FAUNA *of* AUSTRALIA

18. NATURAL HISTORY OF THE METATHERIA

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NATURAL HISTORY

Ecology

Diet. Traditionally, Australian marsupials have been viewed in two dietary categories: the predominantly carnivorous marsupials, with polyprotodont dentition, and the predominantly herbivorous large diprotodonts. Recent observations on feeding (Smith 1982a; Henry & Craig 1984) and analysis of diet (Hall 1980a; Statham 1982) have not altered this view in the broadest sense. They have shown, however, that some polyprotodonts such as the peramelids (bandicoots) (Heinsohn 1966; Lee & Cockburn 1985) and the Bilby, *Macrotis lagotis* (Johnson 1980a), include significant proportions of plant items in their diets. Further, some small and medium-sized diprotodonts are now known to be dependent upon plant products such as nectar, pollen, plant exudates, fruit and seed (Smith 1982a; Mansergh 1984b; Turner 1984a, 1984b; Lee & Cockburn 1985).

Arthropods appear to be the principal food items of most dasyurids (for example, *Antechinus* species, quolls, phascogales and planigales) (Morton 1978d; Blackall 1980; Hall 1980a; Statham 1982; Lee & Cockburn 1985), peramelids (Heinsohn 1966; Lee & Cockburn 1985), the Bilby (Johnson 1980a), the Marsupial Mole, *Notoryctes typhlops* (Corbett 1975), the Numbat, *Myrmecobius fasciatus* (Calaby 1960) and the Striped Possum, *Dactylopsila trivirgata* (Smith 1982b). Arthropods also are consistent, but not predominant, food items of burramyids (pygmy-possums) (Turner 1984a, 1984b), petaurids (ring-tail possums and gliders) (Smith 1982a, 1984a; Smith & Russell 1982) and occasionally occur in the diet of the Common Brushtail Possum, *Trichosurus vulpecula* (Kerle 1984c). Vertebrates appear to be important in the diet of some large dasyurids, although many feed predominantly upon insects (Blackall 1980; Godsell 1982). The largest dasyurid, the Tasmanian Devil, *Sarcophilus harrisii*, feeds principally upon mammalian carrion (Guiler 1970a).

Seeds appear to be an important item in the diet of only one Australian marsupial, the Mountain Pygmy-possum, *Burramys parvus* (Mansergh 1984b), which may cache seeds as an over-winter food resource in its snow-bound alpine habitat (Lee & Cockburn 1985). Seeds also occur in the diet of the Bilby (Johnson 1980a). The paucity of marsupial granivores in Australia has been attributed to ants and birds pre-empting this resource (Morton 1979).

The fruiting bodies of endogenous fungi are a significant dietary component in some bandicoots (Lee & Cockburn 1985) and potoroids (bettongs and potoroos) (Guiler 1971b; Kinnear *et al*. 1979). These marsupials may be important agents in the dispersal of such fungi. The occurrence of fruiting bodies in the soil is influenced by soil moisture and, accordingly, their importance in the diet is likely to be seasonal. They are harvested from shallow (< 60 mm deep) excavations (Lee & Cockburn 1985).

Pollen and nectar are the sole dietary items of the Honey Possum, *Tarsipes rostratus*, (Wooller *et al*. 1981) and important items in the diets of some pygmy-possums (Turner 1984a, 1984b) and petaurids (Smith 1982a; Henry & Craig 1984), all of which harvest pollen and nectar without destroying the flowers. The production of flowers by plants such as *Banksia*, *Dryandra* and *Eucalyptus* species which produce copious quantities of nectar and pollen, probably influences dependence upon them. The Honey Possum is confined to heaths in south-western Australia in which the overlapping flowering of plant species results in a year round supply of pollen and nectar (Wooller *et al*. 1981). In eastern Australian forests and heaths, flowering occurs only in some seasons.

Here, the pollen and nectar feeders, the Eastern Pygmy-possum, *Cercartetus nanus*, and the Feathertail Glider, *Acrobates pygmaeus*, turn to fruit and plant exudates when flowers are not available (Turner 1984a, 1984b).

Plant and insect exudates, including *Acacia* gum, eucalypt sap, manna and honeydew, are important dietary components of petaurids. These exudates are rich in energy, but generally poor in protein. Protein is obtained by feeding on arthropods (Smith 1982b, 1984a; Smith & Russell 1982; Henry & Craig 1984). Both the Yellow-bellied Glider, *Petaurus australis*, and the Sugar Glider, *P. breviceps*, gnaw through the bark of certain eucalypts to sever phloem ducts and may spend long periods at these sites lapping the exuding sap (Smith 1982a; Henry & Craig 1984). *Hakea* gum appears to be an important item in the diet of the Brush-tailed Bettong, *Bettongia penicillata* (Kinnear *et al*. 1979).

