

The feeding ecology of the dingo II. Dietary and numerical relationships with fluctuating prey populations in south-eastern Australia

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Abstract

The dietary and predator-prey relationships of *Canis familiaris* dingo were studied for 9 yr at a coastal site and for 1.5 yr at a montane site in south-eastern Australia. The percentage occurrences of items eaten were obtained from faeces, and the abundances of prey by counting waterbirds, trapping small mammals, and tracking large and medium-sized mammals on specially prepared soil plots. Dingoes were also estimated by tracking.

The diet was broad but predominantly mammalian (23 species). Dietary frequencies were grouped around three weight modes, 0.1, 1.25 and 16 kg, corresponding with bush rat (*Rattus fuscipes*), ringtail possum (*Pseudocheirus peregrinus*) and swamp wallaby (*Wallabia bicolor*). The amplitudes of those frequencies approximately doubled from mode to mode, viz. 4, 13.5 and 28.3%, respectively. Medium-sized mammals have been recognized as the staple prey because of their dependability. Their density estimates fluctuated least among prey-groups, and track records of dingoes in the mountains were significantly related to them. Other categories of prey were supplementary (large mammals), opportune (small mammals) and scavenged.

Although there were general tendencies for dietary frequencies to follow prey abundances, significant functional and numerical responses were obtained only for water-birds (coot and swan). Their super-abundance in the mid-years of the coastal study and their highly clumped distribution were the likely causes.

Predation was disproportionately severe on mammalian prey-classes after an extensive wildfire at the coastal site. Such predation may have suppressed populations of wallabies and kangaroo for 2 yr until the water-birds became super-abundant. The prevalence of wombats in the mountains may have induced heavy predation upon other less numerous large prey. Concepts of profitability in feeding appear to apply to the dingo more than those of optimization of time or energy.

The decline in dingoes was correlated most with long-term declines in water-birds and medium-sized mammals. At the time, abundance estimates of wallabies and kangaroos were increasing and those species increasingly predominated in the diet. The ability to hunt co-operatively was apparently ineffectual in preventing decline in dingo numbers.

It is suggested that pack size is related inversely to the level of temporal instability in the environment. Frequent wildfires may prevent staple (medium-sized) and supplementary (large) prey from being abundant simultaneously, a combination thought necessary for large pack size.

Introduction

The study reported here examines the diet and abundance of the dingo (*Canis familiaris dingo*) relative to the abundance of prey in south-eastern Australia. It was conducted at two study-sites, one at the coast in Nadgee Nature Reserve and the other in the mountains in Kosciusko National Park (Fig. 1). Both populations of dingoes are relatively undisturbed by man because the areas are protected for wildlife. The study at the coast lasted 9 yr and involved three groups of dingoes each containing two or three adults, and that in the mountains lasted 1.5 yr and mostly involved one group of nine adult dingoes (Newsome & Catling unpubl.).

We sought to answer the following questions:

(1) What is the nature of the relationship between the incidence of a prey in the diet and its abundance?

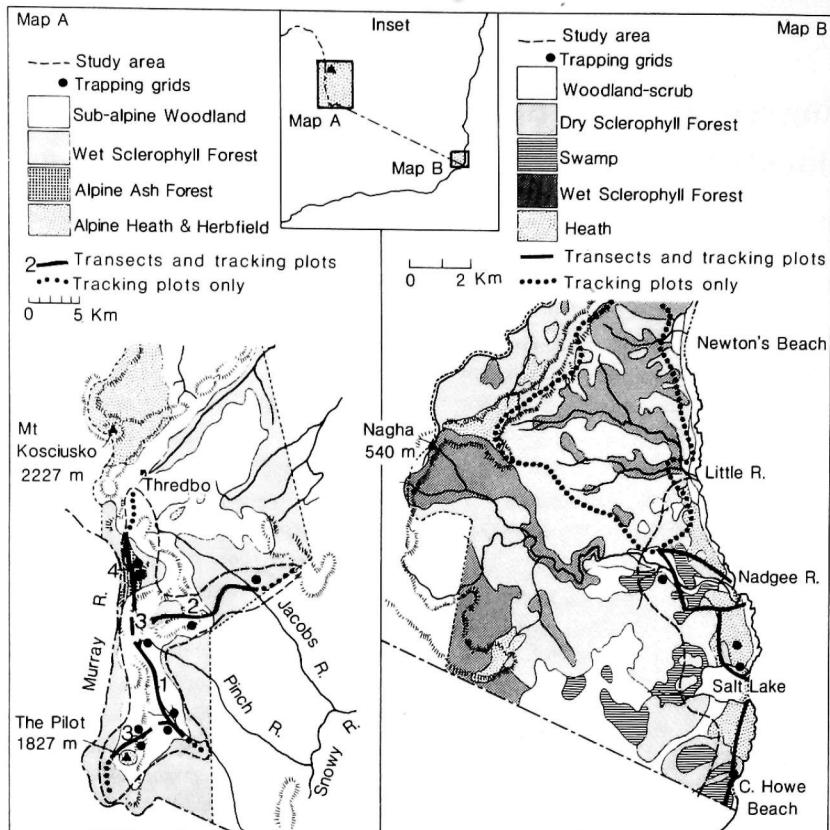


FIG. 1. The Nadgee and Kosciusko study sites showing major habitats, transects along which faeces were collected and soil plots were prepared for tracking medium-sized and large vertebrates, and trapping sites for small mammals.

(2) How does the relationship change with fluctuations in prey abundance?

(3) Do the numbers of dingoes respond to changes in prey abundance?

Since dingoes hunt singly but also form packs (Corbett & Newsome 1975), the range of prey eaten should be broad, as demonstrated by the literature. Thus, prey includes a variety of mammals from small to large and including kangaroos and domestic stock; but it also includes carrion, other vertebrates, invertebrates, and even vegetation in small amounts (Newsome *et al.* 1973; Brunner & Coman 1974; Corbett 1974; Robertshaw 1976; Whitehouse 1977; Newsome *et al.* in press; Corbett & Newsome unpubl.). During the study at the coast, a severe wildfire provided an exceptional opportunity to observe the restructuring of mammal communities (Newsome *et al.* 1975; Newsome & Catling 1979; Catling & Newsome 1981; Newsome & Catling 1983) and the effect of predation upon them.

The dingo has hybridized with the domestic dog (*C. f. familiaris*) in south-eastern Australia to form

mixed populations (Corbett 1974; Newsome & Corbett 1982). All, however, are referred to as dingoes in this paper. The lists of mammals at the two sites were obtained mostly from J. Calaby (pers. comm.) and were confirmed and added to by our observations.

Methods

Study sites, habitats, fauna and climates

The main study was conducted in the south of Nadgee between 1971 and 1980 on a coastal strip of about 25 km² which includes a sub-coastal lake (Fig. 1). There was a subsidiary study of predator and prey abundances also in the north of the Reserve (Fig. 1). The comparative study on about 180 km² in the mountains at about 1300 m altitude at Kosciusko (Fig. 1) was conducted over two summers and a winter during 1975–76.

The extensive habitats at Nadgee are dry sclerophyll forests (mainly *Eucalyptus sieberi*) and

woodland/scrub (characterized by *Banksia serrata*) (Fig. 1). Less extensive habitats include the lake, beaches, heathlands and swamps. The wet sclerophyll forests are mainly in the north of Nadgee. The main vegetation at Kosciusko is montane and subalpine woodlands of mixed *E. dalrympleana* and *E. pauciflora* subsp. *niphophila* on the mountains interspersed with narrow grassy (*Poa* spp) or heathy valleys. There is a small area of alpine ash forest (*E. delegatensis*). Both study sites are well watered.

The dingoes utilized all habitats in both sites, especially the ecotones between the forests and the grasslands and heathlands (Newsome & Catling 1979). At Nadgee the sea and lake beaches were also important. Regardless of the altitude or the vegetation in the two sites, the major potential mammalian prey were basically the same species (Newsome & Catling 1979). The large grazing marsupials, eastern grey kangaroo (*Macropus giganteus*), red-necked and swamp wallabies (*M. rufogriseus* and *Wallabia bicolor*) and common wombat (*Vombatus ursinus*), also favoured ecotones between the forests and grasslands. Of the medium-sized mammals, bandicoots (*Isoodon obesulus*, *Perameles nasuta*) and brushtail and ringtail possums (*Trichosurus vulpecula*, *Pseudochirus peregrinus*) were most

common in forests at the coast but they inhabited coastal thickets also. The long-nosed potoroo (*Potorous tridactylus*) was found in minority habitats there. The European rabbit (*Oryctolagus cuniculus*) was present in most habitats at both sites. The native small mammals, two rodents (*Rattus fuscipes*, *R. lutreolus*) and two marsupial mice (*Antechinus stuartii* and *A. swainsonii*), preferred habitats which combined trees, a heathy understorey, logs, litter and moisture (Newsome & Catling 1979; Catling *et al.* 1982; Newsome & Catling 1983). The feral house mouse (*Mus musculus*) was also present. There were some prey differences. Principally at Nadgee there were the large water-birds on the lake, black swans (*Cygnus atratus*) and Eurasian coots (*Fulica atra*), and the carcasses of mutton birds (*Puffinus tenuirostris* and *P. pacificus*) and penguins (*Eudyptula minor*) washed up on beaches. Additional prey at Kosciusko were the mountain brushtail possum (*T. caninus*), the uncommon mountain pygmy possum (*Burramys parvus*), the broad-toothed rat (*Mastacomys fuscus*) and feral horses (*Equus caballus*). There were no *R. lutreolus* or bandicoots.

