

CHAPTER 1

INTRODUCTION

1.1 Preface

In 1968 the National Parks and Wildlife Service of New South Wales commenced an ambitious task of examining the biology of the dingo in the rugged escarpment east of Armidale. The inaccessibility of the area caused by the rough terrain produced many practical problems in undertaking such a study.

The initial aim of the study was to acquire knowledge of the biology of the dingo in this and other similar types of terrain in order to formulate dingo management policies. Gradually as more knowledge was acquired the aims broadened to study other components of the ecosystem which the dingo may have influenced or may have been affected by. This diversification involved work by postgraduate and honours students from the University of New England. These people, including the author, formed a team. Individually we benefitted from the participation in the joint work and assistance from the N.P.W.S. group with our own work.

1.2 The Dingo

1.2.1 Distribution and Description

The dingo is found throughout mainland Australia (Marlow, 1962). "Vermin fences and vigorous efforts at its destruction" (Wood-Jones, 1925) modify its distribution locally and even regionally. Ride (1970), Marlow (1962) and Macintosh (1956) state that the dingo was absent from central New South Wales, the mid-coastal region of Western Australia and the northern agricultural districts of Western Australia.

Clutton-Brock *et al.* (1976) state that the dingo was found in open country while Wright *et al.* (1966) describes "deep and inaccessible gorges, heavy forest, steep hills and valleys" as a natural haven for dingoes. McIntosh (1928) wrote that dingoes "prefer hilly country where they can get cover". L.E.R. Rhodes (May 21st., 1958) believed the dingo liked "plenty of softwood scrubs [rainforest] for them to camp and breed in". Calaby (1966) also states that dingoes prefer rainforest for shelter in the daytime.

Macintosh (1956) also states that "records of the early navigators and explorers are of tremendous importance", since their sightings and subsequent descriptions would be of "pure" dingoes. He wrote "the first reference to the dingo in European literature appears to have been an observation made in 1623 by Jan Corstenz who observed mastiff-sized tracks on the shores of the Gulf of Carpentaria". (N.B. Iredale (1947) spells Corstenz as Carstenz.) In 1688 William Dampier (Macintosh, 1956; Iredale, 1947; Hudson, 1974) described a couple of dingoes as "hungry wolves - lean like so many skeletons". Such references, and more detailed descriptions of dingo habits and coat colours, for example Sir Thomas Mitchell's 1836 description (Macintosh, 1956), have provided valuable information. Yet 360 years after the first description we still do not know what a dingo is or was like.

Wood-Jones (1925) provides the most comprehensive description of a dingo and is quoted here in full.

"The coat colour varies from black to almost white, the commonest colours being reddish yellow or a dark cream yellow. The coat is straight and fairly close, there being an ample

underfur. The individual hairs of the midline of the back are of an average length of 30mm. The dorsal surface of the head and midline of the back are usually darker than the general coat colour. The ventral surface and inner sides of the limbs are paler. The tip of the tail and the manus and pes are light; in yellow dogs being usually white. The ears are large and pointed at the tips; they are carried erect and are amply clothed and fringed with hairs. The tail is clothed in its whole length with hairs some 60mm. in length, and in the animal as usually seen in the bush is carried at a droop, though in animals reared as pets it is usually erect; when alert the tail is bristled into a fine brush. The naked rhinarium varies from black to pink, with brown as its most usual colour. The iris is varying shades of brown; the pupil is truly circular in all degrees of contraction. The manus and pes are large when comparison is made with common dogs of comparable size and build. An average dingo is some 1500mm. in head and body length, the tail being about 350mm. The skull is that of a typical dog in all respects, and especial note should be paid to that portion of bone which projects over the socket for the eye. This - supraorbital process - is somewhat swollen, so as to be convex on its upper surface".

Within this description there are a few points which need emphasizing.

1. The polymorphism of coat colour is widely reported, mainly by reference to early explorers' descriptions. However, it is still generally believed that dingoes, which are not a golden reddish tan, are hybrids with domestic dogs. St. George J. Mivart (1890) reported that the first white settlers found both black and red dingoes were common. Troughton (1941) states "the range of colour variation is greater than one would suppose, and the early explorers referred to seeing yellowish-white, piebald and blackish individuals". Rhodes (1958) quotes his father as saying that c.1850 the dingo was a brindle colour in 9 out of 10 cases in the upper reaches of the Clarence River. Matschie (1915) describes coat colour variation from reports by several early naturalists and from observations in his examination of material from the Queensland Museum, Berlin Zoological Museum and the Zoological Museum of Landwirtschaftliche Hochschule. Matschie (1915) reported that a "small white stripe on the brow and irregular distribution of the white colouring on the forefeet indicate descent from dingoes bred in captivity". Clutton-Brock (1977) also believed that these "white markings on the pelage" were an indication of the dingoes' past domestication. Thus

"freckled" feet may have been possible in "pure" dingoes and not a characteristic of hybrids.

2. The naked rhinarium colour variation is similar to that found in domestic dogs ranging from pink through light brown to black (Wood-Jones, 1925; Marlow, 1962).

3. The circular contracted pupil and the inflated and convex supraorbital processes are two features by which the members of the genus *Canis* differ from vulpine carnivores (Wood-Jones, 1921).

In addition to the above quotation from Wood-Jones (1925) there are three more points to be mentioned before the dingoes' description is complete. Firstly, the dingoes' first upper molar tooth has an incomplete cingulum (Wood-Jones, 1921 and 1925) and the upper carnassial length is large relative to the basicondylar length. Secondly, a vestigial first digit or dew claw was found on the hind feet of 1 of 15 British Museum skins (Clutton-Brock *et al.*, 1976). Mivart (1890) states that no wild species of canids ever has this vestigial first digit. Clutton-Brock *et al.* (1976) in their review of the family Canidae state that they "have not noticed any example of it [in wild canids], but it is relatively common in domestic dogs". Lonnberg (1916), while discussing the remarkable occurrence of the first hind toe in the common fox, *Vulpes vulpes*, also stated that the vestigial first digit was very rare in wild canids. Thirdly, on the dingo skin possessing the dew claw there was "a slight dark patch on the dorsal side of the tail in the position of the tail gland" (Clutton-Brock *et al.*, 1976). Hildebrand (1952) states that tail glands were found in all canids except *Lycaon pictus* and the domestic dog.

1.2.2 The term dingo

Iredale (1947) states the term dingo was first applied to the Dog of New South Wales in Trench's (1789) "Botany Bay". Trench (1789) briefly mentioned that "the aborigines called their dogs dingoes". The next reference to the dingo was in White's "Voyage to New South Wales"

1790, (Iredale, 1947; Barker and Macintosh, 1979), where the title Dingo appeared with a figure of a dog. Some authors (Le Souef and Burrell, 1926; Brereton, 1968; Hudson, 1974; Barker and Macintosh, 1979) believe that the term dingo, in aboriginal language, may have referred to white mans' dog and that **warrigal** was the name given to "their" dog.

More confusion exists over the dingoes' correct scientific name and authority. The term *Canis dingo* was first used by Meyer in 1793 but was predated by *Canis antarcticus* Kerr 1792 although this latter reference to the dingo of Australia was unused (Iredale, 1947). Tate (1951) asked the International Commission on Zoological Nomenclature to use its Plenary Powers for a fiat ruling on this situation since he believed that this caused *Canis antarcticus* Shaw 1832, the then commonly used name for the Falkland Island Wolf, to fall as a homonym. In 1957 the International Commission on Zoological Nomenclature decreed (Opinion 451, Vol. 15(17) pp. 329-338) "that the specific name *dingo* Meyer, 1793, as published in the combination *Canis dingo*, shall be the oldest available name for the Dingo of Australia (Class Mammalia)".

Prior to Iredale's 1947 paper on the scientific name of the dingo, many referred to the dingo as *Canis familiaris dingo* Blumenbach 1780. However as this predated the arrival of the First Fleet in Australia some thought it was an obvious mistake and should have been 1790 (Iredale, 1947). Examination of the early literature by Iredale and Troughton in 1934 (Iredale, 1947) failed to verify this later date or find a reference to *Canis dingo* by Blumenbach earlier than Meyer's 1793 reference. However Matschie (1915) cites Blumenbach in 1791, in the 4th edition of the Handbook of Natural History page 103, as referring to the Dingo of Australia. (This paper by Matschie (1915) was twice quoted by Iredale (1947)). Not only does this later reference predate both Meyer and Kerr but also refers to the dingo as, the currently accepted subspecies of *Canis familiaris* (Flecker, 1948; Stains, 1975; van Gelder, 1978) instead of a separate species of the genus *Canis* (ie. *Canis dingo*). However, examination of page 103 of this edition failed to verify the statement by Matschie (1915).

1.2.3 Taxonomy of the dingo

It is now generally agreed that the dingo was a feral domestic dog and hence a subspecies of *Canis familiaris* (Wood-Jones, 1921 and 1925; Flecker, 1948; Marlow, 1962; Stains, 1975; Clutton-Brock *et al.*, 1976; Clutton-Brock, 1977; Newsome, *et al.*, 1980; Harden, 1981; Newsome and Corbett, 1982). Dingo taxonomy has been approached by means of blood enzymes, blood antigens, cytogenetics, behaviour and numerical taxonomy.

Blood enzyme studies (Shaughnessy *et al.*, 1975; Clark *et al.*, 1975; Cole *et al.*, 1977) examining 30 loci in total have failed to differentiate between domestic dogs and dingoes. Seal (1975) found separation based on the identification of protein polymorphisms within species and of protein genetic differences between species of the genus *Canis* of only limited value. He concluded that this was due to a substantially lower incidence of polymorphic loci in Canoidea than had been found in other mammalian orders except Pinnipedia.