Leaves are the principal component of the diet of ringtail possums, *Pseudocheirus*, brushtail possums and cuscuses (Phalangeridae), the Koala, *Phascolarctos cinereus*, macropods (for example, kangaroos, wallabies, pademelons) and the wombats (Vombatidae) (Lee & Cockburn 1985). With the exception of some macropodids (mainly *Macropus* species) and wombats which are grazers, all of these leaf-eaters are browsers. There is a tendency for individual species of browsers to feed upon a single family or genus of plant. Forty-five percent of marsupial browsers in Australia feed principally upon leaves of the genus *Eucalyptus* and a number of species (in particular the Koala and the Greater Glider, *Petauroides volans*) show local preference for one or two species within this genus (Henry 1984; Martin & Lee 1984).

Fleshy fruits are uncommon in the eucalypt and acacia dominated forests and woodlands of temperate Australia and marsupials inhabiting these formations rarely include fruit in their diets. Fleshy fruits are more abundant in tropical communities and probably occur in the diets of most, if not all, tropical marsupial folivores (Kerle 1984c; Procter-Gray 1984).

Body size has an important bearing on diet. Vertebrate prey increases in importance in the diet of large dasyurids (Lee & Cockburn 1985). There is also a tendency for these animals to feed upon readily harvested insects such as pasture pests (Blackall 1980) and for the relatively large Numbat and the Striped Possum, *Dactylopsila trivirgata*, to feed on social insects (Calaby 1960; Smith 1982b.

Within the diprotodonts, species which weigh less than 50 g usually feed upon nectar, pollen, insects, fruit, seed and perhaps honeydew and manna. Those in the 100–650 g range also feed upon these items (except seed), but show increasing dependence upon plant exudates. Above an adult weight of 700 g, all diprotodonts are herbivorous (Smith & Lee 1984) (Fig. 18.1). Even among the herbivorous marsupials, feeding patterns change with body size. Small herbivores (such as the Common Ringtail Possum, *Pseudocheirus peregrinus*) tend to feed upon young leaves and may even select the least fibrous part of the leaves (Pahl 1984). Large folivores, such as the Koala, eat young and old leaves, but select certain old leaves (Martin & Lee 1984).

Macroniches and Habitat One way to describe the life styles of marsupials is to classify them according to their needs for substratum (for example aquatic, arboreal) and diet (for example piscivorous, carnivorous). Using this system, Eisenberg (1981) identified 53 macroniches occupied by mammalian genera. Only 18 of these macroniches are occupied by marsupial genera and only 15 by genera of Australian marsupials (Lee & Cockburn 1985). Roughly one-third of Australian marsupial genera occupy the terrestrial insectivore / omnivore macroniche. There are no flying or aquatic marsupials nor any which feed on plankton, fish, crustaceans, molluscs or blood. Very few marsupials are granivorous, carnivorous, fossorial or semi-aquatic. This classification is based upon the predominant tendencies of genera and does not take into account niche

differences between species within genera. Nevertheless, attention is drawn to the limited scope of the marsupial radiation. The macroniches occupied by genera of Australian marsupials are summarised in Table 18.1.

Table 18.1 Macroniches of marsupial genera arranged in order of mean body length of genera. Non-Australian genera marked with asterisk. (Macroniches after Eisenberg 1981). Mean body lengths. (After Lee & Cockburn 1985)