The general climate throughout the study region is cool temperate, but milder at the coast. At Nadgee,

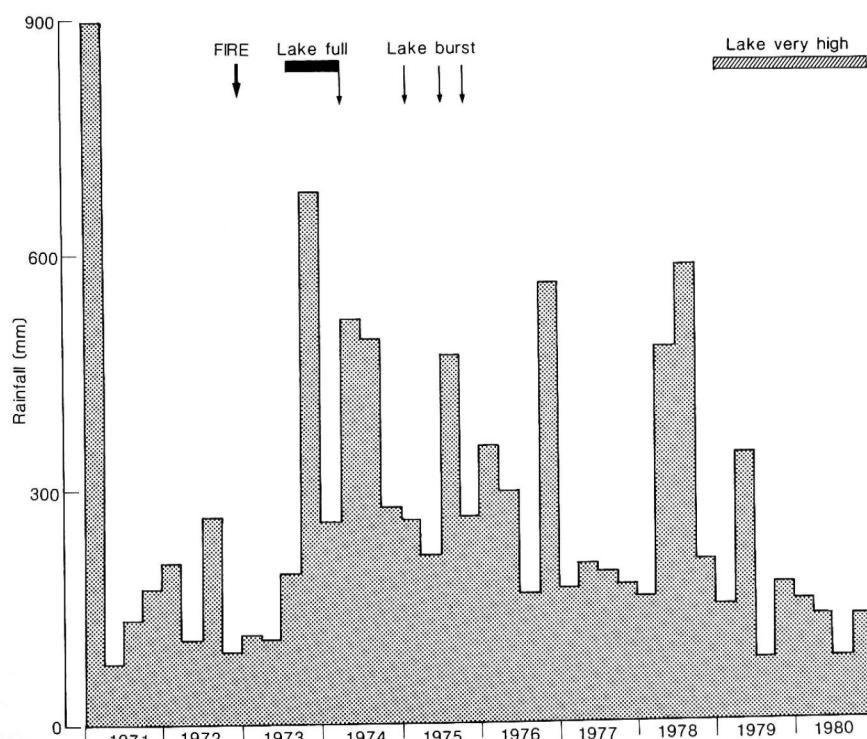


FIG. 2. Nadgee: Rainfall lumped for three monthly intervals during the study.

maximum and minimum mean temperatures ($^{\circ}\text{C}$) are 23 and 14 in January, and 14 and 7 in July, and, at Kosciusko, 20.4 and 7.4, and 4.5 and -3.6 , respectively. Precipitation ranges from 750 to 1000 mm yr^{-1} at Nadgee and from 750 to 2000 mm yr^{-1} at Kosciusko where the study site is in a minor rain and snow shadow. During winter the snow lies above approximately 1400 m. The weather pattern at Nadgee over the nine years of the study went from dry to wet to dry (Fig. 2).

The severe drought in the first two years at Nadgee culminated in the severe wildfire of December 1972 (indicated in Fig. 2). A graphic account of the fire and its effects was presented by Fox (1978). The fire burnt the entire Reserve, destroying all ground and understorey vegetation and much of the tree canopy. The only green vegetation remaining was in wet gullies and along sea-cliffs. From winter 1973 for three years, excellent rainfall on the ash beds regenerated lush dense growth of ground vegetation, shrubs and tree seedlings. Most adult eucalypts sprouted epicormically, and, within two months, there was an outbreak of unidentified large caterpillars which fed on the prolific eucalypt shoots (Fox 1978). In the last years of the study the undergrowth of the woodlands and forests became very dense. Salt Lake (Fig. 1) filled so often that it burst out to the sea four times in 1974 and 1975 (Fig. 2). The water-birds were most abundant during those middle years of the study in association with a bloom of submergent macrophytes (*Ruppia* sp.) (W. Braithwaite, pers. comm.).

Diet

Samples. Faeces were collected along standard transects on tracks and beaches. At Nadgee, there was one transect 10 km long, and, in Kosciusko, four transects totalling 20 km (Fig. 1). Each faecal sample was individually labelled by site and date. At Kosciusko, faeces were not collected when transects were covered by snow (Fig. 1). Habitat characteristics of the Kosciusko transects are presented in Table 2 below.

Since foxes (*Vulpes vulpes*) were also present, faeces were classified on size by eye as dingo (about 2 cm in diameter or more), fox (about 1 cm in diameter or less) and intermediate. Only the former were used for this study. Selection may have been biased by exclusion of small faeces from young dingoes or inclusion of large fox faeces. However, Corbett (1974) found that the incidence of small,

medium-sized and large vertebrates in the stomachs of young and adult dingoes in Gippsland south of the study region did not differ significantly ($P > 0.05$) although insects in particular featured in the small ($n = 11$) sample of young dingoes. If there were fox faeces in our samples, estimates of dietary frequencies for large mammals may have been lowered, those for small mammals and insects increased, and those for medium-sized mammals, largely unchanged.

Identification of ingesta. Cuticle scale impressions of hairs from different parts of potential mammalian prey were prepared on thin films of starch gel on microscope slides. Hair from prey species were either from animals caught alive or from museum specimens in the Australian National Wildlife Collection, Canberra. The scale impressions were satisfactory for our array of species most of the time (L. Corbett, unpubl.), but microscopic cross-sections of hair (Brunner & Coman 1974) were used to help define closely related species. Faeces were oven-dried to kill eggs of the tapeworm (*Echinococcus granulosis*), and then re-moistened and teased apart. Scale impressions of hairs from the faeces were identified mostly to species by comparison with the photographs of the reference collection. Tests comparing random and subjective selections of hair from samples detected no bias in identifications, and so the latter, much quicker, method was employed. Characteristics used for subjective selection were, for example, the tangled hair of possums compared with the straight hair of kangaroos and wallabies.

For cross-comparisons and identification of any additional prey, skeletal fragments were identified independently from prepared sets of skeletons. Teeth were particularly important but so were some anatomical peculiarities, e.g. claws of the koala (*Phascolarctos cinereus*) and toe-bones of macropodids (as a group). Ends of long bones, skull bones and mandibular angles sometimes also proved specific. Sometimes the hair and skeletal remains in one faecal sample were identified to different species. To check for errors, remains were re-identified. Feathers and bones of birds, remains of reptiles, amphibia, fish, insects, crustaceans and plant material were also identified using museum and herbarium specimens. It was more difficult to identify their remains to species than for mammals.

In some samples, particular pairs or trios of prey species were identified together more often than expected by chance. Such samples were always rechecked for mis-identifications. Remains of ring-

tail possum and swamp wallaby, however, remained persistently paired. To test for any systematic error in identification, starch gel impressions were prepared from museum or fresh specimens and included with other specimens without the identifier's knowledge. There were no mis-identifications and so the original identifications were accepted.

The number of faecal samples in which a particular species or group of species was found in any year (July-June) was divided by the total number of faecal samples to provide the percentage occurrence. Because faecal samples often contained remains of more than one small mammal, or other group, the percentage occurrence of a prey group can exceed 100%.

Estimating the abundance of prey. Three methods were employed, counts for water-birds, trapping for small mammals and track records of medium-sized and large mammals. The errors involved would have been least for the counts and most for tracking.

Swans and coots on the lake at Nadgee were counted using binoculars from a vantage point overlooking the entire lake. Counts taken on two to three days consecutively on each visit were averaged to represent abundances. Our methods were confirmed by W. Braithwaite (pers. comm.) at a time of great abundance of coots. To standardize to 'swan equivalents', numbers of coots were divided by 7.3, the differential between the weights of adult swan and coot. A mean estimate of 'swan equivalents' for the year (July-June) was obtained from all counts.

Trapping grids for small mammals were established in four major habitats at Nadgee and in six at Kosciusko (Fig. 1). Each grid had 20 live-traps, 10 set at 7 m intervals in each of two parallel lines placed 10 m apart. In each sampling period traps were set for three consecutive nights. Bait was a mixture of rolled oats and peanut butter. At Nadgee trapping was conducted four to six times per year and always included periods of population lows (August/September) and highs (February/March). At Kosciusko trapping always included the population high (February/March), but there was no trapping in winter. Small mammals (species as above) were identified, sexed, weighed, examined for reproductive condition, individually toe-clipped and released. The total number of individuals captured was expressed per 100 trap-nights annually (July-June). Lumping in this way should help to nullify any seasonal variability in trappability (Fletcher 1977; Cockburn 1981).

Bider (1968) formalized the method of recording animal tracks across specially prepared sand-plots to

census the species present and to indicate their activity. Tracks in snow have been used also to estimate fluctuation in arctic hare (*Lepus timidus*) (Pullianen 1982). That tracks could reflect abundances was shown by removal trapping for the shrew (*Sorex cinereus*) (Sarrazin & Bider 1973) and for the dingo (Newsome *et al.* 1972). Also, tracks of red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) have been successfully calibrated against actual numbers obtained from drives (Dzieciolowski 1976).

In this study, soil plots about 1 m wide were prepared across vehicle tracks, walkways and beaches. They were raked one day and the tracks made by medium sized and large vertebrates were identified the next day for 3–5 days consecutively in each sampling period. At Nadgee there were 65 plots spaced about 0.4 km apart on the study site and 45 plots similarly spaced in the auxiliary northern site; they were prepared and read every second to third month. At Kosciusko, there were 105 plots which were placed 0.8 km apart and read in the summers of 1975 (February and April) and 1976 (February and March). If rain, high winds, and high seas on beaches erased plots, the day's tracking was repeated. The tracks of some species were indistinguishable and so they were recorded as groups, respectively, the macropodids (except for large kangaroos), the possums and the bandicoots.

Two indices of activity were calculated: the percentage of soil plots on which specified tracks were recorded, and the percentages having 0, 1, 2, . . . , n such tracks on them. The former is used here as an estimate of abundance and the latter as supportive evidence. At Nadgee data were lumped annually (July-June), but at Kosciusko data were lumped by transects over time. There are two underlying assumptions: that usage of the narrow roads and beaches is representative and that changes in activity are related most to changes in abundances. The more mobile species appeared to use roads and beaches as rights of way; the dingo certainly did so (Newsome & Catling unpubl.). wombats utilized tracks preferentially soon after the fire because green herbage sprouted there first (Newsome *et al.* 1975).

The second assumption rests on the relatively small home ranges of many species: ringtail possum, 0.37 ha (Tyndale-Biscoe 1973); brushtail possum, 1.1–3 ha (Dunnet 1964); greater glider (*Petauroides volans*), 1.2–2.4 ha (Tyndale-Biscoe & Smith 1969); rabbit, unmeasured for the habitats, but probably 2–5 ha (D. Wood pers. comm.); wombat, 12.4 ha (J. McIlroy pers. comm.);

and swamp wallaby, 5.7 ha (Edwards & Ealey 1975). The number of warren entrances with tracks indicates rabbit abundance (Parer 1981). Since the warrens were mostly inaccessible, we have assumed that tracks around them may be indicators also. There are no published data for bandicoots although their ranges are likely to be small, and none for the red-necked wallaby and grey kangaroo. Our observations indicated that individuals or groups of grey kangaroos tended to be found in the one locality, but that distances of 1 km or so would be easily achieved. Dingoes move further over a mean home range of 10 km² at Nadgee and 17.5 km² at Kosciusko (Newsome & Catling unpubl.).

So, for the large prey, it is less likely that changes in track counts will reflect numbers than for smaller ones. Although possums do spend time on the ground, their tracks may be poor indicators of abundance also. The dingo was mentioned above. In a trial in central Australia (Newsome *et al.* 1972), soil plots prepared around 60 watering points indicated the presence of 183 dingoes. After 137 of them were caught, tracks indicated 64 dingoes remaining. These results indicate that 201 dingoes were watering initially, providing an error of estimation of just under 9%.