Swisher *et al.* (1962) and Bowdler *et al.* (1971) found the red cell antigens of the domestic dog to number eight distinct antigen systems designated A, B, C, D, E, F, G, and Tr. Bull and Bowdler (1972) examined the red cell antigens in several wild species of the family Canidae, including the dingo. They found in eleven dingo specimens A, AC, and C phenotypes but as antisera with activities anti-canine E, F, G, and Tr were not available for their study so the complete array of red cell antigens was not examined. They concluded that the "canine red cell antigens were of considerable antiquity and must have evolved before the domestication of the dog".

Baranov *et al.* (1973) found it was possible to immunologically distinguish seven species of Canidae, including the dingo, from the red fox. The Corsac fox and the Arctic fox were related antigenically to the red fox and so were the domestic dog, wolf and the Raccoon Dog but to a lesser degree. The dingo and the jackal had a higher value of cross reaction in turbidimetry than could have been expected on the basis of double diffusion and classical taxonomy (Baranov *et al.*, 1973). This latter finding indicates more similarity between the dingo and the jackal than the dingo and the wolf even though it is thought that the dingo may

have evolved from the wolf (Wood-Jones, 1921 and 1925; Macintosh, 1975; Barker and Macintosh, 1979). Similarly it suggests differences between the dingo and the domestic dog.

Chiarelli (1965 and 1975) states that no morphological differences in the somatic chromosomes have been found in the different races of the domestic dog or between the different species of *Canis*. Chiarelli (1975) did not include the dingo in his examination of the chromosomes of the *Canidae*. A comparison of the nature of the dingoes' chromosome morphology (Agudo Valero and Barasona Mata, 1971) with that of domestic dog (Chiarelli, 1975) indicated a high degree of similarity. Both had the same diploid chromosome number ($2n = 78$) and a similar arrangement of acrocentric or subacrocentric somatic chromosomes. In both taxa the X-chromosome was large and metacentric and the Y-chromosome small and metacentric.

Macintosh (1956) believed that behavioural differences could separate the dingo from the domestic dog. "Some aspects of his mating behaviour are quite different, his gait is characteristic of neither domestic dog, nor wolf, nor coyote, and is peculiarly his own. His howl and the various other noises he makes are not to be matched precisely by any other canid. His reserved and aloof attitude combined at the same time with a high capacity and apparent desire for affection is almost unique among the canids, (Macintosh, 1956)". These claims are largely unsubstantiated. Dingo vocalisation has been examined by Cohen and Fox (1976) and they made no comment as to its uniqueness among other canids. Further Kleiman (1968) observed dingoes mating on several occasions and recorded mating behaviours common in other canids.

Wood-Jones (1925) believed the ratio of the length of the upper carnassial tooth to the skull length was diagnostically useful in separating the dingo from domestic dog. Newsome *et al.* (1980) applied this criteria to their sample of dingo and domestic dog skulls and concluded that this ratio alone was not adequate to separate the two taxa. Macintosh (1975) initially used 120 skull characters to separate dingoes from domestic dogs. Finally he chose eleven characters to distinguish between the two and stressed the need to use all 11 even though he found the mandibular diastema between the second and third

premolars "absolutely differential in our [his] series of crania". Newsome *et al.* (1980) reaffirmed Macintosh's findings but established separation of taxa and sexes by canonical analysis on six skull characters. These characters were, in order of importance, alveolar distance along lower premolars, maxillary width, bulla volume, crown width of upper carnassial tooth, basal length of upper canine and width of nasal bones. Thus their findings indicated that dingoes had longer muzzles, larger bullae and main teeth, longer and more slender canine teeth, and flatter crania with larger nuchal crest. However, these findings were based on a sample of dingoes from arid Australia and thus may not necessarily be "typical" of all dingoes. (The Australian Native Dog Training Society separates dingoes into several types of which one is the Arid dingo). Newsome *et al.* (1980) concluded by stating "that so clearcut a distinction between dingoes and dogs can be made with so few skull characters, indicates that the name *Canis familiaris dingo* (Blumenbach, 1780) is warranted, at least", and implied full species recognition should be considered.

1.2.4 Arrival of the dingo

There were three main theories on how the dingo arrived in Australia. Some (Mivart, 1890; Ogilby, 1892; Gregory, 1906; Lucas and Le Souef, 1909 (cited by Barker and Macintosh, 1979); Etheridge, 1916) considered the dingo indigenous. Lucas and Le Souef (Barker and Macintosh, 1979; Wood-Jones, 1921) also believed that the dingo arrived unaided, using a landbridge to enter Australia. This latter notion forms the second theory. Supporters of the third theory, that the dingo was a domesticated companion of man, were divided as to whether man and dingo entered Australia by sea or landbridge. Generally it was accepted that man in this instance referred to aboriginal man rather than white man. However some (McGilp, 1921) believed that the dingo accompanied early Dutch explorers.

As it seems unlikely (Wood-Jones, 1921) that the dingo was indigenous, evolving in Australia, deduction of its time of arrival has been used to confirm the likelihood of the dingo accompanying aboriginal man by sea to Australia. It is argued that since the dingo is not found in Tasmania or Kangaroo Island (Wood-Jones, 1921; Macintosh, 1975) it

arrived after the flooding of these respective landbridges. Flooding of the Bass Strait (Tasmanian) link occurred between 12,000 and 13,500 years BP (Jennings, 1959; Macintosh, 1975). Therefore the earliest arrival could not have been before 13,500 years BP. Similarly as the dingo is not found in New Guinea and the separation of Australia from New Guinea was between 8,000-6,500 years BP it is unlikely that the dingo arrived before 8,000 years BP. Furthermore even at the last glacial low sea level 18-20,000 years ago crossings of channels of up to 100km wide would have been required (Jennings, 1971). Thus the dingo would have had to have accompanied man to Australia (Macintosh, 1975).

Fossil evidence of dingo antiquity from Mt Burr (South Australia), Gisbourne and Lake Colongulae (Victoria), Lake Eyre (South Australia), Devil's Lair (Western Australia) and the Wellington Caves (New South Wales) was discounted by Macintosh (1975) and Barker and Macintosh (1979) as having been disturbed or present in unstratified geological layers. The Devil's Lair and Mt Burr findings had indicated that the dingo was present 8,500 and 8,000 years BP respectively. Four dingo fossils have been accurately aged and are all less than 3,600 years old. These finds were at Fromm's Landing (South Australia), 3,000 years BP; Madura Cave (Western Australia), 3,450 \pm 95 years BP; Thylacine Hole on the Nullabor Plains, 2,200 \pm 96 years BP; and at Wombah on the north coast of New South Wales, 3,230 \pm 100 years BP.

With man arriving in Australia earlier than 30,000 years ago (Macintosh, 1975) the dingo must have accompanied a more recent (c. 4,000 years BP) influx of aboriginal man. There is further evidence for this conclusion as Barker and Macintosh (1979) suggested that the dingo is a recent addition to aboriginal mythology.

1.2.5 Biology of the dingo

Dingoes breed annually (Kleiman, 1968; Newsome *et al.*, 1973; Harden, 1978). Breeding generally commences in autumn. A pro-oestrus of two or three weeks duration is characterised by a swollen vulva with a bloody discharge, increased aggressive encounters between males and between females, and more frequent scent marking by both sexes (Kleiman, 1968). Oestrus lasts three or four days with females soliciting

attention from males by presenting and exposing the vulva. After intromission a copulatory tie is formed and the pair may stand back to back for two to twenty minutes (Kleiman, 1967 and 1968). Gestation lasts approximately 63 days (Newsome *et al.*, 1973; Harden, 1978) and Kleiman (1968) reports on the gestation period for four dingo bitches as 59, 62, 62 and 73 days duration. Young are born in late winter and early spring (Marlow, 1962). Litter size has been reported as 4 to 6 by Harden (1978) and 5.2 by Bekoff *et al.* (1981) while Newsome *et al.* (1973) found litter size to vary according to the environmental conditions. Weaning occurs at 1 to 2 months (Harden, 1978; Bekoff *et al.*, 1981) and pups become independent at 3 to 4 months (Corbett and Newsome, 1975; Harden, 1978; Bekoff *et al.*, 1981).

Dingoes may live for upto 10 years in the wild if they survive the high mortality rate in the first year (Newsome *et al.*, 1973). Harden (1978) believed that this mortality was post-independence and "probably caused by a combination of malnutrition and under nutrition, as at this age pups are small and have the additional disadvantage of an inability to hunt effectively while cutting adult teeth".

Most species of the Canidae are solitary with sociality only increasing during the breeding season and Kleiman (1967) states that for the few social species, excepting the bat-eared fox, communal living has probably evolved concurrently with the hunting of large game. Bekoff *et al.* (1981) lists the wolf, bushdog, dhole and the Cape hunting dog as the only social canids. Kleiman (1967) found many behavioural similarities between the dingo and the wolf and this would suggest that the dingo may have a social system like that of the wolf. Newsome *et al.* (1973) stated that dingoes, "though apparently operating alone, probably belong to loosely knit social units that coalesce during the breeding season" and also "function as a pack when the need arises to kill larger prey". This would indicate that dingo social organisation could bridge social and solitary forms of sociality at will depending on the size of the prey they consume. Harden (1978 and 1981) believed that the dingoes have a well developed repertoire of communication via posture, facial expression, vocalisation and olfactory sense which would suggest a more complex social structure than Newsome *et al.*'s (1973) loosely knit social units.

Although Bekoff *et al.* (1981) stated that the dingo was nocturnal, most studies suggest that the dingo was active at all times. Harden (1978) found that high activity periods occurred at sunset and sunrise while the middle of the day tended to be the time of lowest activity.