MACRONICHE	MEAN BODY LENGTH (mm)	GENERA
Semifossorial herbivore/grazer	956	*Lasiorhinus*, *Vombatus*
Terrestrial carnivore	881	*Thylacinus*, *Sarcophilus*
Scansorial herbivore/browser	692	*Dendrolagus*
Terrestrial herbivore/grazer	550	*Lagorchestes*, *Macropus*, *Perodorcus*, *Petrogale*, *Onychogalea*
Terrestrial herbivore/browser	535	*Dorcopsis**, *Dorcopsulus**, *Lagostrophus*, *Setonix*, *Thylogale*, *Wallabia*, *Wyulda*
Arboreal herbivore/browser	469	*Petauroides*, *Phalanger*, *Phascolarctos*, *Pseudocheirus*, *Trichosurus*
Terrestrial fungivore/omnivore	319	*Aepyprymnus*, *Bettongia*, *Potorous*
Semiaquatic insectivore	???	*Chironectes**
Scansorial insectivore/omnivore	285	*Didelphis**, *Dromiciops**, *Philander**
Terrestrial myrmecophage	245	*Myrmecobius*
Terrestrial frugivore/omnivore	236	*Hypsiprymnodon*
Arboreal frugivore/omnivore	221	*Caluromys**, *Caluromysiops**, *Glironia**
Terrestrial insectivore/omnivore	196	*Antechinus*, *Caenolestes**, *Chaeropus*, *Dasycercus*, *Dasykaluta*, *Dasyuroides*, *Dasyurus*, *Echymipera*, *Isoodon*, *Lestodelphys*, *Lestoros**, *Lutreolina**, *Macrotis*, *Metachirus**, *Microperoryctes**, *Monodelphis**, *Murexia**, *Myoictis**, *Neophascogale**, *Ningaui*, *Parantechinus*, *Perameles*, *Peroryctes**, *Phascogale*, *Phascolosorex**, *Planigale*, *Pseudantechinus*, *Rhyncholestes**, *Rhynchomeles**, *Satanellus*, *Sminthopsis*
Arboreal exudivore	195	*Gymnobelideus*, *Petaurus*
Arboreal insectivore/omnivore	164	*Dactylopsila*, *Distoechurus* (?), *Marmosa**
Fossorial insectivore/omnivore	140	*Notoryctes*
Terrestrial frugivore/granivore	112	*Burramys*
Arboreal nectarivore	75	*Acrobates*, *Cercartetus*, *Tarsipes*

Marsupials occur in almost the entire range of terrestrial and arboreal communities found in Australia. Species densities are highest along the relatively wet eastern and south-west coasts, where there is a rich mosaic of open and closed forests, woodlands and heaths. The lowest densities occur in inland Australia (Pianka & Schall 1981). The three families of Australian marsupials with the most species, Dasyuridae, Macropodidae and Peramelidae, occur in a wide range of communities, but their proportional representation in communities differs. Dasyurids attain greatest species richness in communities within the arid zone (45% of species; Morton 1982). Peramelids are spread more evenly across most terrestrial communities. The macropodids attain greatest species richness in open forests (57% of species, including species inhabiting rock outcrops in open forest) and woodlands (33% of species). The largely or

totally arboreal families, the Phalangeridae, Pseudocheiridae and Petauridae, are confined almost entirely to the forests and woodlands of the margins of the continent.

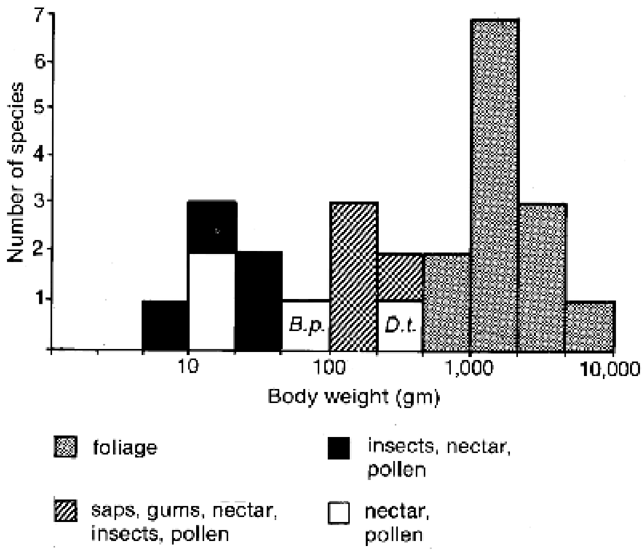


Figure 18.1 Relationships between major dietary preferences and body mass in possums, gliders and the koala. (After Smith & Lee 1984). D.t. Striped Possum (*Dactylopsila trivirgata*) feeds on ants, termites, wood-boring insects and fruit. B.p. Mountain Pygmy-possum (*Burramys parvus*) feeds in captivity on seeds, fruits and insects.

LIFE HISTORIES

Relationships with Body Size

Comparisons of life history traits of different groups of organisms usually take into account the strong influence of body size upon many traits, using the allometric procedure to eliminate this influence. This method allows adaptive trends to be identified while emphasising the importance of body size as an adaptive trait. The relationship between the life history trait (LHT) and body mass (M) is usually expressed in terms of a power function LHT = a M^b where a and b are constants. Logarithmic transformation produces the linear relationship

$$\log (LHT) = \log a + b \log M$$

where log a is the elevation (intercept on the y-axis) and b is the slope of the line. Comparisons of the relationships between LHT and M for different taxa are generally made by comparing the elevations and the slopes of the equations describing those relationships.

Within the Marsupialia there are obvious relationships between increased body size, decreased litter size, increased duration of care by the mother and increased longevity. At present, data are only sufficient to derive allometric equations for a small number of marsupial life history traits and for only a few taxa within the Marsupialia (Table 18.2). Less precise comparisons can be made by inspecting the ranges of life history traits characteristic of taxa, keeping in mind differences in body size (Table 18.3).