Results

Overall diet

A total of 1102 faecal samples were collected at Nadgee and 314 at Kosciusko. Detailed results are presented for some prey in Tables 1 and 2, and for minor dietary items in the Appendix. Twenty-three mammal species were recorded in all, plus nine species of bird, at least two reptiles, and some fish, insects and plant material. Mammals formed the majority of the prey by species and by percentage occurrence at both sites. At Nadgee, 22 different mammals (102.9% occurrence) and nine birds (38.4%) were recorded, and, at Kosciusko, 18 mammals (121.6%) and one bird (0.9%). Large mammals were most common with 48% occurrence at Nadgee and 75.1% at Kosciusko. The commonest species in the diet were swamp wallaby at Nadgee (> 18.5%) and wombat at Kosciusko (51.3%), a difference related directly to differences in abundance estimates. Water-birds (36.9%) were the second most common group at Nadgee, closely followed by medium-sized mammals (34.7%) which were the second most common dietary items at

Kosciusko (35%) also. The high occurrence of birds in the diet was not only in response to the swans and coots on the lake, but also to carcasses of muttonbird and little penguins washed up from the sea.

There were some dietary peaks for some species over time at Nadgee, e.g. 21.1% for ringtail possum in the first year (drought), 31.4% for swamp wallabies, 14% for bandicoots and 21.1% for rodents in the second year (drought and fire), and 20.5% for coots during their abundance in the fourth year. *Solanum* seeds formed 6.9% of faeces in the first year post-fire when the plants proliferated. Despite the array of items eaten, only 10 species were represented in more than 5% of faecal samples at Nadgee, and only five species in more than 10% of them. The respective figures for Kosciusko were four and two species overall.

Some rare species were eaten, e.g. the koala (0.4% occurrence). That species has never been found at Nadgee but it is known in the forests to the west. Three faecal samples (0.3%) contained spines of the short-beaked echidna (*Tachyglossus aculeatus*) which was not tracked on our plots although seven were seen at Nadgee. The potoroo (*P. tridactylus*) was first recorded at Nadgee when we found a dingo kill. Small pockets of them were then found mostly in swampy localities (Newsome & Catling 1979). *Potorous longipes*, known from Gippsland south of our study sites (Seebeck & Johnston 1980), was not recorded by us. At Kosciusko, the rare mountain pygmy possum was not caught in traps although one faecal sample (0.3%) contained its remains.

By contrast, some relatively common medium-sized species were not recorded in faeces, e.g. the lyrebird (*Menura novae-hollandiae*), or were rarely recorded, e.g. the monitor (*Varanus varius*) (0.1%). Monitors were eaten at a similarly low frequency in central Australia (1.7%) (Corbett & Newsome in prep.) The water-rat (*Hydromys chrysogaster*) was present at Nadgee and even tracked away from water on one occasion, but it was not identified from our sample of dingo faeces.

Modality in weight-classes of prey in the diet

The percentage occurrences in the diet for both study sites combined (Tables 1 and 2) are plotted against the logarithms of adult body-weights of various prey in Fig. 3. The distribution has three modes whose values, 4, 13.5 and 28.3%, were related to prey of increasing weight, 0.1, 1.25 and 16 kg, respectively. The first mode corresponded with the large bush rat, the second, with ringtail possum (closely

TABLE 1. Percentage occurrence of prey in the diet (*d*), and estimates of abundance* (*a*) of them and of the dingo per year (July-June) at Nadgee

| | 1971-72 | 1972-73 | 1973-74 | 1974-75 | 1975-76 | 1976-77 | 1977-78 | 1978-79 | 1979-80 | Totals |
|---|----------|----------|----------|----------|----------|----------|----------|----------|----------|-----------|
| | <i>d</i> | <i>a</i> | <i>d</i> | <i>a</i> | <i>d</i> | <i>a</i> | <i>d</i> | <i>a</i> | <i>d</i> | Abundance |
| No. scats | 156 | 71 | 274 | 151 | 50 | 136 | 133 | 86 | 45 | 1102 |
| No. plot nights | 279 | 1189 | 1334 | 952 | 573 | 734 | 644 | 758 | 793 | 7256 |
| No. trap nights | 2109 | 6877 | 4668 | 3018 | 1689 | 2132 | 1730 | 1672 | 2134 | 26,029 |
| No. water-bird counts | 6 | 10 | 8 | 5 | 4 | 5 | 3 | 4 | 5 | 50 |
| Birds | | | | | | | | | | |
| Little penguin (<i>Eudyptula minor</i>) | 3.8 | — | 0 | — | 12.4 | — | 5.3 | — | 8.1 | — |
| Mutton bird (<i>Puffinus spp.</i>) | 3.2 | 0 | — | 6.2 | — | 7.9 | — | 16.0 | — | 6.7 |
| Swan (<i>Cygnus atratus</i>) | 0.6 | 188 | 1.4 | 205 | 0.7 | 51.0 | 2.6 | 306 | 8.0 | 205 |
| Eurasian coot (<i>Fulica atra</i>) | 0 | 0 | 0 | 0 | 0.7 | 0 | 20.5 | 7000 | 2.0 | 1000 |
| Large water-bird index. | 6.4 | — | 9.9 | — | 5.5 | — | 13.9 | — | 10.0 | — |
| Mammals | | | | | | | | | | |
| Brown antechinus (<i>Antechinus stuartii</i>) | 0 | 1.4 | 1.4 | 0.9 | 0 | 0.3 | 0 | 0.1 | 0 | 0.4 |
| Dusky antechinus (<i>A. swainsonii</i>) | 0.6 | 1.3 | 1.4 | 0.4 | 0.4 | 0.1 | 0 | 0.1 | 0 | 0.4 |
| Marsupial mice index. | 3.8 | — | 1.4 | — | 0 | — | 0.7 | — | 0.7 | — |
| Long-nosed bandicoot (<i>Potorous ocellatus</i>) | 1.9 | — | 4.2 | — | 2.2 | 0.7 | 4.0 | — | 2.9 | — |
| Southern brown bandicoot (<i>Isoodon obesus</i>) | 1.3 | 7.9 | 8.4 | 1.2 | 0.4 | 1.6 | 0 | 2.0 | 0 | 0.7 |
| Bandicoot index. | 0 | — | 1.4 | — | 0.4 | 0.7 | 0.7 | — | 0.7 | — |
| Common wombat (<i>Vombatus ursinus</i>) | 1.3 | 1.1 | 8.4 | 0.8 | 1.8 | 1.6 | 1.8 | 0 | 1.0 | — |
| Common ringtail possum (<i>Pseudochirulus peregrinus</i>) | 21.1 | — | 8.4 | — | 10.9 | 12.6 | 6.0 | — | 0.7 | — |
| Common brushtail possum (<i>Trichosurus vulpecula</i>) | 1.3 | 5.4 | 9.9 | 1.9 | 5.8 | 1.4 | 0 | 1.7 | 0 | 0.7 |
| Possum index. | 7.0 | 11.3 | 11.3 | 4.0 | 1.3 | 0 | 2.0 | 0 | 7.3 | — |
| Long-nosed potoroo (<i>Potorous tridactylus</i>) | 0.6 | 2.1 | 1.4 | 0.7 | 2.2 | 0.1 | 0.7 | 0 | 0 | 0.5 |
| Swamp wallaby (<i>Wallabia bicolor</i>) | 23.1 | — | 12.7 | 31.4 | 19.2 | 8.0 | 4.4 | — | 10.5 | 18.5 |
| Red-necked wallaby (<i>Macropus rufogriseus</i>) | 5.1 | 7.5 | 2.8 | 8.1 | 9.8 | 4.2 | 6.9 | 2.9 | 14.7 | — |
| Wallaby index. | 14.7 | — | 22.5 | — | 23.0 | 15.9 | 6.0 | — | 3.7 | — |
| Eastern grey kangaroo (<i>Macropus giganteus</i>) | 1.3 | 1.1 | 0 | 2.1 | 0.4 | 0.5 | 0.7 | 0 | 2.2 | — |
| Large macropod index. | 0 | — | 0 | — | 1.8 | — | 0 | — | 10.3 | — |
| Bush-rat (<i>Rattus fuscipes</i>) | 1.3 | 1.2 | 8.4 | 0.6 | 1.1 | 0.3 | 2.6 | 1.3 | 8.0 | — |
| Swamp-rat (<i>Rattus lutreolus</i>) | 5.8 | 0.8 | 2.8 | 0.8 | 0.4 | 0.02 | 1.3 | 1.0 | 2.0 | — |
| Rat index. | 6.4 | — | 9.9 | — | 0.7 | — | 4.6 | — | 10.0 | — |
| House mouse (<i>Mus musculus</i>) | 0.6 | 0 | 0 | 0.03 | 0.4 | 2.0 | 4.0 | 4.8 | 1.2 | — |
| Rabbit (<i>Oryctolagus cuniculus</i>) | 5.8 | 17.9 | 5.6 | 15.2 | 12.8 | 21.1 | 9.3 | 22.8 | 10.0 | 26.7 |
| Hair, hide and bone index. | 16.0 | — | 11.3 | — | 12.8 | — | 14.6 | — | 16.0 | — |
| All large mammals | 45.5 | 9.7 | 46.4 | 11.0 | 68.2 | 6.3 | 39.8 | 9.3 | 16.0 | 11.4 |
| All medium mammals | 40.4 | 33.3 | 52.1 | 20.1 | 40.5 | 24.1 | 26.5 | 30.0 | 34.2 | 26.5 |
| All small mammals | 18.5 | 4.7 | 25.3 | 2.8 | 3.6 | 2.7 | 13.2 | 7.4 | 24.0 | 7.9 |
| All water-birds | 14.0 | — | 11.3 | — | 25.9 | — | 50.2 | — | 58.0 | — |
| Dingo (<i>Canis familiaris dingo</i>)† | 0.6 | 21.5 | 0 | 27.5 | 3.3 | 30.1 | 1.3 | 33.1 | 0 | 24.9 |

* Small ground mammals: No./100 trap nights; large and medium-sized vertebrates: percentage soil-plots with tracks; swan and coots: mean counts; July-June annually.

† Assumed to be from grooming.

followed by the rabbit and mutton-birds but not the bandicoots of similar weight), and the third, with the swamp wallaby (but not the red-neck wallaby of similar weight). The frequency curve declined sharply for prey heavier than swamp wallabies, and, at the other extreme, for very small prey (insects). There are anomalies masked by lumping data from Tables 1 and 2, notably for the wombats. Peak frequencies probably reflected abundances, availability and preferences for prey, although dingoes may not have taken adults always.