Newsome *et al.* (1973) and Harden (1978) found the dingo to be sedentary with irregular shaped home ranges of 2,500 to 5,000 hectares. The former study reported 75% of the resightings to be within 6.5 kilometres of the initial capture site. In the escarpment country of north-eastern New South Wales (Harden, 1978) where the shape of the home range may have been determined in part by the topography of the area, two types of activity were recognised by biotelemetry. Firstly there was a "searching movement" where activity was confined to a small area and secondly an "exploratory movement" where a substantial area of the home range was covered. Harden (1978) also suggested that those areas searched were areas of relatively high prey abundance, especially of high swamp wallaby density within his study area.

Despite the statement by Newsome (1983) that only 60% of the diet of the dingo was mammalian and the remainder consisting of birds and reptiles, over 90% by occurrence of the food items taken by dingoes were mammalian species (Coman, 1972; Newsome *et al.*, 1973; Whitehouse, 1977; Newsome *et al.*, 1983; Robertshaw and Harden, 1984). Members of the family Macropodidae were the most important species in all studies and the majority of the diet was made up of the larger native species, (see Table 1.1). The proportion of the other mammalian species varied from study to study as a result of geographical distribution and the variation in species abundance. A large array of species was taken by the dingo in all studies. The most diverse array, (35 species), was recorded by Robertshaw and Harden (1984) of which three species were not previously known to be present in the area.

The occurrence of domestic stock in the diet was low in all studies. Robertshaw and Harden (1984), whose field area contained only free ranged cattle, found less than 1 percent. Coman (1972) and Newsome *et al.* (1983) in eastern Victoria had the highest occurrence (7%). In the former study this occurrence consisted of 4% sheep and 3% cattle

while the latter contained 2% cattle and 5% sheep. However, in both studies the diet was determined from stomach contents from dingoes which may have been lured to a trap by the presence of domestic stock carcasses. In Newsome *et al.* (1983) 12% of dingoes caught were captured using sheep and cattle carcasses as lures. Newsome *et al.* (1973) found that in east Gippsland 3% of the diet consisted of sheep while in central Australia they reported 0.5% and 4% occurrence of cattle during good and drought seasons respectively. Whitehouse (1977) concluded that since sheep were as numerous in his study area as the red kangaroo and the euro, and only a minor dietary item, dingoes prefer game species over livestock.

TABLE 1.1
SUMMARY OF DIET STUDIES FOR THE DINGO

CATEGORY	DIET STUDIES (% OCCURRENCE)				
	A	B	C	D	E
LARGE NATIVE SPP.					
Macropods	31	43	69	57	54
Wombats	20	27	--	13	--
ARBOREALS	7	5	--	12	14
SMALL MAMMALS	2	1	4	2	20
DOMESTIC STOCK	7	3	5	7	<1
OTHER MAMMALS	12	11	14	22	17
SAMPLE SIZE (g=stomachs, s=scats)	204g	137g	160g	372g	1993s

A = Coman (1972) [34 stomachs were empty]
 B = Newsome *et al.* (1973)
 C = Whitehouse (1977)
 D = Newsome *et al.* (1983)
 E = Robertshaw and Harden (1984)

Robertshaw and Harden (1984), examining the diet of the dingo over a number of years when dingo numbers were increasing, inferred a change in the dingoes' hunting strategy from changes they observed in the diet during this period as an outcome of reduced prey availability. They proposed that the dingo population, by changing their selection of prey from a diverse array of prey species to the larger native species, may be

buffered against either increases in their own population or decreases in the wallaby population. They found that not only did the percentage occurrence of the larger native species increase (especially in the macropods), but the degree of carcass utilisation also increased. Their conclusions were based on the assumption that the dingoes did not concurrently alter their diet to take smaller and hence younger individuals of these larger native species. Shepherd (1981) found that in north-western New South Wales the group of dingoes in his study "clearly preferred juvenile animals as prey" and "when adults were taken they were females at the lighter end of the weight range". Robertshaw and Harden (manuscript) aged the macropods consumed by the dingo from an analysis of the same scats used in their previous study. They found from the aged bone fragments that the dingoes were taking a greater number of older macropod individuals. This they believed suggested that not only were more larger native species being consumed but also the larger individuals of these species. This finding reinforces the claim by Robertshaw and Harden (1984) that the dingo population may be buffered from changes in relative prey abundance by varying the hunting strategy and adapting their social organisation. Newsome *et al.* (1973) also postulated that the dingo had the ability to change its social structure depending on the size of the prey in the area but they saw such changes as differences between areas rather than a dynamic system within an area.

Robertshaw and Harden (1984) also showed that the diet of the dingo varied within a year. They believed that the increase in the diversity of prey items in the scats from May to October was related to behavioural and physical limitations imposed on the dingo as a result of breeding. Initially the breeding pair were limited to an area close to the den thus restricting the availability of prey and later the growing pups because of their size, were restricted to smaller game.

1.3 The Swamp Wallaby

1.3.1 Distribution and description

The swamp wallaby is found along the coastal strip of all eastern mainland states and the south-eastern tip of South Australia (Poole, 1981). Brazenor (1950) states that it is found throughout Victoria while Kirkpatrick (1970) and Poole (1981) extend its distribution inland upto 804 km in southern Queensland (Carnarvon Ranges) and in northern New South Wales (Warrumbungle Ranges).

The swamp wallaby inhabits a wide variety of habitat types. It has been commonly found in woodland and heathland (Poole, 1981) as well as in dense dry sclerophyll, wet sclerophyll forests (Calaby, 1966; Kaufman, 1974) and rainforest (Kaufman, 1974; Johnson, 1977).

The swamp wallaby is also known as the Black-tailed Wallaby (Lydekker, 1894) or the Black Wallaby (Kirkpatrick, 1970; Ride, 1970) and colloquially as the "stinker" (Kirkpatrick, 1970). It is a medium sized wallaby which has been described as stocky, thickset and robust (Wood-Jones, 1925). The recorded weights for adult males have ranged from 17kg (Merchant, 1983), 18kg (Kirkpatrick, 1970), 19kg (Edwards and Ealey, 1975) to 20kg (Poole, 1981) while adult female weights for these studies were respectively 13kg, 11kg, 17kg, and 14kg. The ears are relatively short and the fur is long, thick and soft but rather coarse (Lydekker, 1894). Both Wood-Jones (1925) and Poole (1981) restate this description of the fur being coarse but the fur has only a marginally thicker cross-section than the other macropods (Brunner and Coman, 1974). The following description of coat colour has been given by Lydekker (1894), Wood-Jones (1925), Kirkpatrick (1970), Ride (1970) and Poole (1981). The coat colour is generally dark brown or black with a lighter belly and chest, often orange in colour. The face anterior to the eyes is black with a light yellow to brown cheek stripe rising from the upper lip to the ear. The crown is a rufous orange while the paws, toes and terminal two thirds of the tail is black. The tail may have a white tip. Lydekker (1894) and Kirkpatrick (1970) mention the conspicuous black mark on the body behind the elbow. Lydekker (1894), Ride (1970) and Poole (1981) state that this description varies slightly according to the

geographic location of the specimen. Lydekker (1894) describes the northern or Queensland variety as having shorter coarser fur, more sharply defined markings, especially the cheek stripe, the rufous of the lower back being richer and brighter and the tail generally white-tipped.

1.3.2 Taxonomy of the swamp wallaby

The swamp wallaby (*Wallabia bicolor* Desmarest, 1804) is considered the sole extant member of the Genus *Wallabia* Trouessart 1905 (Calaby, 1966; Bartholomai, 1976). One other member, *Wallabia indra* De Vis 1895 is now extinct. Fossil remains of *Wallabia indra* were from the Pleistocene fluviatile deposits and from the Chinchilla Sand of the late Pliocene age in the eastern Darling Downs (Bartholomai, 1976).

The monotypic distinction arises from three unique features. Firstly, the mode of reproduction is characterised by preparturition fertilisation (Sharman *et al.*, 1966) or prepartum oestrus (Russell, 1974). Secondly, the chromosome number is peculiar to the swamp wallaby. While other macropod species usually have 16 chromosomes in each of the sexes, male swamp wallabies have 11 and the females only 10 (Sharman, 1961; Tyndale-Biscoe, 1973). Thirdly, the dental morphology is typical of a browsing habit and unlike that of the dental morphology of the Genus *Macropus*. A large sectorial premolar is retained throughout life and the whole tooth row is in occlusion in adults and there is no molar progression (Sanson, 1980).

Serological studies (Kirsch, 1968 and 1977) link *Wallabia bicolor* with *Macropus rufus* and other *Macropus* species in a close group. Martin and Hayman (1967) and Kirsch (1977) also suggest that *Wallabia bicolor* has been derived from the *Macropus* group by a continued process of reduction in chromosome number. Bartholomai (1975) indicated that this could not be verified from the then known fossil records. Bartholomai (1978) believed the genus *Wallabia* was distinct from the other Macropodidae in the late Miocene.

1.3.3 Biology of the swamp wallaby

The breeding season of the swamp wallaby has been reported by Kirkpatrick (1970), Frith (1973) and Poole (1981) as being continuous throughout the year. However, weight and size of pouch young in the New England escarpment (N.S.W.) have indicated a summer peak of births (Harrington, 1976; Jones, pers. comm.). Edwards and Ealey (1975), at Coranderrk Reserve near Healesville in Victoria, found all 11 female swamp wallabies to be carrying young of which the majority were to have left the pouch in early summer. Edwards and Ealey (1975) also concluded from the weights of 12 pouch young that the breeding season was not sharply defined.