Table 18.2 Constants for allometric relationships for marsupial life history traits (LHT = a M^b). Sources: Lee & Cockburn, 1985[1]; Russell, 1982[2]; Smith & Lee, 1984[3]; M equals maternal body mass (kg).

LHT	TAXON	a	b	SOURCE
Mass of individual at birth	Marsupialia	0.00014	0.56	2
Mass of litter at birth	Marsupialia	0.00026	0.35	1
Mass of litter at birth (litter = 1)	Marsupialia	0.00026	0.32	2
Mass of individual at weaning	Marsupialia	0.357	0.96	2
Parental investment (= mass of litter x 100/maternal body mass)	Marsupialia	78.60	-0.29	1
Time from conception to weaning (excluding bandicoots) (days)	Carnivorous omnivorous marsupials	151.40	0.093	1
Pouch life (days)	Marsupialia	16.80	0.27	2
	Dasyuridae	29.60	0.13	2
	Macropodidae	15.70	0.29	2
Age at weaning	Marsupialia	35.70	0.22	2
	Dasyuridae	59.50	0.12	2
	Macropodidae	11.10	0.37	2
Litter size (litters >1)	Phalangeridae	4.78	-0.17	3
	Dasyuridae	9.72	-0.12	3

Table 18.3 Ranges of some life history traits of families of Australian marsupials. Sources: Lee *et al*., 1982; Russell, 1982; Smith & Lee, 1984; Lee & Cockburn, 1985; Friend & Whitford, 1985; *higher in continuously breeding tropical species; **laboratory raised animals.

FAMILY	NO. OF SPECIES	E BODY MASS (g)	USUAL LITTER SIZES	LITTERS/ YEAR	INTERVAL BETWEEN LITTERS	AGE OF E AT FIRST PARTURITION (m)
Dasyuridae	40	4.3-6 000	4-12	1-2*	2-12	6**-11
Notoryctidae	1	55				
Myrmecobiidae	1	416	4	1	12	12
Peramelidae	7	190-1 700	2-4	2-5	2	4-6
Thylacomyidae	2	311-950	1-2			
Tarsipedidae	1	11	2-3	2-3	3	6
Burramyidae	6	7-40	2-4	1- 3	2-12	5-12
Petauridae	6	115-1 700	1-2	1-2	12	8-24
Pseudocheiridae	6	700-2 000	1-3	1- 2	5-12	8-24
Phalangeridae	6	1 300-3 500	1	1-2	6-12	12-36
Phascolarctidae	1	7 900	1	1	12	24-36
Vombatidae	3	26 000	1	1		
Potoroidae	8	660-350	1-2	2-3	4-5	6->12
Macropodidae	37	1 070-35 000	1	1- <2	6-13	9-25

Comparisons of Marsupial and Eutherian Life Histories

Of the various life history traits, only one character, the relative investment by mothers in young at birth (weight of young at birth as a percentage of the weight of the mother), clearly sets marsupials aside from eutherian mammals (Russell 1982; Lee & Cockburn 1985). Even in Brown Bears (*Ursus arctos*), in which the litter at birth is 0.6% of maternal body mass (Millar 1981), the investment by mothers is several orders of magnitude greater than the value predicted for marsupials of similar size (Lee & Cockburn 1985). In no marsupial does the weight of the litter exceed 1% of the mother's body mass. Low investment by the mother is reflected in the size of individual young, the largest of which weighs only about 1 gram at birth. It also is reflected in the development of the young. Development is conspicuously altricial in features other than those associated with the passage from the birth canal to the pouch and attachment to the teat and suckling. Such features include the well-developed musculature of forelimb and shoulder and the functional alimentary tract.

Whereas there is a substantial difference between the relative investment by the mother in litters at birth, relative investment at weaning is remarkably similar to eutherians (Fig. 18.2; Russell 1982; Lee & Cockburn 1985). Individual young in marsupials have a mean value of 35% of the mother's body mass (range 9–60%; Russell 1982) compared to 37% (range 10–65%) in eutherians (Millar 1977). Russell (1982) concluded that similar limitations exist on additional investment by the mother at this stage in both marsupials and eutherians.