Seasonal and annual trends in diet

Because there was seasonality in the abundance of

swans and sea-birds, and because the coots were spasmodic in abundance, dingoes may have had to change their diet at Nadgee accordingly. Dietary frequencies for the major classes of prey are sorted by season in Table 3. There were significant peaks ($P < 0.001$) for large and medium-sized mammals and for large birds occurring in different seasons, spring, summer and autumn, respectively. At any season, the diet was not overwhelmingly one prey class or another. The highest seasonal frequency (61.7%, for large mammals) coincided with the period in the wild when most young grey kangaroos (Poole 1973), red-necked wallabies (J. Merchant unpubl.) and swamp wallabies (Harden & Fletcher

TABLE 2. Percentage occurrence of prey in the diet (d), and estimates of abundance* (a) of them and of dingo on four transects at Kosciusko, 1975-76

| | Transects 1. Ingeegood-bee | | 2. Jacobs River | | 3. Cowombat | | 4. Cascade | | Totals | |
|--|----------------------------|-----------|---------------------------------|-----------|--|-----------|--------------------------------------|------|-----------|------|
| | Altitude (m) | 1200-1500 | 800-1600 | 1200-1500 | Montane forest with heathy understorey | 1300-1600 | Moist sub-alpine forest; winter snow | Diet | Abundance | |
| Main habitats | | | Dry montane savannah; woodlands | | | | | | | |
| Woodland/grassland ecotone | | | | | | | | | | |
| Length (km) | 17.7 | d | 18.5 | d | 11.3 | d | 12.9 | d | 60.4 | |
| a | | | a | | a | | a | | | |
| No. scats | 161 | | 72 | | 65 | | 16 | | 314 | |
| No. plot nights | | 322 | | 341 | | 220 | | 241 | | 1121 |
| No. trap nights | | 1000 | | 400 | | 720 | | 320 | | 2440 |
| <i>Mammals</i> | | | | | | | | | | |
| Brown antechinus | 1.2 | 0.5 | 2.8 | 0.7 | 1.5 | 5.1 | 0 | 1.9 | 1.6 | 2.1 |
| Dusky antechinus | 0 | 0.4 | 1.4 | 0 | 0 | 0 | 6.3 | 0.3 | 0.6 | 0.2 |
| Marsupial mice indet. | 2.5 | — | 0 | — | 0 | — | 12.5 | — | 1.9 | — |
| Common wombat | 54.6 | 15.7 | 33.3 | 13.2 | 66.1 | 20.3 | 37.5 | 20.3 | 51.3 | 16.8 |
| Common ringtail possum | 6.8 | | 12.5 | | 9.2 | | 18.7 | | 9.2 | |
| Common brushtail possum | 1.2 | 0.6 | 5.5 | 1.5 | 3.1 | 6.3 | 1.2 | 2.9 | 0.6 | 1.3 |
| Mountain brushtail possum | 0 | | 2.8 | | 0 | | 0 | | 3.8 | |
| Possum indet. | 2.5 | | 6.9 | | 3.1 | | 6.3 | | | |
| Swamp wallaby | 4.3 | | 9.7 | | 6.1 | | 0 | | 5.7 | |
| Red-necked wallaby | 2.5 | | 1.4 | | 0 | | 6.2 | | 1.9 | |
| Wallaby indet. | 13.0 | 1.5 | 11.1 | 5.0 | 9.2 | 0.5 | 12.5 | 2.1 | 11.8 | 2.5 |
| Eastern grey kangaroo | 3.7 | | 0 | | 4.6 | | 0 | | 2.9 | |
| Broad-toothed rat (<i>Mastacomys fuscus</i>) | 2.5 | 0.4 | 0 | 0 | 3.1 | 0 | 0 | 0 | 1.9 | 0.2 |
| Bush-rat | 0.6 | 0 | 5.5 | 1.5 | 3.1 | 2.1 | 6.3 | 5.3 | 2.5 | 1.6 |
| House mouse | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 0 | 0 | 0.1 |
| Rabbit | 18.0 | 38.8 | 29.2 | 32.5 | 9.2 | 21.7 | 0 | 10.8 | 17.8 | 27.7 |
| Horse (<i>Equus caballus</i>) | 1.2 | 9.0 | 0 | 3.5 | 3.1 | 5.3 | 0 | 1.6 | 1.3 | 5.1 |
| Hair, hide and bone indet. | 11.2 | — | 5.5 | — | 20.0 | — | 0 | — | 11.1 | — |
| All large mammals | 79.5 | 26.2 | 56.9 | 21.7 | 89.2 | 26.1 | 56.2 | 24.5 | 75.1 | 24.4 |
| All medium sized mammals | 30.4 | 39.5 | 61.1 | 34.0 | 30.8 | 24.1 | 31.2 | 12.0 | 37.6 | 29.1 |
| All small mammals | 6.8 | 1.3 | 11.1 | 2.2 | 7.7 | 7.5 | 25.0 | 7.5 | 8.9 | 4.2 |
| Dingo† | 0.6 | 25.3 | 0 | 24.6 | 0 | 11.1 | 0 | 2.1 | 0.3 | 17.5 |

* Abundances estimated as for Table 1.

† Assumed to be from grooming.

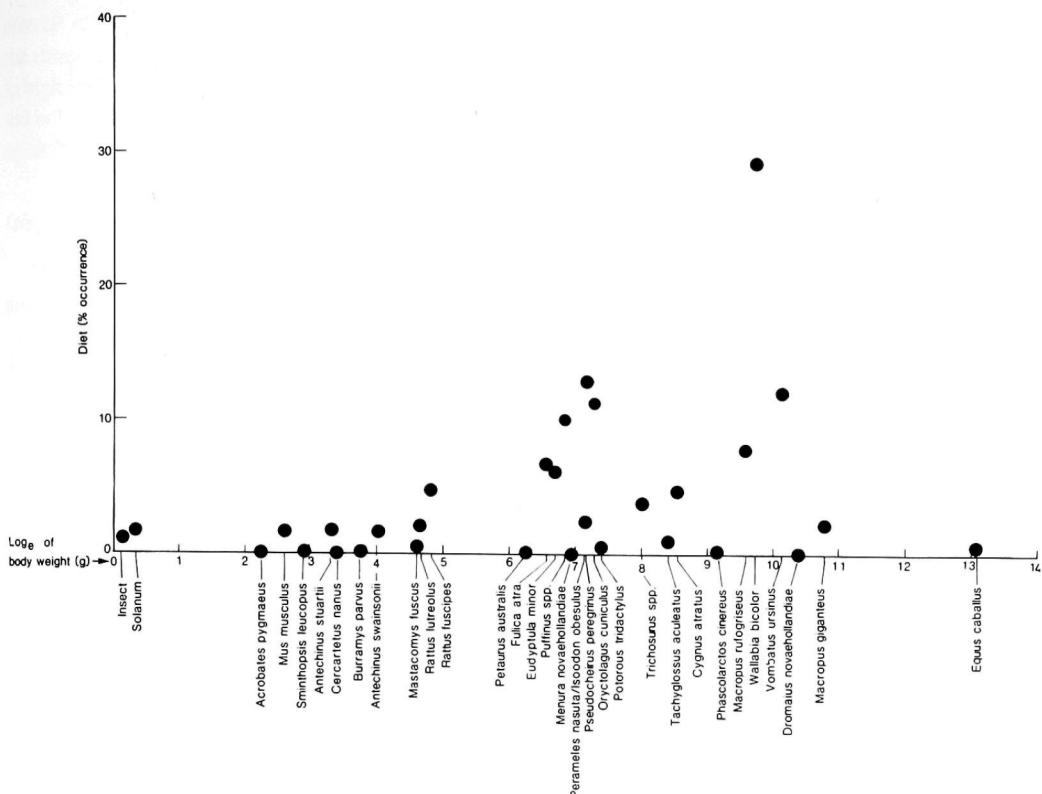


FIG. 3. Nadgee and Kosciusko: Modality in weight classes of prey identified in the diet combined. Identifications to genus only in Tables 1 and 2 are apportioned to species according to their respective percentage occurrences.

unpubl., quoted in Robertshaw & Harden unpubl.) leave the pouch.

Over time, the dietary frequencies for large mammals were inversely related to those for large birds and small mammals ($P < 0.1$) (Fig. 4). Although other prey abundances may have been partly involved in those trends, the great influx of water-birds appears to have been the major influence and to have relieved heavy predation upon wallabies and kangaroos.

At Kosciusko, seasonal differences were significant ($P < 0.05$) on Transect 1 where sample sizes were best, and highly significant overall ($P <$

0.001) (Table 4). Transect 2, which was not affected greatly by winter snows, provided no seasonal trend. Seasonal differences were due mostly to higher dietary frequencies for macropods and possums in winter. The dietary frequency for wombats did not change seasonally ($P > 0.05$). Differences between Transects 1 and 2 were significant ($P < 0.05$) only in summer.

Breadth of diet

At Nadgee, the number of prey species identified in faeces in any year was strongly related to the sample

TABLE 3. Seasonal trends in the diet of the dingo at Nadgee (Percentage occurrence)

| | July-Sept | Oct-Dec | Jan-Mar | Apr-June | Differences |
|------------------------|-----------|---------|---------|----------|-------------|
| Large mammals | 55.2 | 61.7 | 44.3 | 29.9 | $P < 0.001$ |
| Medium-sized mammals | 34.2 | 36.9 | 51.6 | 25.5 | $P < 0.001$ |
| Small mammals | 16.6 | 19.8 | 19.2 | 23.9 | NS |
| Water and sea-birds | 11.9 | 20.3 | 24.7 | 36.2 | $P < 0.001$ |
| No. of identifications | 455 | 301 | 306 | 290 | |
| No. of faeces | 386 | 217 | 219 | 251 | |

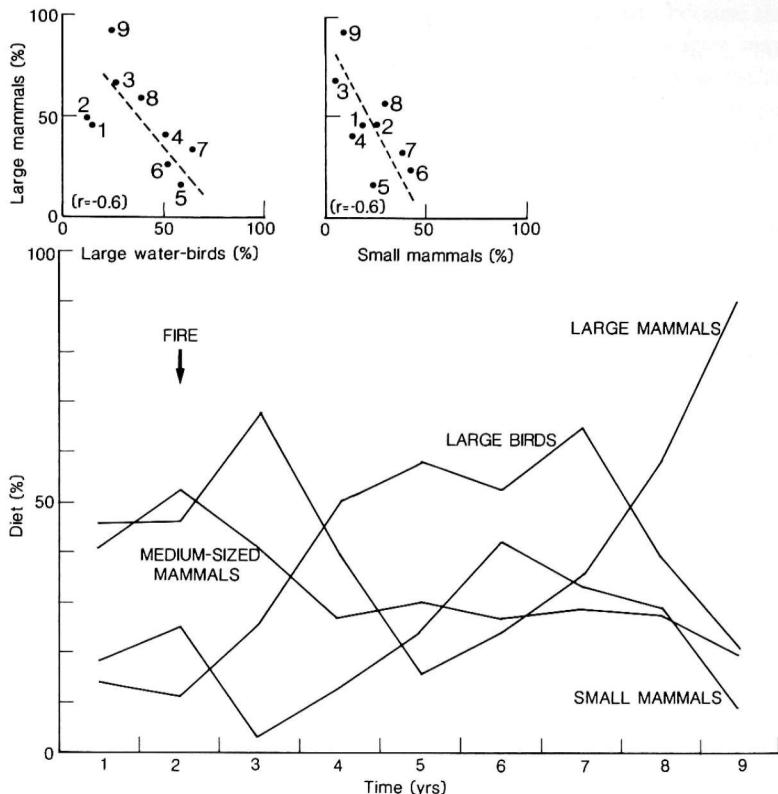


FIG. 4. Nadgee: Interrelationships between dietary trends of major prey-groups.