Preparturition fertilisation was reported by Sharman *et al.* (1966) and Merchant (Calaby and Poole, 1971). Calaby and Poole (1971) amalgamated the findings from these studies but the sample size from which the length of the oestrus cycle and gestation period were taken was small (see Table 1.2 reproduced from Calaby and Poole (1971)).

TABLE 1.2

LENGTH OF CYCLIC REPRODUCTIVE PROCESSES

	Oestrus Cycle	Gestation Period	RPY to Oestrus	RPY to Birth
Range	29-34	35-38	21-27.5	28-32.5
Mean	31	36.8	23.21	29.93
Sample Size	4	5	7	8

where RPY = removal or loss of pouch young
(reproduced from Calaby and Poole, 1971)

With the duration of the oestrus cycle less than that of the gestation period, pregnant females have the potential to come into

oestrus and be fertilised before giving birth rather than just after as in most other Macropodidae (Sharman and Berger, 1969). Under such a condition the two separate uteri would be in use concurrently, one containing a near term embryo and the other a segmenting egg. The latter embryo then undergoes a period of discontinuous development (embryonic diapause) during the birth of the former embryo and subsequent suckling of the resultant pouch young.

The length of the pouch life has been reported as 8 months (approximately 245 days) by Kirkpatrick (1970), 250 days by Merchant (Calaby and Poole, 1971) and 256 days by Sharman *et al.* (1966). (Russell (1974) misinterprets Sharman and Berger's (1969) Figure 1 concluding that the length of pouch life for a full term swamp wallaby was 290 days). The termination of the pouch life by loss or removal of the pouch young causes the onset of the development of the hitherto dormant blastocyst, the recommencement of the oestrus cycle 23 days later, and the birth of this young in a further 7 days.

Sexual maturity was reported in both sexes at 15 months (Kirkpatrick, 1970). Although not reported specifically for the swamp wallaby it is likely that survival to this age is low as it is in most other macropod species (Frith and Sharman, 1964; Poole, 1973). Frith and Sharman (1964) demonstrated that this mortality occurred largely in the older pouch young and young-at-foot groups. Russell (1974) stated that this mortality was due to three factors. These factors were :-

- 1) Inadequate nutrition of large young during drought conditions,
- 2) Mechanical loss from the pouch of large pouch young in a disturbed female at flight, and
- 3) Separation of both older pouch young, which are spending short periods out of the pouch, and young-at-foot from the mother leaving the young subject to starvation and predation.

Apart from mother/young pairs, swamp wallabies are generally solitary (Calaby, 1966; Kirkpatrick, 1970; Frith, 1973; Edwards and Ealey, 1975; Southwell, 1976). Behavioural observations have been limited to the examination of group structure since the dense vegetation inhabited by the swamp wallabies makes direct observations difficult and their solitary nature further reduces the chance of observing intraspecific interactions (Southwell, 1976). Edwards and Ealey (1975)

aided by biotelemetry deduced that swamp wallabies were not markedly nocturnal but remained active throughout the day. However, this activity was interspersed with short periods of repose. They also found that males and females shared overlapping home ranges which were essentially dumbbell or rectangular in shape. Edwards and Ealey (1975) concluded that it was possible for individuals to have overlapping ranges and yet remain "solitary", avoiding continual encounters through the temporal use of their home range.

Edwards and Ealey (1975) found the long axis of the home range was up to 610m and the area enclosed by the widely separated radio-located points was 4.5 hectares for males and 7.2 hectares for females. This area was half of the theoretically predicted area needed for a home range of an animal the size of a swamp wallaby (Edwards and Ealey, 1975). Johnson (1977) radio tracked two 16kg male swamp wallabies at Dorrigo N.S.W. and found that the home range of one male was similar to the area found in the study by Edwards and Ealey (1975) but the other area was considerably larger (approximately 20 hectares). Johnson (1977) did not place any importance on these "ranges" since he thought they may be atypical. However Poole (1981) refers to Johnson's (1977) work as indicating that the swamp wallaby had a 20 hectare home range.

Johnson's (1977) home range data may be considered as atypical since he was working in an area where agricultural practices have altered the natural habitat. Improved pastures and crops interfaced with dense forest have resulted in various macropod species, at Dorrigo and in other areas, feeding in these man-modified areas and hence becoming pests. Not only has the swamp wallaby pest status in these areas but also in areas of reforestation (Baur, 1958; Floyd, 1980). Despite this pest status and attempts at eradication the swamp wallaby is still one of the most abundant species of macropod in eastern Australia (Edwards and Ealey, 1975). This may be a result of the rugged terrain and dense vegetation it inhabits and because its skin is unattractive to commercial shooters (Kirkpatrick, 1970).

1.4 Predator-prey interactions

1.4.1 General

This topic has generated much interest both scientifically and anecdotally. The scientific interest springs from a curiosity to understand both the biology of particular species and why certain species interactions are stable while others are unstable producing large fluctuations of numbers in the species involved (Pulliam, 1974; Murdoch and Oaten, 1975). Much of this knowledge is useful for the formulation of management policies for "game" and wildlife species (eg. Hornocker, 1972; Filinov, 1980) and for economic pests (Murdoch and Oaten, 1975).

Predator-prey studies can be divided into two categories. They are field oriented research (like the studies on wolves by Mech, 1966 and Jordan *et al.*, 1967) and mathematical modelling studies. These latter studies may be purely theoretical modelling (Schoener, 1971; Estabrook and Dunham, 1976; Parker and Stuart, 1976; Hughes, 1979; Caraco, 1980; Palmer, 1981; Lucas, 1983), modelling supported by a laboratory simulation (Emlen and Emlen, 1975; Charnov, 1976; Cook and Cockrell, 1978; Sih, 1980a and 1980b; Collier and Rovee-Collier, 1981) or modelling supported by the interpretation of field data (Pulliam, 1974; Werner and Hall, 1974).

There has been criticism of both fields of research. Many scientists believe that the development of models has vastly outstripped the study of the real situation they were meant to illuminate (Pulliam, 1974; Murdoch and Oaten, 1975). Furthermore, Oaten (1977) states that predictions based on deterministic models for the biological world of stochastic processes were often misleading. Most mathematical models in population biology have been deterministic with events as random variables instead of being represented by fixed probabilities per unit time as in stochastic models. Caraco (1980) suggests that multivariate utility theory, which can express preferences over attributes on a single scale representing an integrated response to variation in several different components of fitness, may be a better model foundation when there is stochasticity. However, Oaten (1977) points out that it may not be "optimal" for a predator to develop the memory and computing ability

needed to carry out the optimal foraging procedure if other abilities were thereby neglected. He goes on to suggest that a simpler suboptimal procedure that requires only minimal memory and computation may be better than learning to use Lagrange multipliers. Charnov (1976) concludes by stating that optimal foraging is not a theory but a point of view; a way of gaining insight into the behaviour of foraging organisms. Murdoch and Oaten (1975) were also critical of the field oriented research. They stated that "no satisfactory field analysis of the important components of the predator-prey interaction, that have been analysed so intensively mathematically and in the laboratory", have been undertaken.

1.4.2 Modelling

a) Historical preface

Mathematical models of predator prey systems were first developed by Thompson and Lotka in 1922 and 1923 (Pulliam, 1974) and by Volterra in 1926 (Maynard Smith and Slatkin, 1973). "Lotka-Volterra" equations were derived to predict population response to varying predator and prey numbers. These differential equations were based on three assumptions (Maynard Smith and Slatkin, 1973). Firstly, the breeding of both predator and prey were assumed to be continuous and dependent on the rate of food intake. Secondly, the rate at which prey were consumed was assumed proportional to the product of the densities of predators and prey. Thirdly, it was assumed that there was no self-limitation of the prey population. (Maynard Smith and Slatkin (1973) could also have reasonably included in the premise, that predators were not self-limiting). These assumptions were probably too simplistic with other objections being that all effects were instantaneous with no allowance for time lags, there was no randomness, and many key properties of the model were fixed or constant (Oaten and Murdoch, 1975a).

In the ensuing 60 years a large data base on the theory of predation has been accrued (Huffocker, 1970; Pulliam, 1974; Lucas, 1983). Pulliam (1974) states this was primarily due to an attempt to describe the fluctuations often observed in predator and prey numbers. However, Murdoch and Oaten (1975) stated that this interest was an attempt to explain the "apparent paradox" that many natural predator-prey systems

seemed stable, with no noticeable large fluctuations in their numbers, while attempts to add observed predator-prey interaction components, (eg. time lags and predator satiation), to the simple models of predation, caused the predicted populations to become unstable.

Two changes to the theory of predation occurred in this 60 year period. Firstly, Solomon (1949) divided the predator response to changes in the number of prey into two components, the "functional response" and the "numerical response". The former described the way in which the number of prey eaten per predator changed as a function of prey density. The latter described the way the number of predators changed as a function of prey density. (Murdoch and Oaten (1975) noted a third response type, "developmental", where the predators' growth rate and rate of development changed as a function of prey density.) The second change was a major shift in perspective in the 1960's as predator theory became more predictive than descriptive and concentrated more on the functional response of predation following the work of Ivlev (1961 cited by Pulliam, 1974) on prey selection in fish. This shift in perspective became quantified in 1966 when both Emlen (1966) and MacArthur and Pianka (1966) viewed prey selection in terms of energy expenditure and time allotment. MacArthur and Pianka (1966) defined optimal diet as one that minimised total search, pursuit and handling time per food item captured. (Schoener (1971) described these predators as "time-minimisers".) Tullock (1971 cited by Estabrook and Dunham, 1976) defined optimal diet as maximising food value per unit foraging energy following Emlen (1966). (Schoener (1971) described these predators as "energy-maximisers".) Whether a time-minimiser or an energy-maximiser, the net rate of energy intake while foraging was maximised (Pyke *et al.*, 1977). Such theory became known as Optimal Foraging Theory.

b) Aims of optimal foraging models

The main aim was to specify for a given animal that complex of behaviour and morphology best suited to gather food energy in a particular environment (Schoener, 1971). Since in practice this became quantified by measuring feeding performance as net energy yield per feeding time, the aim became modified to examine how, through natural selection, an animal maximises or optimizes four aspects of feeding

strategy (Schoener, 1971; Pyke *et al.*, 1977). These aspects were :-

- 1) the optimal diet, or choice of available prey,
- 2) the optimal foraging space, or where to feed,
- 3) the optimal foraging time, or when to feed, and
- 4) the optimal foraging pattern, or how to feed.

