-542

White, J.P. & O'Connell, J.F. (1982). *A Prehistory of Australia, New Guinea & Sahul*. Academic Press : Sydney 286 pp.

Whitehouse, S.J. (1976). Bounty systems in vermin control. *Journal of Agriculture of Western Australia* 17: 35-89

Whitehouse, S.J.O. (1977). The diet of the dingo in Western Australia. *Australian Wildlife Research* 4:145-150

Wood, D.H. (1980). The demography of a rabbit population in an arid region of New South Wales, Australia. *Journal of Animal Ecology* 49: 55-79

Wordall, P.F. (1983). Distribution & population dynamics of dingoes (*Canis familiaris*) and feral pigs (*Sus scrofa*) in Queensland, 1945-1976. *Journal of Applied Ecology* 20: 85-95

Young, J.Z. (1962). *The Life of Vertebrates*. 2nd edn Clarendon Press : Oxford 820 pp.