TABLE 4. Comparisons of diets by seasons and transects at Kosciusko (No. faeces containing prey items)

| Transect Season No. faeces | 1. Ingeegoodbee | | 2. Jacobs River | | 3. Cowombat | | Totals | |
|----------------------------------|-----------------|--------|-----------------|--------|-------------|--------|--------|--------|
| | Summer | Winter | Summer | Winter | Summer | Winter | Summer | Winter |
| Possums | 2 | 15 | 4 | 16 | 0 | 10 | 6 | 41 |
| Wombat | 40 | 48 | 7 | 17 | 1 | 42 | 48 | 107 |
| Macropodids | 11 | 27 | 2 | 14 | 1 | 12 | 14 | 53 |
| Rabbits | 14 | 15 | 10 | 11 | 0 | 6 | 24 | 32 |
| Other | 14 | 12 | 5 | 7 | 5 | 10 | 24 | 29 |
| Total prey items | 81 | 117 | 28 | 65 | 7 | 80 | 116 | 262 |
| χ^2_4 Winter vs Summer | 11.43* | | 7.16 NS | | — | | 19.33† | |
| χ^2_4 Transects 1 & 2 | Winter 6.54 NS; | | Summer 12.08* | | | | | |
| χ^2_8 Transects 1, 2 & 3: | Winter 15.04 NS | | | | | | | |

*P < 0.05; † P < 0.001.

size ($P < 0.01$) but not to prey abundances. When the annual abundances of prey were ranked from low to high and scored from 1 to 9, a multiple regression did not show any significant influence of abundance upon diet breadth.

Diet relative to abundance estimates of prey

Abundance estimates for specified prey and prey groups are shown in Tables 1 and 2, and dietary frequencies are plotted against them in Figs 5 and 6. The percentages of soil plots with tracks of medium sized and large mammals are used in those tables and figures. Data for the other estimate of abundance, the frequency of tracks on plots, are presented for peaks and troughs in those first estimates for selected species in Table 5. There were significant frequency shifts in tracks per plot between troughs and peaks in the percentage of plots with tracks for bandicoots, possums, rabbit, wallabies, large kangaroo, horses and dingoes.

Nadgee The dietary response was significantly functional only for the water-birds (Fig. 5(d); ($P < 0.01$) although dietary frequency did not reach much beyond 20%. The swans congregated on the lake in the summer months with few remaining in winter. About 30 000 coots arrived in Year 4 to augment an already high population of 1000 swans. Their presence was not seasonal. In that year 20.5% of faeces contained coot remains. The indeterminata for large water-birds in the diet at that time were probably mostly swans and coots also which could have increased their percentage occurrence overall from 23.1% to 37%. When sea-birds were included, the dietary frequency for all large birds in that year exceeded 50%, as it did from Years 4 to 7 (50.2–64.7%) (Table 1). The severest winter storm for 40 yr occurred in Year 5 killing many sea-birds including little penguins which were identified in 22% of faeces. Mutton birds were recorded at their highest level in dingo faeces in that year (16%), as were fish (22%), presumably scavenged also.

TABLE 5. Frequency distributions of tracks on soil plots for the highest and lowest values in the percentage of plots with tracks (as Tables 1 and 2)

| Species | Years | Plots with tracks (%) | Track frequency (%) | | | | | No. of plot-nights | |
|------------------|-----------|-----------------------|---------------------|------|------|-----|-----|--------------------|------|
| | | | 0 | 1 | 2 | 3 | 4 | | |
| <i>Nadgee</i> | | | | | | | | | |
| Bandicoots | 1 | 7.9 | 92.1 | 5.4 | 1.8 | 0.3 | 0.3 | 0 | 279 |
| | 2 | 1.2 | 98.8 | 0.8 | 0.1 | 0.3 | 0 | 0.1 | 1189 |
| Possums | 1 | 5.4 | 94.6 | 3.2 | 2.2 | 0 | 0 | 0 | 279 |
| | 3 | 1.4 | 98.6 | 1.2 | 0.2 | 0 | 0 | 0 | 1334 |
| Rabbit | 2 | 15.2 | 84.8 | 2.4 | 2.5 | 1.8 | 1.6 | 6.8 | 1189 |
| | 5 | 26.9 | 73.1 | 2.8 | 4.4 | 2.1 | 3.1 | 14.5 | 573 |
| | 9 | 15.3 | 84.7 | 5.3 | 1.9 | 1.4 | 0.9 | 5.8 | 793 |
| Wallabies | 7 | 24.2 | 75.8 | 14.9 | 5.9 | 2.5 | 0.6 | 0.3 | 644 |
| | 3 | 4.2 | 95.8 | 3.7 | 0.2 | 0.2 | 0.1 | 0 | 1334 |
| Large kangaroos | 8 | 4.1 | 96.0 | 2.6 | 1.3 | 0.1 | 0 | 0 | 758 |
| | 3 | 0.5 | 99.5 | 0.5 | 0 | 0 | 0 | 0 | 1334 |
| Dingo | 4 | 33.1 | 66.9 | 17.5 | 7.1 | 2.7 | 2.6 | 3.0 | 952 |
| | 9 | 9.8 | 90.2 | 5.7 | 2.5 | 0.9 | 0.5 | 0.2 | 793 |
| <i>Kosciusko</i> | Transects | | | | | | | | |
| Rabbit | 1 | 38.9 | 61.1 | 16.9 | 10.2 | 5.1 | 1.8 | 4.8 | 332 |
| | 4 | 10.8 | 89.2 | 5.4 | 3.3 | 0.4 | 0.4 | 1.2 | 241 |
| Macropodids | 2 | 5.0 | 95.0 | 3.8 | 0.3 | 0.9 | 0 | 0 | 341 |
| | 3 | 0.5 | 99.5 | 0.5 | 0 | 0 | 0 | 0 | 207 |
| Horse | 1 | 9.0 | 91.0 | 1.2 | 3.9 | 2.1 | 0.9 | 0.9 | 332 |
| | 4 | 1.6 | 98.3 | 0 | 0 | 1.2 | 0.4 | 0 | 241 |
| Dingo | 1 | 25.3 | 74.7 | 11.7 | 6.3 | 3.6 | 1.5 | 2.1 | 332 |
| | 4 | 2.1 | 97.9 | 0.8 | 0.4 | 0.8 | 0 | 0 | 241 |

All species significantly different at $P < 0.002$ except for Macropodid in Kosciusko, $P < 0.01$. Species with non-significant distributions not presented.

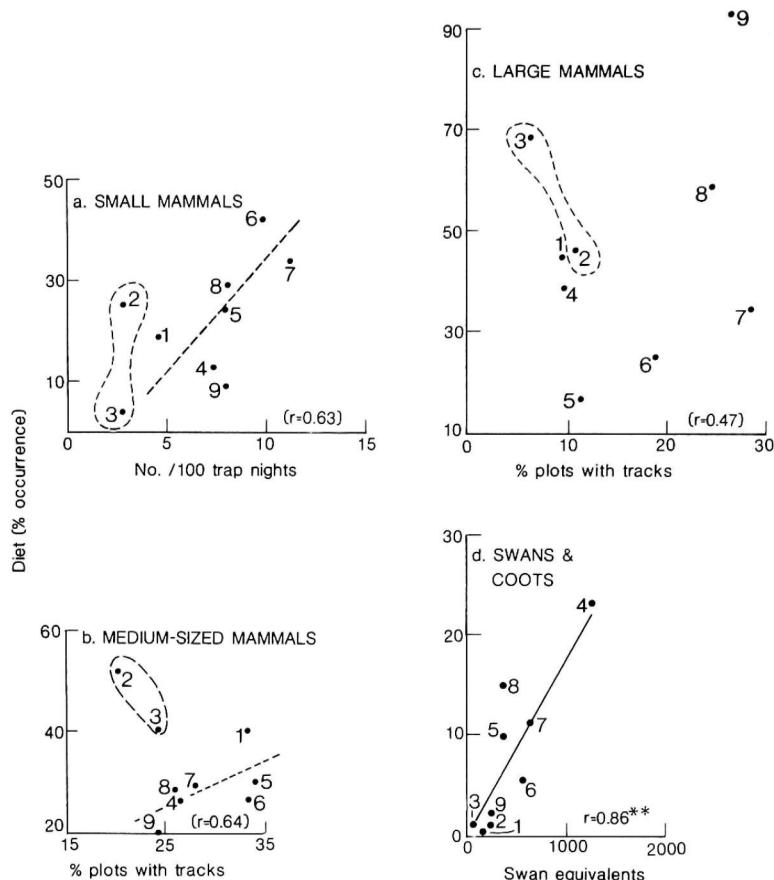


FIG. 5. Nadgee: Diet relative to estimated prey abundances. Numerals represent the years of study. $^{**}P<0.01$; r at $P(0.05)=0.67$. Values for r were calculated excluding data for Years 2 and 3 in Figs. 5 (a)-(c).