These aspects have been assumed independent of each other (Pyke *et al.*, 1977) but it is obvious that they will interact to some extent. The following sections will deal primarily with the first aspect, the optimal diet, and the other aspects only where they influence optimal diet.

c) Assumptions of optimal diet models

There are numerous simplifying assumptions for the various models but Pyke *et al.* (1977) states that they all assume "that the fitness of a foraging animal is a function of the efficiency of foraging measured in some 'currency' - usually energy - and that natural selection has resulted in animals that forage so as to maximise this fitness".

Some other assumptions raised by various authors are as follows :-

- 1) that there is a certain abundance and distribution of prey in the environment (Pulliam, 1974),
- 2) that there is a certain feeding pattern for predators in the environment (Pulliam, 1977),
- 3) that all prey are available at all times (Murdoch and Oaten, 1975),
- 4) that preference is independent of the time since the last meal (Oaten and Murdoch, 1975b),
- 5) that the different kinds of prey are distributed independently of one another (Estabrook and Dunham, 1976),
- 6) that individual prey are encountered one at a time (Estabrook and Dunham, 1976),
- 7) that elapsed times between successive encounters by the predator of prey individuals are equal (Estabrook and Dunham, 1976),
- 8) that the handling time per prey type is constant for

- each predator (Estabrook and Dunham, 1976),
- 9) that the predator recognises all prey types instantaneously (Hughes, 1979),
 - 10) that the constant handling time per prey type is independent of the rate of encounter or the accumulated number of encounters between predator and prey (Hughes, 1979),
 - 11) that the predator consumes all of the prey item (Sih, 1980a) and lastly
 - 12) that there was unlimited foraging time (Lucas, 1983).

d) Predictions of optimal foraging diets

There are three general predictions for optimal diets (Pulliam, 1974; Werner and Hall, 1974; Charnov, 1976; Estabrook and Dunham, 1976; Pyke *et al.*, 1977; Lucas, 1983). The first prediction was that prey types should be ranked according to the energy derived from the prey divided by its handling time (Lucas, 1983). Thus whether or not a food type should be consumed is independent of the absolute abundance of the food type and depends only on the absolute abundance of the food types of higher rank (Pyke *et al.*, 1977).

The second prediction was that prey types should either be eaten on every occasion or not at all (Lucas, 1983). Hence animals should never exhibit "partial preferences" except where theory is extended to include dietary constraints (Pulliam, 1975) or random variation in prey abundance (Pyke *et al.*, 1977). The third, and most examined, prediction states that a prey type should be added to the diet solely on the basis of the absolute frequency of encounter with higher ranked prey types (Lucas, 1983). The third prediction has been more clearly restated by a number of people. Schoener (1971) words this property in terms of the lower the absolute abundance of food, the greater the range of items that should be eaten. Hughes (1979) restates this as "the most valuable prey are always eaten when encountered but if their encounter rates are too low the diet expands to include less valuable prey".

Some models have extended optimal theory to include finite prey recognition time or the probability of the predator mistaking

nonpreferred prey for preferred prey (Estabrook and Dunham, 1976; and Hughes, 1979). Hughes' (1979) model predicted that "less valuable prey should be eaten when their relative abundances are high even when preferred prey are plentiful if there is a finite recognition time or alternatively, there is a significant probability of the predator mistaking them for the preferred prey". Palmer's (1981) model went further in that it predicted that predators whose prey varied primarily in handling time, would be expected to make fewer errors in the type of prey selected than predators whose prey varied primarily in net energy because the cost of making an error would have been greater.

Pulliam's (1974) model placed more emphasis on the addition of prey items to the diet being independent of the absolute density of the higher ranked items. With this belief predominating, he modified the third prediction to read: an increased density of preferred items will increase specialisation on those items, however an increased density of nonpreferred items will not change the probability that a preferred item was eaten given that it was encountered. However, Estabrook and Dunham (1976) predicted from their modified model that determination of optimal diet was not independent of the relative abundances of all the possible prey but that a small change in the relative value or ranking was more effective in changing the optimal diet than was a small change in the relative abundance of the potential prey.

Several further model variations have produced predictions concerning the breadth of the optimal diet. Sih (1980a) predicted from a model including partial consumption of prey, that a lower proportion of each prey item should be eaten if food availability increased. The model by Lucas (1983), incorporating varying foraging times and varying prey encounter rates, makes two predictions. Firstly, that animals should become more catholic in their diet choice as the amount of uninterrupted foraging time decreased. Secondly, as variance in prey encounter rates increased for a forager with patchily distributed prey, fluctuations in the number of prey types in the diet would also increase.

One reason for the varying foraging time may be the need for the forager to avoid certain risks, such as its own predation. Palmer (1981) predicted that such risks would be greater for a predator who consumed

prey which varied in handling-time as opposed to prey which varied in net energy. This was because a greater proportion of the total foraging time would be spent in the act of consuming the prey, and risk while feeding would likely be proportional to handling time (Palmer, 1981). Palmer (1981) also predicted that predators, in environments where prey availability fluctuates in space and in time, would be expected to re-evaluate their average yield over a shorter time interval or over fewer individuals if their prey varied in handling-time as opposed to net energy.

One type of foraging strategy not predicted by the optimal foraging models was "switching". Murdoch (1969) was the first to introduce this concept and defined switching as follows. "As a prey species becomes more abundant, switching occurs if the relative amount which that species forms of the predators' diet increases disproportionately in comparison with the expected amount. The expected amount is based on the proportion that the species forms of the food supplied and on the observed diet when both prey are equally common". A less rigorous definition is now generally accepted (Murdoch and Oaten, 1975; Cornell, 1976). Cornell (1976) defines predator switching "as the ability of a general predator to become conditioned to its most abundant prey so that the number of attacks on that prey are disproportionately greater than would be expected by chance encounters. Thus the predator exhibits a flexible search image influenced by learning. If switching were to be included in optimal foraging theory, the third prediction (that prey types were added on the basis of the absolute frequency of encounter with higher ranked prey items) may have to be modified to include the learned enhancement of the capture of the most frequently encountered prey item.

1.4.3 Canine predator-prey interaction

a) General

Many studies have placed an adaptive value on a particular species' social organisation, particularly in regard to the exploitation of a resource/prey or the avoidance of predators (for example, Crook, 1970; Barash, 1974; Jarman, 1974). Furthermore, species are not necessarily characterised by one type of social organisation (Kruuk,

1972; Macdonald, 1983) but may exhibit a plasticity of social structure as is evident in many mammalian carnivores (Messier and Barrette, 1982). Diverse selective pressures have contributed to this plasticity of social groups in carnivores (Macdonald, 1983). These pressures include, the benefits of greater numbers for the defence of kills and territory (Lamprecht, 1978; Bekoff and Wells, 1981; Bowen, 1981; Macdonald, 1983); the increased efficiency and greater hunting success when utilising larger prey species (Fox, 1975; Kruuk, 1975; Zimen, 1976; Macdonald, 1983); the potential for information transfer and social learning and the advantages of alloparental behaviour patterns (Macdonald, 1983).

Available prey size has been highly correlated with group formation in social canids (Bowen, 1981) but it is not clear whether this was a result of a direct response or as an indirect response to the other selective pressures (Messier and Barrette, 1982). Messier and Barrette (1982) reported that prey size may only facilitate the cohesion of groups formed for other reasons and that the co-operative hunting hypothesis was not sufficient to explain the social system of the coyote or even other canids.

b) The coyote (*Canis latrans* Say 1832)

Description

The coyote is smaller than the Gray wolf but larger than a jackal. The average weight of an adult male coyote is 12kg (Mech, 1970) but the weight is subject to geographical variation with coyotes weighing 11.5kg in the Mexican desert and up to 18kg in Alaska (Gier, 1975). (Thus coyotes and dingoes have a similar weight range.) The following description is quoted from Clutton-Brock *et al.* (1976). "The coyote stands nearly as high at the shoulder as the wolf but is much more lightly built with long slender legs, large ears and a bushy tail. Pelage characters are variable as with all canids that cover a wide geographical range. The coat is usually long and has an overall buffy-grey colour with long dark-banded guard hairs. Legs and sides may be fulvous. Under-parts and chin are pale or nearly white. Tip of tail was usually black."

Distribution

Since the recognition of the coyote as a separate species in 1832, the coyote has been noted as extending its distribution (Gier, 1975). In the 1850's the coyote was found west of the Mississippi River into the Sierra Nevada mountains, north into Alberta and south to southern Mexico through California but absent from the Gulf States (Gier, 1975; Clutton-Brock *et al.*, 1976). It now occurs north of Costa Rica through Canada and Alaska (Stains, 1975) but is still not common in the eastern regions of North America (Clutton-Brock, 1976).