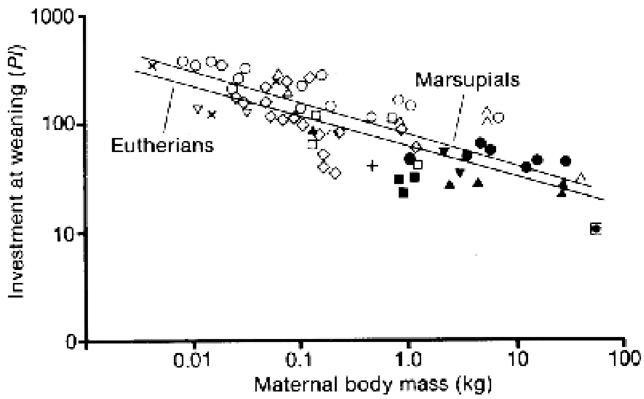


Figure 18.2 Relative investment in litters at weaning (PI) as a function of maternal body mass in eutherians and marsupials. (After Lee & Cockburn 1985). Symbols for marsupials: open triangles, Didelphidae; open circles, Dasyuridae, Myrmecobiidae; filled squares, Peramelidae, Thylacomyidae; inverted open triangles, Tarsipedidae, Burramyidae; open squares, Petauridae; inverted filled triangles, Phalangeridae; filled triangles, Phascolarctidae, Vombatidae; filled circles, Macropodidae. (Sources of data, see Lee & Cockburn 1985)

In other life history traits, marsupials and eutherians differ only in degree. In some instances these differences appear to influence strongly the range of life histories exhibited by the taxa. Traits which appear particularly significant are: the longer duration of investment by the mother and the slower pace of growth in marsupials (Braithwaite & Lee 1979; Russell 1982; Lee & Cockburn 1985). Braithwaite & Lee (1979) used the interval between conception and weaning as a measure of the duration of nutrient transfer between mother and young (duration of the mother's investment) and argued that this interval was longer in small marsupials than in similar sized eutherians. This measure has certain

weaknesses. It includes periods of stasis during the uterine life of the embryos of certain marsupials when nutrient transfer is presumably negligible (Russell 1982). It also excludes maternal care after weaning. At present, however, data for a more precise assessment are not available. A recent comparison of the interval between conception and weaning in marsupials and eutherians based upon a restricted data set (carnivorous and omnivorous species excluding eutherians with delayed implantation and peramelids; for reasons, see Lee & Cockburn 1985) has confirmed that these marsupials and eutherians are different and that this difference is greatest in species of small body mass (Fig. 18.3; Lee & Cockburn 1985).

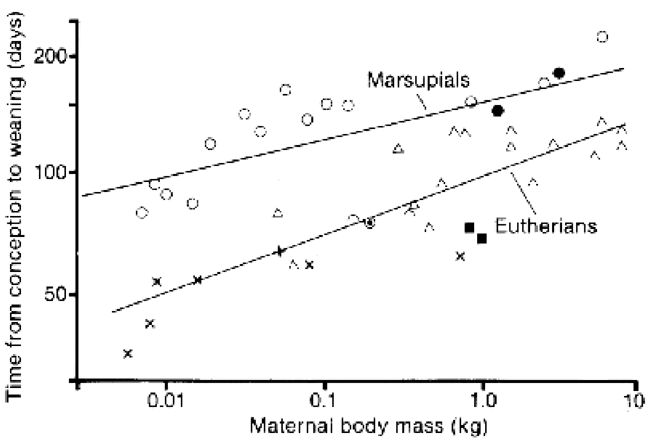


Figure 18.3 Time from conception to weaning (tcw) as a function of maternal body mass in carnivorous/omnivorous eutherians and marsupials. (After Lee & Cockburn 1985). Symbols as in Fig. 18.2. (Sources of data, see Lee & Cockburn 1985)

Comparisons of growth of marsupials and eutherians based upon the Gompertz growth equation show that the growth rates of marsupials tend to be lower than those of eutherians and that this difference is again greatest for species of small body mass (Fig. 18.4; Lee & Cockburn 1985). One consequence of the slow pace of growth appears to be the low incidence of marsupial species which reproduce in the season of birth. Most marsupials breed in the season after their birth. In species of large body mass, maturation and reproduction may be delayed for several years (see below). Exceptions occur among the peramelids, which have extremely rapid growth and may reproduce first at 4–5 months of age (Heinsohn 1966), the Honey Possum, *Tarsipes rostratus*, which first reproduces at 6 months of age (Wooller *et al*. 1981) and certain burramyids (pygmy-possums) which reproduce first at 5–8 months of age (Fleming & Frey 1984; Lee & Cockburn 1985). Some dasyurids, such as the Fat-tailed Dunnart, *Sminthopsis crassicaudata*, can attain sexual maturity at 6 months of age, but do not appear to reproduce naturally at this age (Morton 1978d).