Dietary frequencies for small, medium-sized (mostly rabbits) and large mammals (mostly wallabies) were high at Nadgee during Year 2, Years 2 and 3, and Year 3 respectively, despite low abundance indices (Fig. 5a-c). Thus, there was every indication of heavy predation upon those groups towards the end of the drought and after the fire. Deleting data for Years 2 and 3 for consistency, caused the trends for diet on abundance estimates of small and medium-sized mammals to be positive but not significant ($P > 0.05$). The overall trend for large mammals was U-shaped. With the arrival of the coots dietary frequencies for large mammals fell sharply from 68.2% in Year 3 to 16% by Year 5. Then, as track records for the large mammals began to increase rapidly, so did their dietary frequencies which reached 93.3% in Year 9. The dietary frequencies of large mammals had the widest range of any group.

Kosciusko. In Kosciusko, the sample size for Transect 4 was small ($n = 16$) but that was where the tracking records for dingoes were also least (Table 2). Abundance estimates for the wombat, the predominant prey, were very similar on all four transects (16.7–20.7%) but dietary frequencies were not significantly related to them (Table 2; $P < 0.05$). However, dietary frequencies for the wombat, kangaroo and horse were significantly correlated ($P < 0.05$) regardless of their specific abundance estimates. Thus, the presence of one prey in abundance appears to have induced heavy predation upon scarcer prey. Small mammals were not important in the diet (8.9%). The only strong correlation between dietary occurrence and abundance estimate was for the rabbit ($r = 0.91$; Fig. 6a), although it too was non-significant ($P < 0.1$). Overall, dietary and abundance estimates for medium-sized mammals were similar at Kosciusko and Nadgee. The abun-

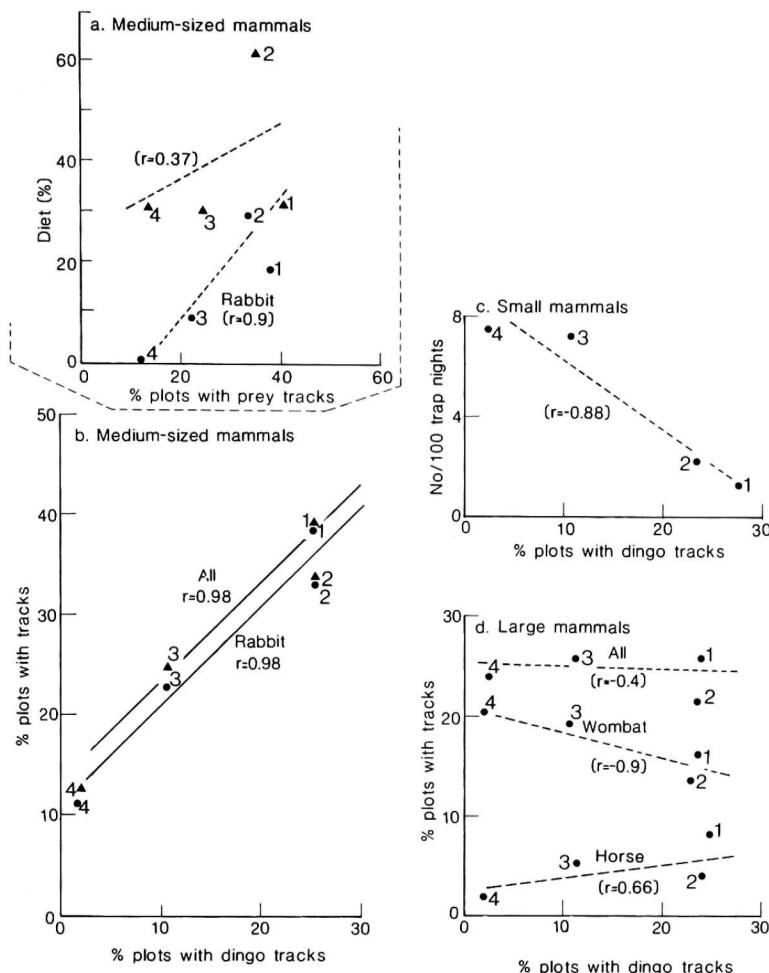


FIG. 6. Kosciusko: (a) Diet relative to estimated prey abundance for medium-sized mammals; (b,c,d) Relationships between estimates of predator and prey abundances. Numerals represent different transects (see Table 2). r at $P(0.05) = 0.95$.

dance estimate for the wombat in Kosciusko was 12.9 times larger than at Nadgee and the dietary frequency 24 times higher.

The relationships between abundance estimates of predator and prey

Nadgee. Time trends for estimates of abundance for major groups of prey and for the dingo, and the relationships between them, are presented in Figs 7 and 8 for Nadgee Nature Reserve. Trends for all mammalian prey indicate post-fire declines but regeneration subsequently to levels well beyond those prevailing pre-fire.

Coot and swan were the only prey for which a numerical response was measured (Fig. 7i). The peak in dingo estimates overall for the southern

study site coincided with the mass influx of coots to the lake and the peak in swan numbers in Year 4. The increase in dingo tracks was greatest near the lake. A pair of dingoes whelped there in that year (Newsome & Catling unpubl.) but dingoes also appeared to congregate about that great source of food. There was no similar increase in dingo numbers in the north of Nadgee at the time (Fig. 8). However, abundance estimates of dingoes throughout Nadgee Nature Reserve began increasing in the previous year before the coots and swan had arrived in any numbers. Other prey were scarce as a result of the fire and so perhaps the dingoes were travelling more in search of food. Predation upon all mammalian classes appears to have been severe at the time (Fig. 5).

Abundance estimates of small mammals declined immediately post-fire (Newsome *et al.* 1975;

Catling & Newsome 1981) and stayed low for two breeding seasons. Their increase lasted through Years 4–7, but there was no simple response in the abundance estimates of dingoes. The overall trend between the two estimates was negative and anti-clockwise over time (Fig. 7f).

Trends for tracks of medium-sized mammals were similar in the two sectors of Nadgee except that estimates peaked a year earlier in the north, in Year

4, for unknown reasons. Trends for rabbits, which comprised the majority of tracks, were, however, significantly similar ($P < 0.05$). Tracks of medium-sized mammals indicate that that group was the first to recover from the fire to peak in abundance in Year 5 (Fig. 7c). No linear trends were discernable between their abundance estimates and those of dingoes (Figs 7g, 8d). Changes in abundance estimates of medium-sized mammals were less marked than

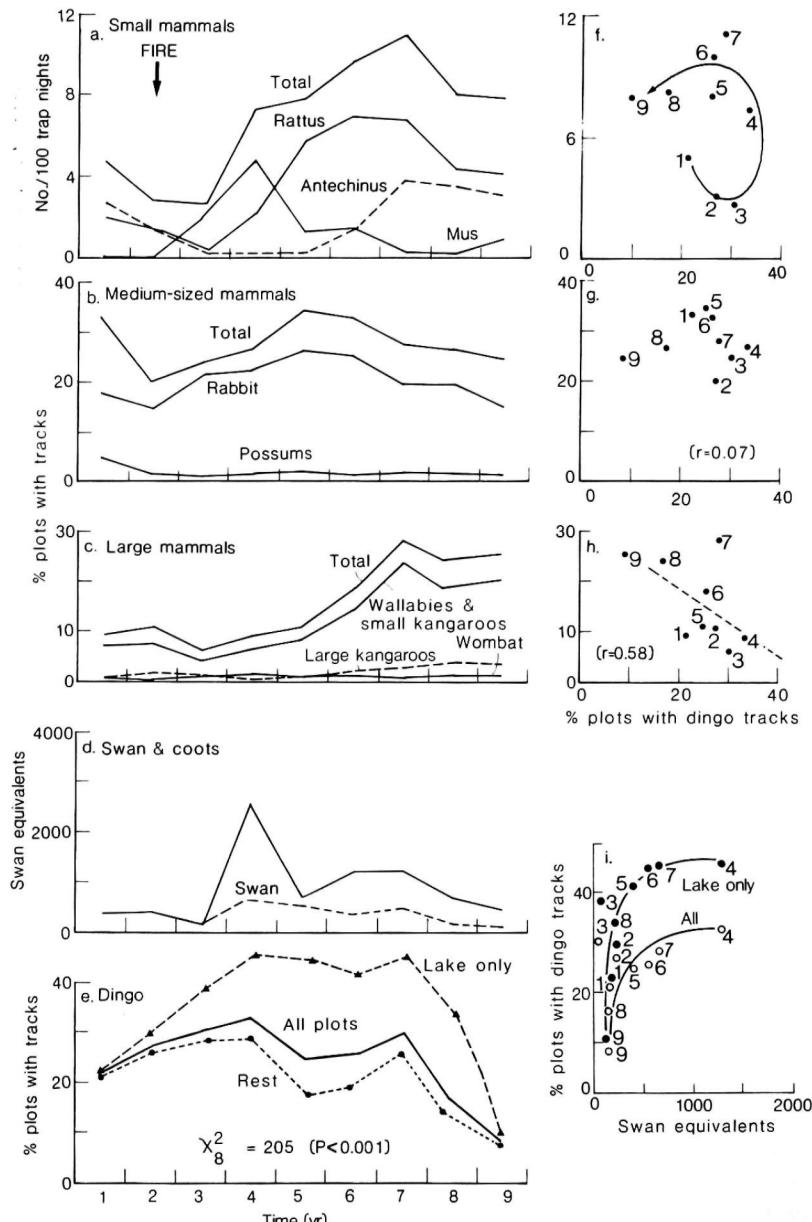


FIG. 7. Nadgee: Predator and prey abundances and their relationships at the main site. Numerals represent the years of the study. Curves were fitted by eye. One adult coot equals 0.14 of an adult swan by weight.

for other groups. As stated above, estimates for a principal prey, the possum, were probably poor.

Abundance estimates of large mammals declined significantly from autumn to autumn, and spring to spring, from before to after the fire throughout Nadgee (Newsome *et al.* 1975), and the decline is evident in the data as presented here (Figs 7c, 8b). That decline in tracks is in accord with the known large losses of life among kangaroos and wallabies during the fire (Fox 1978). Abundance estimates for large mammals (mostly wallabies) took longest to indicate recovery and reached a peak in Year 7 (Figs 7c, 8b). The recovery came only after the advent of so many water-birds and an increase in their dietary frequency in the dingo. While estimates for large mammals remained low in early years, those for dingoes were increasing and the incidence of large mammals in their diet was high, especially in Year 3 (Fig. 5). Those relationships were reversed later in the study. While tracks of large mammals were increasingly abundant and the incidence of large mammals in the dingo's diet was increasingly predominant, there was every sign (tracks, faeces, howling and sight records) that dingo populations were in decline. The general relationship between dingoes and large prey was negative on the study site though not significant ($P < 0.05$), and was not discernable to the north. Overall the decline in

abundance estimates of dingoes on the study site coincided best with declines for medium-sized prey, both mammals and birds (Fig. 7).