Food habits

Coyotes are generally regarded as solitary predators of rodents and lagomorphs (Bowen, 1981; Springer and Smith, 1981). Gipson (1974) summarised the findings of western coyote dietary components and found that rabbits and rodents occurred in 41.1% and 36.2%, respectively, of the 16,355 stomachs and scats. However, coyote diets vary markedly within and between habitats (Gier, 1975; Bekoff, 1977). Where the biota was relatively simple, single species (eg. the jackrabbit) may constitute as much as 75% of the diet (Clark, 1972). In Arkansas, poultry carrion (34%) and persimmons (23%) were the main dietary items (Gipson, 1974) thus illustrating the adaptability of this species. While ungulates were generally not considered important, Cook *et al.* (1971), White *et al.* (1972), White (1973), Springer and Smith (1981) and Bowen (1978 cited by Bowen, 1981) reported that large ungulates may be the dominant species in the diet in some regions. In the latter study (Bowen, 1981) 86.5% of the summer diet and 94.9% of the winter food consisted of 18 mammalian species. But despite the diversity of prey eaten, three species accounted for 71.5% of the diet in winter and four species accounted for 68.7% of the summer diet. These species were elk, mule deer, *Microtus* spp. and Columbian ground squirrels. Although the diversity of prey items was not as great as that found for the dingo in eastern Australia the percentage of mammalian and the high percentage of a few dietary items was similar.

The interaction of group structure and prey selection

Coyote populations may have similar diets yet differ in social organisation and in particular group structure. In Texas (Andelt, cited by Macdonald, 1983) and the Rocky Mountains (Bekoff and Wells, 1980) coyotes fed mainly on rodents. In the former area they lived in groups while in the latter area they lived in pairs. Cook *et al.* (1971) and White *et al.* (1972) working in another part of Texas found that deer comprised a high percentage of the diet of coyotes which were essentially group-living. Thus it was also possible for the coyotes to have a similar group structure while having a markedly different array of prey items. Elsewhere they fed predominantly on ungulate carrion and in such cases the larger packs were more successful at defending these carcasses from rival packs (Bekoff and Wells, 1980). Yet in other areas coyotes may kill some large ungulates and live singly or in groups (Bowen, 1981). Bowen (1981) found that all coyotes were in good nutritional condition but the group-living coyotes spent less time hunting and more time resting suggesting that their energy requirements were met more efficiently than solitary or paired coyotes. Hence while some studies may have shown a high correlation between prey size with increased efficiency of utilisation and group formation it does not hold for all coyote studies. In some studies group size was considered supra-optimal for hunting and the presence of such groups has been interpreted to mean that group size was determined by other selective pressures (Macdonald, 1983).

In some studies man had previously and concurrently depressed group size by reducing coyote numbers and/or created vacant territories reducing the cost of dispersal (Macdonald, 1983). This latter effect of man and the rapid expansion of coyote geographic range may have resulted in coyote populations not obtaining a balance in the studied systems. Thus group size may only be transitional in some studies and not reflect group size under equilibrium, if such a state is obtainable.

c) The wolf (*Canis lupus* L. 1758)

Description

The gray or timber wolf is the largest extant canid, weighing from 27kg to 80kg (Stains, 1975). Thus it is generally twice as heavy as the dingo (Bekoff *et al.*, 1981). The following description comes from Clutton-Brock *et al.* (1976). The wolf has a heavy body with a large head, long legs, long bushy tail and erect ears. The pelage is variable from white to black, but generally grey agouti and tawny colours are more common. The legs, muzzle, ears and underparts are usually pale or reddish and there is often a dark saddle and a dark patch over the tail gland. The fur is thick with long guard hairs.

Distribution

The distribution of the wolves has contracted as a result of mans' direct attempts at eradication and indirectly from other activities of man. The wolf was widespread in the northern hemisphere and did not show particular habitat preferences (Clutton-Brock *et al.*, 1976) but was absent from deserts and rainforest (Pimlott, 1975). Today there are a few isolated populations in Europe and south-western Asia and it is almost extinct from the U.S.A. except in wildlife parks and Alaska. As in Alaska, it is still widespread in the U.S.S.R., western China, northern India and Canada.

Food habits

The wolf is primarily a predator of large mammals (Mech, 1970; Pimlott, 1975; Van Ballenberghe *et al.* 1975; Holleman and Stephenson, 1981). In winter they exhibit a dependence on large ungulates (Pimlott, 1967 and 1975), while in summer they take a wider variety of prey items although ungulates remain as the major component of the diet, often in excess of 75% (Murie, 1944; Thompson, 1952; Mech, 1966; Pimlott *et al.* 1969; Van Ballenberghe *et al.* 1975; Fuller and Kieth, 1980). Pimlott (1975) citing Hall (1971) and Tener (1954) state that there were only two cases where a single species was more important than the ungulates. In the former study beavers, only available in the summer, occurred in more

than 75% of the scats for that season as a result of declining white-tailed deer numbers. In the latter study arctic hare predominated in the diet from Ellesmere Island. Fuller and Kieth (1980) also found that the beaver was an important (13% - 52%) prey item and its inclusion in the diet was related to its local abundance.

The interaction of group structure and prey selection

Wolves are highly social creatures and are usually observed in groups of 2 to 8 (Mech, 1970). Only 12 % of 7,477 wolves were observed singly (summarised from Mech 1970) and such cases may have been the result of temporary group splitting (Mech, 1970). The upper limit to pack size is unknown but Rausch (1967) reported sighting a pack of 36 wolves (the largest reliable report - Mech, 1970) in southern central Alaska. With relatively so few lone wolves and the difficulty and danger associated with capturing prey much larger than the predator it was considered rare for a lone wolf to hunt and kill these large mammals (Mech, 1970; Pimlott, 1975). Such individuals were usually found scavenging from carcasses left by packs (Jordan *et al.*, 1967). However, Cowan (1947) believed a lone wolf in his study had managed to kill an elk indicating that such an event was possible.

While most wolves exist in groups and prey upon ungulates there is little evidence to suggest that group-living was or was not correlated to the size of the prey consumed. However group size variation would suggest that packs were formed as a result of other selective pressures rather than the ability to kill the large ungulates and defend their carcasses. Stephenson and Ahgook (1975) stated that not all the wolves in a pack play equal roles in killing ungulate prey. They further stated that "usually 2 wolves in a pack of 5 do the great majority of killing, the remaining wolves in a pack playing peripheral roles in the hunt" or if very old or young taking no active part. This further indicates that packs may be larger than they need to be simply for the killing of their prey.

1.5 Aims and design of the study

The prime aim of this study was twofold, firstly to document the effects of predation by the dingo on the swamp wallaby and secondly to examine prey selection by the dingo. This was to be achieved by comparing two sites in which the relative numbers of dingoes varied markedly and for which the potential prey diversity was similar.

Within each site the diet of the dingo was to be determined as well as several swamp wallaby reproductive and morphometric parameters. Between sites the relative numbers of dingoes, and the three largest macropod species, were to be estimated. By a comparison of sites it was hoped to determine how the prey selection of dingoes responded to changes in dingo numbers and what the effect of greater predation was on the swamp wallaby.

Site modification, division into two parts, became necessary when a portion of the site with a relatively high number of dingoes was found to have too few swamp wallabies present to make the proposed comparison possible. Diet and macropod density data were still collected from the portion with the low number of swamp wallabies so as to assess the effect of the proposed shooting of swamp wallabies for reproductive material.

CHAPTER 2

MATERIALS AND METHODS

2.1 Description of the study area

2.1.1 Location

The study area was located in the north-east corner of New South Wales approximately fifty kilometres due east of Armidale (30° 32'S, 152° 20'E). It consisted of three distinct sites. The first site was part of the Styx River State Forest (S.R.S.F.) that lay to the north of the Armidale to Kempsey road. The remaining sites, Diamond Flat and Petroi, were east of the first site but separated only by a steep valley drained by George's Creek. The border between Diamond Flat and Petroi was a ridge running due east from "Petroi Hill" to the edge of the escarpment (see Figure 2.1).

2.1.2 Topography and vegetation

The area was dissected by four major drainage systems. They were the Dyke and Styx Rivers and George's and Cunawarra Creeks. This dissection and the area's position on the edge of the Great Dividing Range has produced a rugate surface with an altitude range of 1300 to 300 metres above sea level (a.s.l.). Within this larger area, all sites had a similar altitude range of 900 - 1200 metres a.s.l..

The three sites had a similar array of habitat types. These were grassy woodland, shrubby open forest, tall open forest, closed forest, herbfield, and heath (Specht, 1970). Tussock grassland, although present in the eastern sites did not occur in the Styx River State Forest site.