A consequence of the long duration of care by the mother may be the unusually high incidence of monoestry (females ovulate once a year) in the Dasyuridae and the strong tendency towards semelparous life histories (single reproduction in a life time) among species in the dasyurid genera *Antechinus* and *Phascogale* (Lee, Wooley & Braithwaite 1982). Braithwaite & Lee (1979) attributed these trends to the restriction that the long period of maternal care places upon the opportunities for repeated reproduction in highly seasonal environments. In many marsupials, the energetically demanding periods of late lactation and weaning coincide with the period of maximum food abundance (Tyndale-

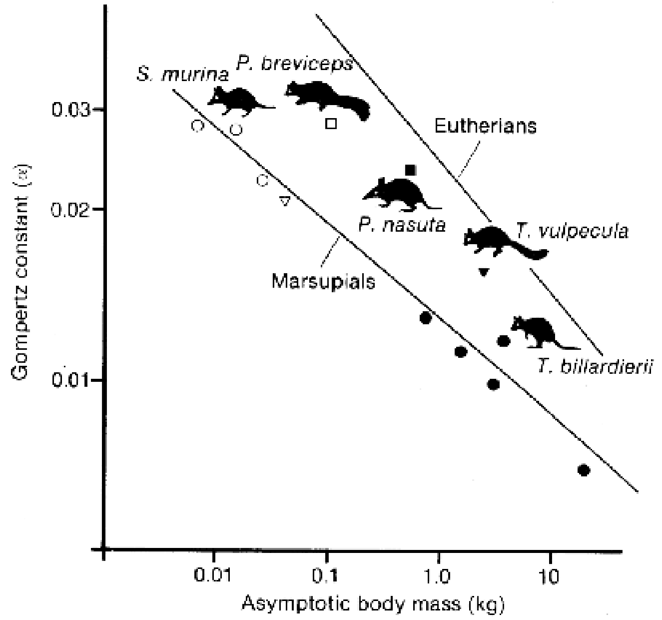


Figure 18.4 The Gompertz constant α as a function of asymptotic body mass in marsupials and eutherians. (After Lee & Cockburn 1985). Open circles, Dasyuridae, Myrmecobiidae; filled squares, Peramelidae, Thylacomyidae; inverted open triangle, Tarsipedidae, Burramyidae; open square, Petauridae; inverted filled triangle, Phalangeridae; filled circles, Macropodidae. The species of special interest are *Sminthopsis murina*, *Petaurus breviceps*, *Perameles nasuta*, *Trichosurus vulpecula* and *Thylogale billardierii.* (Sources of data, see Lee & Cockburn 1985)

Biscoe 1979a; Lee & Cockburn 1985). Where the period of maximum food abundance is limited, such as in temperate forests, a second litter will be weaned when food is scarce and may place the litter and the lactating mother at risk. These circumstances may favour monoestry; and semelparity in species where the probability of surviving to a second rut at approximately 23 months of age is low (Braithwaite & Lee 1979). Iteroparity (repeated breeding in a life time) and polyoestry (females ovulate more than once annually) appear to be the rule among small eutherians and among most small marsupials. In small, iteroparous marsupials the interval between litters and the duration of the period suitable for breeding are usually such that more than one litter is produced annually.

Life Histories of Marsupials

Whereas many of the differences between the life histories of marsupials can be related to differences in body size, there are some that cannot be accounted for in these terms. For example, peramelids (and petaurids) have a higher relative maternal investment in young at birth than other marsupials, despite a gestation of 12–14 days duration in peramelids which is the shortest yet recorded for a mammal (Stodart 1977). Peramelids also grow more rapidly than other marsupials, are weaned at an early age (about 65–70 days) and may first reproduce at an early age (5–6 months; Russell 1982; Lee & Cockburn 1985). The interval between litters, about 70 days, is much shorter than in any other similar sized marsupial. Females return to oestrus when the pouch young are about 50 days of age. A litter conceived at this time is born a few days after the previous litter leaves the pouch (Stodart 1977). This life history is associated with a pattern of parental care involving retention of the young in a well-

developed pouch until they are almost independent (see below; Russell 1982). Only a short period is spent in the maternal nest before the precocious young disperse. The peramelid strategy of producing relatively small litters, usually of 2–4 young at short intervals, associated with early dispersal and maturation of the young, appears adaptive for life in ephemeral habitats such as certain successional stages in heathland. Maximum longevity in peramelids appears to be about 3 years (Stoddart & Braithwaite 1979).