There was a marked secondary peak for dingoes in the north of Nadgee in Year 7 when abundance estimates of large mammals peaked (Fig. 8c). In Year 7, a pair of dingoes suddenly took up residence near a grassy flat and began to prey upon the 10–14 kangaroos living there. The dingoes whelped there which could explain the increase in their tracks. On average, tracks of large mammals were more numerous in the north than on the study site by a factor of 1.76. The factors for medium-sized mammals and dingoes were similar (0.59 and 0.52)

Kosciusko. The abundance estimates for the dingo were positively and significantly correlated ($P < 0.05$) with those for the rabbit and for medium-sized mammals of which they formed the majority (Fig. 6b). There were no significant relationships with estimates for large mammals (Fig. 6d). The strongest relationship was with the wombat, but track records for wombats did not change much between transects. There was a positive relationship with the horse (Fig. 6d) which would have been predominant if biomass were estimated. Where horse tracks were most prevalent, those of wombats and large kangaroos were least, the vice versa ($P < 0.05$). The abundance estimates of dingoes and

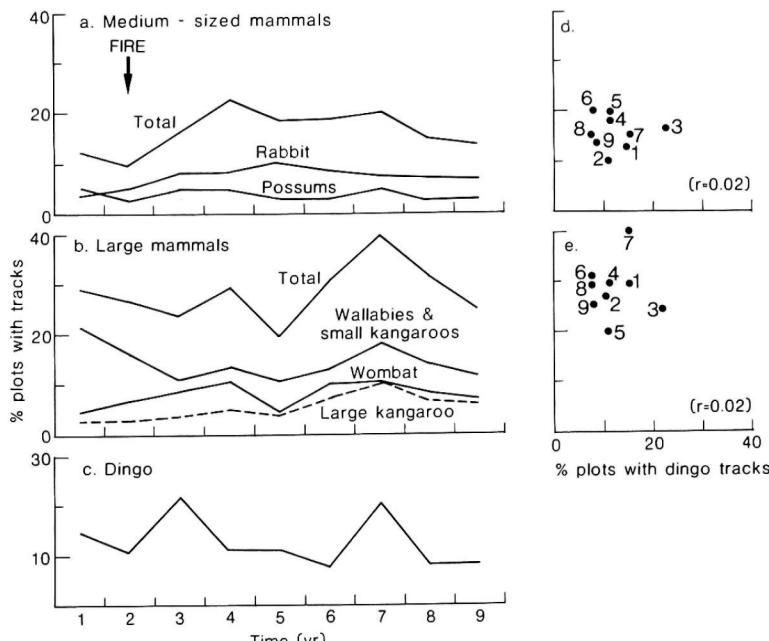


FIG. 8. North Nadgee: Predator and prey abundances and their relationships in the ancillary coastal study-area. (No trapping for small animals conducted, and no water-birds present.)

small mammals were related inversely but not significantly (Fig. 6c).

Examples of predation and scavenging and of amounts eaten

Although we occasionally saw dingoes feinting at swans, killing was witnessed only once. A dingo had six moulting swans cornered in a small shallow inlet. When the swans made a break for open water, a second dingo rushed out of the fringing scrub and the pair of them swiftly killed all six swans by biting them across the back behind the wings. Each dingo took two swans to the shore to feed, and two dingoes returned to feed on them for the next two days. On four other occasions, swan carcasses (4, 3, 2 and 1 of them) were found with similar injuries to those seen killed. No attacks on coots were observed, but dingoes probably rushed those at the edge of the lake just as they did for swans and flocks of gulls (*Larus spp.*) and terns (*Sterna sp.*).

On one occasion fresh tracks on the beach indicated that two dingoes had chased a swamp wallaby out of the scrub and killed it. Only the skin remained. On another occasion, however, one dingo was seen to chase, catch and kill a swamp wallaby along Nadgee Beach (R. Breckwold pers. comm.). Macropods were seen to escape on three occasions by taking to water. A grey kangaroo was found standing chest deep in a creek with a dingo sitting on the bank watching it. Both were disturbed by the observer. Another grey kangaroo, first heard crashing through the scrub, suddenly plunged into the creek to stand shoulder deep facing back to the scrub. A dingo appeared and sat on the bank watching the kangaroo for about 7 min before the kangaroo swam across the creek and disappeared.

The third pursuit involved a swamp wallaby and two dingoes. The wallaby burst out of the scrub and swam out into Salt Lake. Two dingoes appeared from the same fauna trail as the wallaby but disappeared back along it after becoming aware of the observer. The wallaby swam around for about 30 min before returning to the shallows where it stood waist deep. The observer waded out but it made no attempt to escape and was still there in an exhausted state 75 min later.

Predation upon the group of 10–14 kangaroos was mentioned above. Once dingoes entered the area, there were signs of chases and fights in the adjacent undergrowth and well-chewed remains of several kangaroos were found, and the numbers of kangaroos dwindled. In another location, an old male

kangaroo was killed and fed upon by two dingoes for five days.

In Kosciusko, several dingoes were heard howling in a valley over two consecutive days when two with radio-collars were located there. On the third day we investigated. Six dingoes emerged from the forest just on sundown, first to surround two wild horses which were grazing a grassy valley. The horses were alarmed but stood their ground. After a few minutes the dingoes left and joined two other dingoes, which, as we found the next day, were feeding on the carcass of a freshly killed six-month old foal. The damaged vegetation indicated quite a chase, with the foal being killed finally in a sphagnum swamp where it had become bogged. Only the well-chewed bones of the foal remained.

Dingoes were often seen scavenging along the beaches in Nadgee either singly or in pairs, and searching across moors, presumably for small lizards, rodents or perhaps insects. We know of seven cases of scavenging on macropod carcasses, five on birds and six on fish. In September 1975, a large Australian fur seal (*Arctocephalus forsteri*) was washed up dead. After it had been lying there for five days, the dingoes in the area (probably three of them) ate it in five days.

The amount of rabbit eaten by captive dingoes weighing 16.2 ± 1 kg has been measured at 0.45 ± 0.2 kg day $^{-1}$ (Green 1978). The consumption of free-living dingoes has been measured at approximately three times that amount, 1.4 kg day $^{-1}$, representing about 7% of the dingoes' body weight per day (Green & Catling 1977). The amounts eaten by dingoes in these examples of witnessed or assumed predation far exceed those amounts, and far exceed the food provided by a possum or a rabbit. Also, on 23 occasions between sampling periods from October 1973 to November 1975, food was placed on beaches to study sociality (Newsome and Catling, unpubl.). (The effect of that free-feeding may have influenced the track counts on two occasions only, in October 1973 and July 1975, by lowering them due to dingoes congregating on the free food. Averaging over a year diminished the influence of those lowered counts.) Carcasses comprised 17 legs from cows, two sheep, two grey kangaroo and two red-necked wallabies. All meat disappeared within 1–10 days. On at least three occasions the meat on cow legs weighing more than 20 kg were eaten in one night by two or three dingoes. The evidence from watching at carcasses was that dingoes gorged themselves continually, often over a series of days, until all food was eaten.

Discussion

There was only one consistent set of significant relationships between the estimates of diet, prey abundance and numbers of dingoes — that for water-birds. The super-abundance of water-birds over the middle years of the study appear to have allowed dingoes to increase beyond densities which could be supported at other times on the study site or in the north where there were no water-birds. The increase in dingo tracks was probably due to aggregation as well as breeding. The advent of water-birds in such abundance appeared to alleviate severe post-fire predation upon all size-classes of mammals. That post-fire predation may have been sufficiently severe to control some populations, e.g. the macropodids, for a period of two to three years. The fire-opened habitats may have increased the availability and vulnerability of prey.

Water-birds are really a special case of medium-sized prey of which the mammals provided the most consistent element of the diet at Nadgee. Their estimated abundances fluctuated least and the distribution of dingo tracks was most strongly related to those of rabbits at Kosciusko. However, there was an inconsistency between the predominance of the ringtail possum in the diet and possum tracks. Ring-tails often make their nests in low *Melaleuca* scrub, and dingoes may learn to flush them out. Nevertheless, the tracking method probably underestimated the abundance of possums. Most tracks of medium-sized mammal tracks were of rabbits which now live throughout the forests but concentrate on dunes around the lake and beaches. Medium-sized vertebrates as a whole, from reptiles to mammals, number at least 20, and any individual is a meal for a dingo.

Changes in numbers of large macropodid tracks after the fire had killed so many and after dingoes had killed most of the group of kangaroos in the north of Nadgee indicate that changes in tracks reflect changes in abundance. We have assumed also that macropodids bred up in the regenerated habitats post-fire after the apparent heavy predation declined after Year 3. However, the swamp wallaby, which is a solitary species (Kaufmann 1974), was the main macropodid preyed upon at Nadgee. Floyd (1980), studying the distribution of the species, found faeces at low densities throughout the two year old eucalypt plantations but concentrated at the edges of denser and taller 10 year old stands and in native forest, i.e. at the ecotones. Floyd

suggested the importance of food and cover as determinants. The distribution of all large mammals in this study favoured ecotones (Newsome & Catling 1979). The vehicle tracks along which we placed soil plots provided minor ecotones in the forest. Thus, clumped dispersion may have contributed to the increase in macropodid tracks in the last half of the study. Such proposed clumping of wallabies would constitute a real increase to dingoes utilizing tracks.

The decline in dingo tracks over the last three years of the study is thought to be real. Compared with the middle years of the study, few dingoes were ever seen and hardly any howling heard then, and fewer and fewer faecal samples were found. The apparent decline took place at a time when large mammals were increasingly predominant in the diet and their tracks were most numerous. These data are difficult to interpret. The increased frequency in the diet of dingoes indicates that there may well have been a real increase in the numbers and/or availability of large macropodids. That would mean, however, that dingoes may not have been able to maintain their numbers despite good populations of macropodids. If track records grossly overestimated macropodid abundance, then the dietary data indicate increasing and selective predation upon large prey which is hard to understand if dingo numbers were declining. Although some other factors than food may have been involved, the decline for dingoes was correlated with declines in abundance of water-birds and in track records of medium-sized mammals. At Kosciusko also, the track records of dingoes was poorly related to those of large mammals. In regions where wombat tracks were most abundant and where they were so important in the diet, tracks of medium-sized mammals were least abundant, and so were those of dingoes.