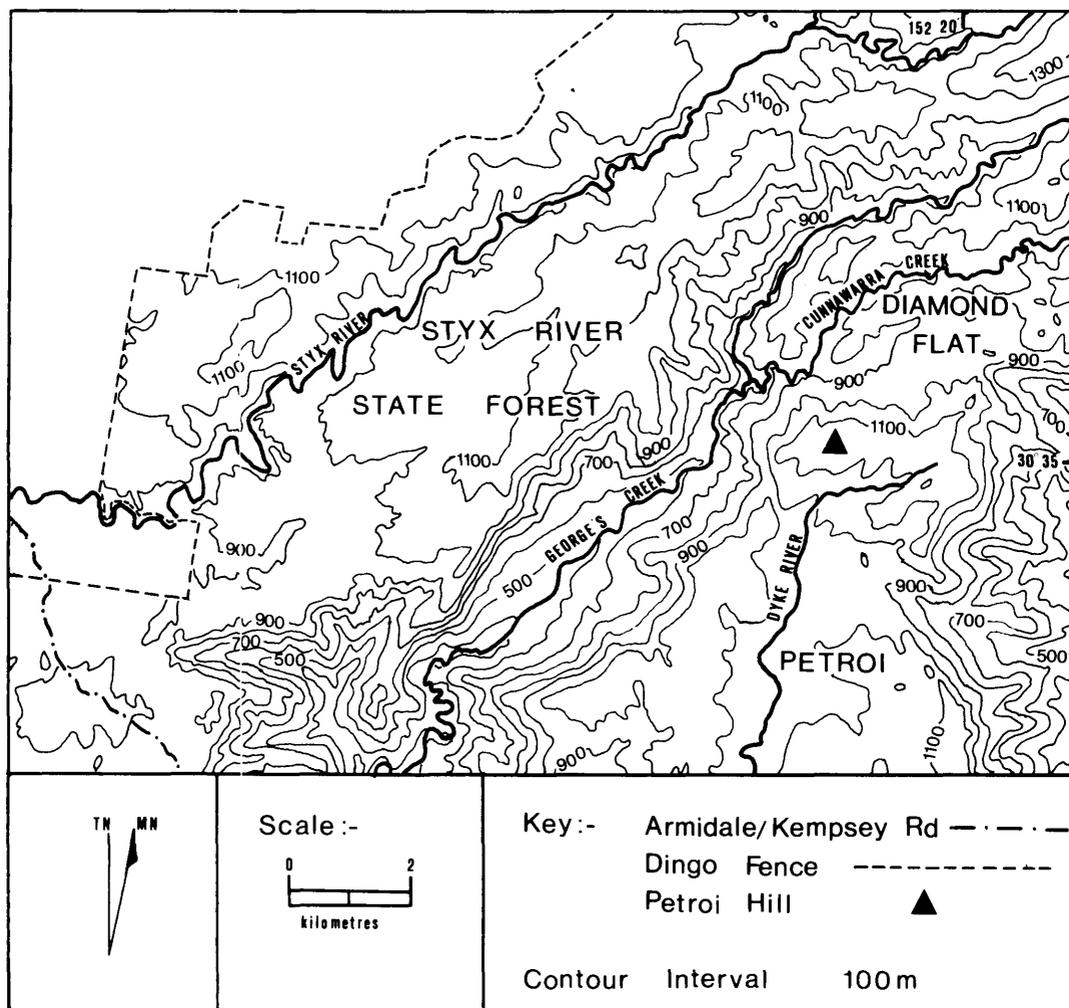


FIGURE 2.1 The study area.

Both forestry and grazing activities marked all three sites. While there was no logging in the S.R.S.F. site during the study it had been selectively logged in previous years. Logging occurred concurrently with the study at Petroi and Diamond Flat. While both these sites had previously been logged in selected regions the current logging at Petroi resulted in almost clear-felling of a portion of the south-western corner of that site. At Diamond Flat, the forestry activity was not extensive. In all three sites the forestry activity was marked by the presence of a network of fire trails and snig tracks. The effect of free-range grazing of cattle on the vegetation was less obvious and no differences were observed between the three sites.

2.1.3 Climate

Although the region was declared drought-stricken throughout the period of the study there is normally a marked summer rainfall accompanied by moist easterly winds. The average annual rainfall was 1800 mm. In winter cold dry westerly winds prevailed. Summer temperatures were mild (mean minimum 12° c, mean maximum 27° c) while winters were cold (mean minimum 1° c, mean maximum 14° c).

2.2 Dingo scat analysis

2.2.1 The collection of the dingo scats

A systematic preliminary examination of the snig tracks and fire trails within each study site revealed the presence of dingo spoor. Spoor consisted of three types: tracks, scats (the faecal droppings), and rakes (the backward scratching of the ground usually associated with urination). The frequency of each of the spoor types was recorded each month on a map. The fire trails and some snig tracks in the three sites were cleared of scats in March 1979. This clearing assured that the subsequent monthly collections were deposited within a similar duration of time. In the S.R.S.F. site the Forest Way and Loop Road fire trails were not suitable for scat collection since they were too wide and received too much traffic. Collections were concluded in September 1980.

All scats collected were placed in individual plastic bags. They were then labelled according to the date and site of collection.

2.2.2 Identification of prey species

a) Contents of a scat

The common components of dingo scats included hair, feathers, bones, plant material, chitinous exoskeletons and digested material (Coman, 1972; Robertshaw, 1976; Robertshaw and Harden, 1984). Of these components only hair, bone and digested material occurred frequently. The diagnostic value of these three items varied significantly. The digested material has been deemed of little use in identifying the prey

species (Brunner and Coman, 1974). The bone material was of two types: fragmented or whole (Coman and Brunner, 1971). Bone fragments have not been successfully used in prey identification. Identifications that used whole bone have been limited to those vertebrates with bones small enough to pass through intact or whose teeth and claws were easily recognised (Coman and Brunner, 1971; Pearson, 1964). Usually such findings have been used in conjunction with other means of identifying prey. Of these other methods most have been indirect in the respect that they relied on observations of kills compared to the examination of stomach or faecal contents (Kruuk, 1972). For predators of mammals, hair identification provides a suitable alternative to the above methods, and hair identification has been successfully used in dingo scat analysis (Coman, 1972; Robertshaw, 1976; Robertshaw and Harden, 1984). This success was due to the presence of hair in ninety percent of the scats and the speed of application of Coman and Brunner's technique of identification.

b) Hair identification

Coman and Brunner's method of hair identification makes use of the structural appearance of a hair. A hair is a cylindrical epidermal structure composed of three layers of dead cells. The inner core of hair, the medulla, is surrounded by the cortex which in turn is enclosed by a scaly cuticle (de Beer, 1966). Not all hair was of practical diagnostic value. Brunner and Coman (1974) recognised five types of hair. The first three types (vibrissae, bristle-hairs and overhairs), they found of little or no diagnostic value while the fourth type, underhair, was of limited use in the identification of some species eg. Brush-tail and Ringtail possums. The fifth type, guardhair, was diagnostically the most useful. Brunner and Coman (1974) used the between species structural variations of guardhairs as a means of identifying mammalian prey species. These structural variations were the shape of the cross-section, the appearance of the medulla and the pattern of the scales forming the cuticle. They also showed that the greatest variation between species was associated with the shield region of the guardhair.

c) Procedure

The technique, briefly described here, was adapted from Coman and Brunner (1972) and Brunner and Coman (1974). Both references give a complete coverage of their methods used and the latter source has an extensive array of photomicrographs of various mammalian hair encountered in the course of their studies.

To produce the hair cross-section a stainless steel plate 0.4mm thick and containing a number of 0.8mm holes was used. A loop of nylon thread was passed through a hole, and placed within this loop were several cellulose acetate fibres. The loop was tightened around the fibres and partially pulled through the hole to raise the ends of the fibres. A tuft of an unknown hair sample was then placed within the fibre ends. These fibres were then pulled further through the hole so as to pull the hair tuft into the hole. The distance the hair was pulled through depended on the average position of the shield region within that sample of hair. Once the sample was positioned in the hole the cellulose acetate fibres were dissolved by adding a drop of acetone to each side of the slide beside the hole. This released the pressure on the hair and set the hair sample within the hole. (It was important not to attempt to section too many hairs in one hole since this distorts their cross-sections). Once the plug had dried and set, it was sectioned by running a razor blade across the two faces of the slide. The section was then viewed *in situ*. The various types of cross-section that could be seen are illustrated in Figure 5 of Brunner and Coman (1974).

When the prey item was not positively identified from the cross-sectional appearance, the medulla and the nature of the scale pattern were examined. (See Figures 6 and 7 of Brunner and Coman (1974) for examples of these structures). To view the medulla single hairs were embedded in 50% polyvinyl acetate (p.v.a.) on a glass cover slip. When the solution was dry the hairs were viewed under low power on the microscope. To obtain an impression of the scale pattern the hairs used in the whole mounts were removed. This left a cast in the p.v.a. which was inverted on a glass slide and examined.

The characteristics observed were then compared with photomicrographs of prepared samples from known species. These photomicrographs and an associated key to the identification of mammalian hairs found in the study area were developed for a previous study, Robertshaw (1976). In that study a reference collection of furs was established from animals taken within or in close proximity of the present field area. This precaution was taken to negate any chance of geographical variation affecting the identification of the prey species.

Before identification could proceed a hair sample was obtained by soaking and breaking down the scat in boiling water. Once the scat was broken up it was placed on a 220 μ m sieve and washed under cold running water to remove the digested material. The material caught by the sieve, hair and/or bone material, was then separated accordingly into vials and preserved in 50% alcohol. While separating the hair from the bone material the hair was examined visually for differing hair types or the presence of feathers in the scat. Where observed differences or feathers were found the vial was marked noting this. A selection of hair drawn from random sites within the scat, including any hair thought different from the rest, was then placed at the top of the vial. This sample was then identified using Coman and Brunner's technique.

d) Test of consistency

In previous studies, Robertshaw (1976) and Robertshaw and Harden (1984), 20% of the scats were chosen at random and the hair reidentified. As all the cases of reidentification verified the previous finding the percentage chosen for reidentification in this study was reduced to 10%.

2.2.3 Examination of the macropod bone material found in the scats

Robertshaw and Harden (manuscript) found it was possible to separate bone material, from an array of differing sized macropod species, into two age classes. These classes were dependent and independent (Kaufmann, 1974). The former class included pouch young and young-at-foot while the latter included sub-adults and adults. The criteria established from a reference collection of skeletal material were then

used to allocate the bone material to each age class. Such criteria were, the dimensions of the bones (particularly the ribs, ulna, radius, metacarpals and non-caudal vertebrae), the degree of fusion of the articulating cartilage caps (epiphyses) and the changes in the shape of muscle insertion sites, the articulating surfaces with age and the strengthening of joints.