Peramelids show little variation between species in life history traits such as litter size and intervals between litters. Populations do differ in the duration of the breeding season and, in consequence, young may breed at an earlier age in some populations (Lee & Cockburn 1985). In contrast, the dasyurids show considerable variation between species in life history traits, but their strategies tend to be rigid and show little interpopulation variation (Lee *et al*. 1982; Lee & Cockburn 1985). Furthermore, the intervals between litters tend to be long in dasyurids and, as already noted, this has favoured a high incidence of monoestry and a tendency towards semelparous life histories among species which occur where the climate is reliable, but strongly seasonal. Four-fifths of the dasyurid species are, however, unquestionably iteroparous and breed either once annually, twice annually or continuously throughout the year. These iteroparous species occur where the climate is relatively variable; or in tropical regions in the case of continuously breeding species (Lee *et al*. 1982).

In comparison to other marsupials, the female dasyurids have large litters and invest heavily in them. At weaning, the young of small species may have a mass as much as three times that of the mother (Russell, 1982). This investment is accompanied by a very different pattern of parental care. The young initially are attached to the teat, but later are placed in a nest while still naked, ectothermic and with their eyes closed. At this stage the litter has attained at least half the mass of the mother. The young spend more than half the period of lactation in the nest and are suckled by the mother between bouts of foraging (Russell 1982). Age at first reproduction also is delayed and few species appear to breed naturally until about 11 months (Lee *et al*. 1982). Longevity of small dasyurids (< 300 g) is generally less than 3 years (Lee *et al*. 1982). Longevity for large dasyurids has not been ascertained.

The influence of body size on reproductive traits is conspicuous among the diprotodont marsupials. Among the burramyids, which are similar in size to small dasyurids, litter size is small, usually two to four young. These are, however, iteroparous species and most produce two or three litters a year at minimum intervals of 60–90 days. In addition, age at first reproduction may be as little as 5–6 months. Young born early in the breeding season may produce a litter before the season ends (Lee & Cockburn 1985; Smith & Lee 1984). The pattern of parental care appears to resemble most clearly the dasyurid pattern, although the pouch is well developed in burramyids and the period in the pouch is longer than that in the nest (Russell 1982).

The petaurids are an order of magnitude larger than the burramyids and, in these, litter size is reduced to one to two young. One or, at most, two litters are produced a year (Smith & Lee 1984). The pattern of parental care is similar to that of burramyids. First reproduction occurs at 1 year of age. Natural longevity is 5–7 years (Henry & Suckling 1984; Smith & Lee 1984; Lee & Cockburn 1985).

Except for the pseudocheirids, which are the smallest of the herbivorous marsupials and most closely resemble the petaurids in life history traits, the largest diprotodonts in the families Phalangeridae, Potoroidae, Macropodidae, Phascolarctidae and Vombatidae usually produce a single young annually. Additionally, the age of reproduction is delayed in many of the largest herbivores until their second or third year. Longevity is greater and often

exceeds 10 years (Smith & Lee 1984; Lee & Cockburn 1985). In many of these species the pattern of parental care differs from previous patterns. The female has a well-developed pouch and the young remain in the pouch after release from the teat. They become furred, endothermic and the eyes are open before they venture from the pouch. Among the macropodids, at final pouch exit the young is able to follow close by the mother, which it does at least until weaning (Russell 1982) when the weight of the litter may be only 20 percent of maternal mass. Total relative investment is low, but investment in individual young is relatively high (Russell 1982).

Interspecific Interactions

Two types of interspecific interaction involving marsupials have received recent attention. These are mutualism, where both species benefit through their association, and competition, where coexistence reduces some aspect of the species' fitness.

Some marsupials, such as the Honey Possum burramyids and possibly petaurids, appear to play a mutualistic role as pollinators of proteaceous and myrtaceous plants (such as *Banksia* and *Eucalyptus*), benefiting by harvesting pollen and nectar (Turner 1982). In fact, the Honey Possum is reliant on these resources (Wooller *et al*. 1981). Pollen is transferred from anther to fur and from fur to stigma while the marsupials probe deeply into inflorescences to obtain nectar. Pollen also is harvested from the fur by the burramyids during periodic bouts of grooming. Plants visited by these marsupials generally produce copious quantities of nectar and pollen. There has been speculation as to whether certain characteristics of some plants are particular adaptations which attract non-flying mammals (Rourke & Wiens 1977), but on balance these characteristics also would appear effective in attracting avian pollinators (Turner 1982). Competition for pollen and nectar between mammalian and avian visitors to flowers may not occur as the former are nocturnal and the latter, diurnal.

Another potentially mutualistic association occurs between marsupials which eat fungi (peramelids and potoroines) and sporocarpic mycorrhizal fungi (Lee & Cockburn 1985). Fungal spores are resistant to digestion and the fruiting bodies of these fungi are often odoriferous and highly attractive to mammals. In this largely unexplored relationship, marsupials facilitate spore dispersal and benefit by ingesting the nutrient-rich fruiting body.