There are problems in nominating for the dingo what is primary, or secondary, or alternative prey. We recognize four categories of prey: *staples*, *supplementary*, *opportunistic* and *scavenged*. We argue that the most important prey are those upon which dingoes can rely over time and not necessarily those which comprise the highest average percentage occurrence (cf. Fuller & Keith 1980). In this study, we have called such prey the *staples*, and they appear to have been the medium-sized mammals. The water-birds were a special case among medium-sized vertebrates, and clearly highly prized. Medium-sized mammals comprise the largest suite of prey species, 11 of them, although some are rare.

The suite is likely to be enlarged by the young of large mammals which are also of medium-size. We were unable to tell what proportions of the wombats, wallabies and kangaroo in the diet were young animals; but during the season when the proportion of large mammals in the diet was highest, most young macropodids leave the pouch. In semi-arid Australia, Shepherd (1981) found that 80 of 83 red kangaroos (*M. rufus*) killed by dingoes were juveniles. Coyotes (*Canis latrans*), which are about the size of a dingo, kill more lambs than adult sheep in north America (Sterner & Shumake 1978). Wolves (*C. lupus*), however, take disproportionately high numbers of old deer (*Odocoileus virginianus*) (Hall 1971) but proportionate numbers of young (Pimlott *et al.* 1969; Fuller & Keith 1980).

Supplementary prey were mainly the large mammals. Although comprising major proportions of the diet at times and the highest on average, they were minimal at others and generally ancillary to the water-birds at Nadgee. Small mammals are an example of *opportune* prey. Although preyed upon functionally, there was no numerical response from the dingo to them. There is no way, either, that dingoes could depend upon such prey over time. Nor could they depend upon *scavenged* food which is a special category of opportune prey.

Dietary frequencies were grouped around three size modes in prey (Fig. 3) (assuming adult weights). The amplitude of those frequencies approximately doubled for every order of magnitude increase in prey size. One dingo should be able to hunt successfully for prey in the first and second modes (small and medium-sized); but we consider that two or more would usually be required for adults of the third mode (large mammals) (although an example of one dingo for one wallaby was mentioned above). We do not know whether dingoes purposely organize group hunts for large prey as observed in hyaenas (*Crocuta crocuta*) (Kruuk 1972) (although groups of hyaena can be much larger than known for dingoes). Presumably, communal hunting such as we have seen for small prey could be transformed immediately into cooperative hunting should a suitable target present itself. The examples of group killings could have arisen in either way. Group hunting appears to obtain much more food per dingo than the daily requirements. The success rate of such hunting, however, is unknown. Shepherd's (1981) observations indicate that, in favourable circumstances, the kill rate can be very high, 0.38 kg of prey (*M. rufus*) per kg of dingo, although only a fraction of the food was

eaten. As Shepherd points out, such a kill rate far exceeds that for wolves (*Canis lupus*) on moose (*Alces alces*), 0.12–0.19 kg prey/kg predator (Pimlott 1975; Fuller & Keith 1980). Group hunting for large prey improves both success rate and food obtained (Mech 1970; Schaller 1972; Bertram 1978; Kruuk 1972). Kruuk's data are best. For every doubling in the weight of prey killed, three times the number of hyaena were fed, and each obtained just about double the amount of food. Hyaena specially grouped into large packs to hunt zebra (*E. burchelli*).

The confrontation between six dingoes and two horses in Kosciusko appeared to have been coincidental. The dingoes had been resting in the adjacent forest in the afternoon, and happened to emerge onto the grassy valley just where the horses were grazing. The confrontation may have been indicative. It may have needed several of the eight dingoes gathered there to have cooperated to catch the foal on which they were feeding. Also, for the wombat to predominate in the diet in the mountains implies considerable amounts of cooperative hunting although individuals can suffer from debilitating mange (*Sarcoptes scabiei*) and presumably become easy prey. Moreover, there was a close association between dietary occurrences of large mammal there regardless of their respective densities. Purposeful group hunting of calves (*Bos taurus*) (Corbett & Newsome unpubl.) and red kangaroos (Shepherd 1981) has been seen in inland Australia.

Dietary frequencies were related to abundance estimates of prey at some times but not others, indicating a high level of opportunism in the dingo's feeding strategy. There may be little meaning in attempting to apply optimal foraging theory to so versatile a predator especially in so changeable an environment with its different prey populations fluctuating out of phase. Nor did the dingo increase the breadth of its diet during times of low abundance of food, as might be expected (MacArthur & Pianka 1966). Rather, the reverse seemed to be true: at such a time predation increased on medium-size and large mammals. Royama's (1970) concept of profitability appears to apply to the dingo more than optimization of time or energy in feeding (see Schoener 1971 and Krebs 1978).

In the breadth and composition of its diet, the dingo resembles most another medium-sized canid, the coyote (*C. latrans*). Large, medium-sized and small mammals comprised respectively 54.3, 35.1 and 17.8% of the diet in the dingo (this study overall) and 68.8, 52.9 and 29.9% in the coyote

[data lumped from Andrews & Boggess (1978) and Berg & Chesness (1978)]. The number of items recorded (> 45) were also very similar. However, dingoes appear to eat much less vegetable matter (2.3% in faeces only) than the coyote (41.9% in faeces and stomachs) (Gier 1975). Functional and numerical responses to abundances of medium-sized prey have been demonstrated for the coyote also (Clark 1972; Todd *et al.* 1981), and numerical responses to population changes in rabbits and microtine rodents (Gier 1975).

The much larger wolf (*C. lupus*) is a dietary specialist in North America compared with the dingo and coyote. For six areas overall, the dietary frequency of large ungulates was 85.1% (Mech 1970; Peterson 1977; Fullen & Keith 1980). Beaver (*Castor canadensis*) can be important also (Kolenosky 1972) possibly related to their abundance (Fuller & Keith 1980) but inversely to the abundance of white-tailed deer (*Odocoileus virginianus*) (Hall 1971; Petersen 1977). Medium-sized prey like the arctic hare (*Lepus arcticus*) are eaten (Tener 1954), and even small prey, rodents, birds, reptiles, and even insects, earthworms and berries (Mech 1970; Pimlott 1967) especially in summer.

The smaller prey are regarded as more the preserve of smaller canids. For the red fox (*Vulpes vulpes*) in Scotland, Burrows (1968) reported rodents at 5–42% occurrence, rabbits at 2–26%, and birds at 2–18% throughout the year, plus scavenging on deer. In Kosciusko National Park, insects and small, medium-sized and large mammals were found in 79.8, 33.3, 1.7, and 0.3% of faeces, respectively at alpine altitudes (Green & Osborne 1981) and in 18.8, 36.4, 37.6 and 17.6%, respectively in our study area at lower altitudes (Newsome & Catling unpubl.). At Nadgee, insects were unimportant and small prey most important to the fox at 2.9 and 51.9% occurrence, with medium-sized and large mammals comprising 29 and 30.3% occurrence, respectively. The large mammals may have been carrion on our study site because dingoes were present; but the fox can kill yearling macropodids (Hornsby 1982). Flexibility as predators appears to be a hallmark of canids whatever their size, so that the concepts of staple, supplementary, opportune and scavenged foods may apply broadly.

Despite flexibility for hunting alone or in groups for different prey, the study at Nadgee indicates that the dingo may lack the flexibility to increase group size to exploit a long-term change from a predominance of medium-sized prey to that of large prey. Under what circumstances, therefore, might

large groups develop? Although the different pack sizes at Nadgee (2–3) and Kosciusko (9) may have been fortuitous, they were probably related to food supplies in some way. Predation upon horses may be unusual, but such large prey represent an enormous food source. In themselves, they may induce formation of large packs. However, an apparent abundance of macropodids at Nadgee was associated with an apparent and severe decline in dingo numbers. Nadgee, with its frequent fires and fluctuating lake level, has an unstable environment. As a consequence, prey classes were never estimated at peak abundances simultaneously. In the Kosciusko region, extensive fires are half as frequent as at Nadgee, once every 5–12 years (Walker 1979), and there had been none in the study area for many years. There, both medium-sized and large prey were estimated to be simultaneously abundant on the adjacent Transects 1 and 2 which was where the large pack of dingoes lived.

It is therefore suggested that large packs may be a function not so much of high food availability *per se*, as of high availability of staple (medium-size) and supplementary (large) prey simultaneously over a number of years. That is, pack size may be related inversely to the level of temporal instability in the environment.

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Appendix 1. Minor items in the diet (percentage occurrence).

| | Nadgee (n=1102) | Kosciusko (n=314) |
|---|--------------------|----------------------|
| <i>Plants</i> | | |
| Seeds (mainly <i>Solanum</i>) | 2.3 | 0 |
| <i>Crustacea</i> | | |
| Freshwater crayfish (<i>Parastacidae</i>) | 0 | 1.3 |
| Indet. | 1.6 | 0 |
| <i>Insects</i> | | |
| Beetle (Coleoptera) | 0.4 | — |
| Insect indet. | 0.8 | 1.9 |
| <i>Fish</i> | | |
| Indet. | 6.9 | 0 |
| <i>Reptiles</i> | | |
| Monitor (<i>Varanus varius</i>) | 0.1 | 0 |
| Lizard indet. | 0.3 | 0 |
| Snake (<i>Elapidae</i>) | 0 | 0.3 |
| <i>Birds</i> | | |
| Fairy prion (<i>Pachyptila turtur</i>) | 0.1 | — |
| Cormorant (<i>Phalacrocorax</i> spp.) | 0.1 | 0 |
| King parrot (<i>Aprosmictus scapularis</i>) | 0.1 | 0 |
| <i>Crested tern</i> | | |
| (<i>Sterna bergii</i>) | 0.3 | — |
| <i>Superb blue wren</i> | | |
| (<i>Malurus cyaneus</i>) | 0.1 | 0 |
| Small bird indet. | 0.8 | 0.9 |
| <i>Mammals</i> | | |
| Short-beaked echidna (<i>Tachyglossus aculeatus</i>) | 0.3 | 3.2 |
| Koala (<i>Phascolarctos cinereus</i>) | 0.4 | 0 |
| Mountain pygmy possum (<i>Burramys parvus</i>) | — | 0.3 |
| Sugar glider (<i>Petaurus breviceps</i>) | 0.1 | 0 |

| | | |
|--|-----|-----|
| Yellow-bellied glider (<i>Petaurus australis</i>) | 0.2 | 0 |
| Glider indet. | 0.5 | 0 |
| Black rat (<i>Rattus rattus</i>) | 0.3 | 0 |
| Fox (<i>Vulpes vulpes</i>) | 0.2 | 0 |
| Cat (<i>Felis catus</i>) | 0.4 | 0.3 |
| Pig (<i>Sus scrofa</i>) | — | 0.3 |

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