Following the methods of Robertshaw and Harden (1984b and 1984c) the bone material separated from the hair and digested material was boiled in a 3% hydrogen peroxide solution. This boiling bleached and further cleaned the bone material aiding in both the separation of the material into age classes and the identification of the sections of the carcass consumed. These sections were divided into eleven zones. These zones were the skull, neck, shoulder (top of the humerus, scapula and clavicle), arm (lower humerus, top of the ulna and radius), hand (lower ulna and radius and the phalanges of the fingers), thorax (ribs, sternum and thoracic vertebrae), lumbar region (lumbar vertebrae), pelvic region (pelvis, associated vertebrae and the top of the femur), leg (lower femur and the top of the tibia and fibula), foot (lower tibia and fibula, metatarsals and the phalanges of the toes) and the tail. The presence or absence of these zones was recorded for each scat in each age class.

The bone material was air dried and then placed in an oven at 50° c for 72 hours and weighed.

2.2.4 Equitability index as a comparison of food habits

Hurtubia (1973) used the diversity index

$$H = -\sum_{i=1}^s P_i \log P_i \quad \text{where } H = \text{estimate of diversity,}$$

P_i = proportion in the ith species.

to illustrate the species richness and abundance of the prey species of three sympatric species of lizards. He found this approach useful where there were numerous prey species as it showed general changes in the number of prey species and the relative occurrence of each species.

In this study an equitability (J) index (Pielou, 1966) was used. Equitability was related to H (diversity) such that

$$J = H / \log S$$

where S was the total number of species.

Criticism of diversity and equitability indices by Hurlbert (1971), Fager (1972), Goodman (1975) and Peet (1975) was countered by Robertshaw and Harden (1984a). Firstly Robertshaw and Harden (1984a) standardised the number of species (S) to include all species known to have been present in the area, not just the sample total. Secondly, they calculated the indices cumulatively as the second and subsequent scats were added to the sample. If the resultant curve failed to reach a plateau value the sample size was considered too small and excluded from subsequent analyses.

An equitability index of 1 occurs when all species are present in the sample and in equal numbers. Hence high equitability indicates a high species richness and an evenness of species abundance. A low equitability results from a low species richness and/or an uneven spread of species.

2.2.5 Index of abundance

As well as obtaining information on the movements and diet of the dingoes from the spoor, the frequency and location of the spoor was used to develop a relative index of dingo abundance. This index was derived from the number of scats deposited per kilometre of fire trail or snig track, per day. The index was calculated for each monthly collection from each site to examine seasonal differences.

2.3 Macropod abundance

Only the respective abundances of the three largest macropod species common in the study area (Harrington, 1975; Bradley, 1977; Harden and Statham, unpublished data) were estimated. These three species were the swamp wallaby (*Wallabia bicolor*), the red-necked wallaby (*Macropus rufogriseus* Desmarest) and the grey kangaroo (*Macropus giganteus* Shaw).

All three were conspicuous during the daylight hours. To estimate the abundances of the other common macropod species, the parma wallaby (*Macropus parma* Waterhouse) and the red-necked pademelon (*Thylogale thetis* Lesson), would have required night driven transects with unavailable additional manpower and vehicle mileage.

With further consideration of resources and time allocation, transects were a more practical means of estimating the density of the macropods, than pellet plots even though the latter method was potentially more accurate (Bradley, 1977). Transects were walked morning and afternoon and the density calculated using the formulae $n/2Lx$ derived by Leopold et al. (1951), where n = number observed,

L = length of transect, and

x = mean perpendicular sighting distance.

The morning transect commenced half an hour after sunrise while the afternoon transect was planned so that it would finish half an hour prior to sunset. This formula, according to Bradley (1977), gave the closest approximation to the density values obtained from pellet plot estimates. Southwell (1981) also found Leopold's formulae to be the best suited to "the conflicting requirements of appropriateness of the underlying model, precision, and accuracy".

A precision set at $\pm 20\%$ of the density estimate required approximately 36 kilometres of walked transect to sight a large enough sample of macropods. This was derived from data presented by Bradley (1977), whose field area was encompassed by the S.R.S.F. site. In an attempt to obtain this precision at the S.R.S.F. site two transect routes were chosen. Each was walked one morning and afternoon with both transect routes run on consecutive days once a month. The combined distance of these four transects totalled 34.6 kilometres. A similar transect design was established for Petroi and Diamond Flat combined, as initially they were to have been the one site. However when so few macropods were seen at Petroi in the first three transect runs it was decided to separate Petroi and Diamond Flat into two sites. Unfortunately Diamond Flat lacked sufficient length of fire trail to run the same length of transect through the variety of vegetation types passed in the S.R.S.F. transects. As a result of this only one transect, 6 kilometres long, was walked at Diamond Flat. At Petroi the transect distance was cut to 5 kilometres in

order to be more time and labour efficient. These two transect routes were then walked morning and afternoon one day a month. This produced a total of 12 kilometres for Diamond Flat and 10 kilometres for Petroi compared to the 34.6 kilometres per month from the S.R.S.F. site.

2.4 Some aspects of the biology of the swamp wallaby

This information was obtained by shooting a number of swamp wallabies monthly in each of the study sites. For each month and a particular site an attempt was made to obtain a minimum of three females with pouch young and three males. An upper limit of approximately ten animals was set in the S.R.S.F. site by Forestry Commission licence restrictions, permit number 069. Animals were shot at Diamond Flat and on other private property under licence from the N.S.W. National Parks and Wildlife Service which also covered the Service's licence requirements for the shooting in the Styx River State Forest.

2.4.1 Morphometrics

The following measurements were made on all the swamp wallabies shot where the wound did not distort the reading.

- | | |
|--------------------|-------------------------|
| 1) Ear length, | 8) Back length, |
| 2) Head length, | 9) Tail length, |
| 3) Neck diameter, | 10) Tail butt diameter, |
| 4) Paw length, | 11) Tibia length, |
| 5) Forearm length, | 12) Pes length, |
| 6) Bicep diameter, | 13) Weight, |
| 7) Chest diameter. | |

For further explanation see Figure 2.2 .

In addition to this list the date, location and time shot, sex, and general comments were also recorded for each wallaby.

2.4.2 Age structure

From each shot animal the head was removed, skinned, placed in a plastic bag and labelled with its sample number (eg. Wb 47). Each monthly sample was soaked in water to aid defleshing. To further facilitate the defleshing the bags were perforated and the skulls placed in a sealed black drum located in the sun. The water was changed several times before the skulls were sufficiently defleshed before the final cleaning.

This cleaning was started by boiling the skulls in a 3% hydrogen peroxide solution within a pressure cooker. It was then completed by washing the skulls in a beaker of boiling detergent to degrease them.

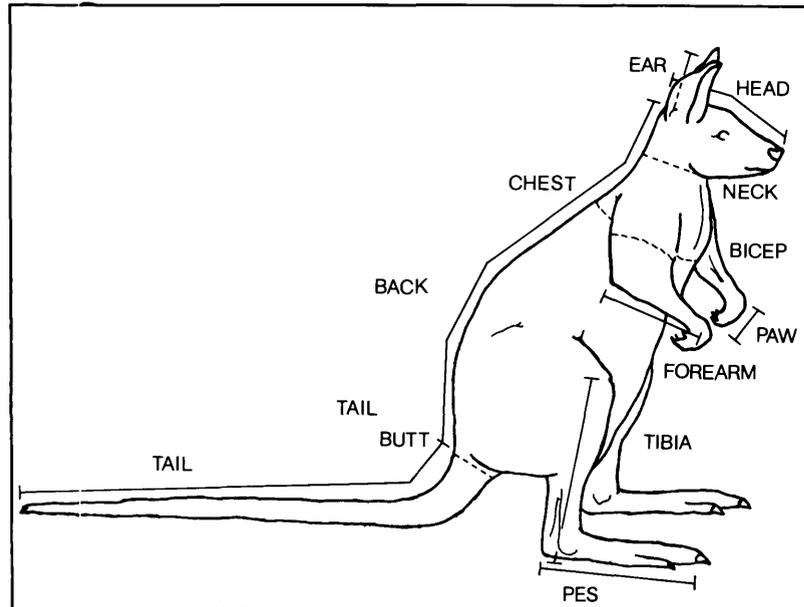


FIGURE 2.2 Morphometric measurements.

A "Molar Index" for each of the cleaned skulls was then derived following Kirkpatrick's (1964) methods. Dudzinski et al. (1977) found the molar index to be a reliable relative index of age.

2.4.3 Reproductive condition

The testes and epididymi from each shot male were removed and preserved in formalin acetic acid and alcohol solution (F.A.A.). Until they were weighed and prepared for sectioning they remained in the fixative. From each male specimen, sections $9\mu\text{m}$ thick were cut from a sample of testis and epididymis dehydrated and embedded in paraplast. Several sections were then mounted on labelled slides, hydrated and stained with Mason's Tricolour Stain and examined for the presence of sperm.

The reproductive condition of the shot females was first assessed by an examination of the pouch. The pouch was noted as either dirty or clean and the number of everted teats was recorded as well as the location and number of lactating teats. If there was more than one lactating teat special note was taken of the teat to which the pouch young was attached. For each of the pouch young the sex and morphometric measurements were recorded. Some parameters of the small pouch young were not measured; but all pouch young under 700g were preserved intact in F.A.A.

The reproductive tract of the female was then removed and preserved in F.A.A. The ovaries and uteri were subsequently dissected out and labelled noting the side of origin and the female's sample number. Before the ovaries were sectioned they were weighed. After dehydration and impregnation with paraplast each ovary and uterus was serially sectioned every 9 μ m. From these sections every tenth one was mounted, hydrated and stained with Mason's Tricolor Stain. The uterine slides were examined for the presence of a blastocyst which would indicate whether the female was pregnant. From the ovarian slides it was hoped to count the number of *corpora albicantia* and *corpora lutea* within the ovary to have an index of the number of past pregnancies.