Several studies have implicated competition in structuring communities of Australian mammals (Fox 1981; Dickman 1984). These include range reductions and extinctions of peramelids and potoroines as a consequence of introduction of the European Rabbit (Ovington 1978) and the exclusion of marsupials from granivory by ants and birds (Morton 1979). Much of the evidence is inferential and some equivocal (see Dickman 1984; Lee & Cockburn 1985, for reviews). The only experimental test of these hypotheses (Dickman 1986b) demonstrated that competition may restrict the habitat used by the smaller of two coexisting *Antechinus*. Although there is circumstantial evidence that rabbits may have exploited burrows and, perhaps, food more efficiently than some peramelids and potoroids (Ovington 1978), this need not imply that marsupials are competitively inferior to eutherians.

Diseases and Parasites

The incidence of diseases and parasites and their significance as factors influencing numbers in wild populations of marsupials is known for only a few species. The parasites which may be present are known for many species from investigation of a few animals from road deaths and other opportunistic sources. These studies indicate a diverse fauna of protozoan, platyhelminth and

nematode parasites. Many of these parasites are known only from Australian marsupials, are specific to one or a few related species and many still are undescribed. Only in the Brown Antechinus, *Antechinus stuartii*, and the economically important large kangaroos have the parasite burdens and associated pathology for populations been surveyed in the wild. These studies indicate that individuals carry a diverse parasite burden, especially of nematodes, some of which may be present in very large numbers. Only a few species are known to produce detectable pathological changes (Arundel, Barker & Beveridge 1977; Arundel, Beveridge & Presidente 1979; Lee & Cockburn 1985). In the Koala, widespread reproductive tract disease of bacterial origin leads to infertility in females of reproductive age, with important consequences for the production of offspring in a population (Bolliger & Finckh 1962; Martin 1981).

Many studies of disease in marsupials relate to captive animals at high densities where transmission of diseases and parasites is enhanced and immune responses to them are reduced by stress. Important diseases of captive animals, such as the infective condition of the bones and soft tissues of the head known as Lumpy Jaw, are almost unknown in the wild (Burton 1981). The Parma Wallaby Herpes Virus (PWHV) causes outbreaks of sudden deaths in captive colonies of many species of kangaroos (Callinan & Kefford 1981). Antibodies to PWHV are present at high frequencies in wild populations, suggesting that the virus is present in natural populations but not normally fatal (Webber & Whalley 1978; Kerr, Whalley & Poole 1981).

The increased susceptibility to disease of captive animals is similar in many ways to the situation documented in the wild for those species of *Antechinus* in which all males die after the mating season. The increased levels of active corticosteroids, which are partly intrinsic and partly the result of social interactions during the mating period, lead to suppression of immune responses and a greater effect of disease and parasites already present (Lee & Cockburn 1985).

BEHAVIOUR

Activity Patterns

The pattern of activity in marsupials appears to be related to a variety of factors including diet, body size, season, habitat and predators. Most marsupials are mainly nocturnal. The amount of diurnal activity varies with season and species. Only a few species are strictly diurnal, in particular the Numbat, *Myrmecobius fasciatus*, (Friend & Burrows 1983; Christensen, Masey & Perry 1984). Bandicoots, possums, gliders and many dasyurids are predominantly nocturnal. These are frequently reported to have a peak of activity just after dusk and sometimes another before dawn (Hall 1980b; O'Reilly, Armstrong & Coleman 1984). The nature of activity changes throughout the active phase. Periods of feeding are interspersed with grooming, social interaction or travel. Dusk and dawn peaks of activity may be periods when animals travel to and from dens. Less active periods in between may be times of feeding or grooming as in the Common Brushtail Possum (McLennan 1984). Activity may be spread throughout the 24-hour cycle, as in the Dusky Antechinus, *Antechinus swainsonii*. In this species, Hall (1980b) relates such activity to continuous availability of prey in leaf litter. The larger kangaroos such as *Macropus giganteus*, *M. parryi*, *M. robustus* and *M. rufus* (Eastern Grey Kangaroo, Whiptail Wallaby, Common Wallaroo and Red Kangaroo) are active to some extent in daylight. Feeding starts before sunset and continues through the night until after sunrise. In most species, more diurnal activity occurs in winter than in summer (Kaufmann 1974a; Croft 1981a, 1981b). The Musky Rat-kangaroo,

Hypsiprymnodon moschatus, is predominantly diurnal (Johnson & Strahan 1982). Laboratory experiments on activity patterns show that in many species there is precise control of the timing of activity by external cues, particularly light/dark transitions (Lyne 1981; Goldingay 1984; O'Reilly *et al*. 1984).

Grooming

Cleaning and maintenance of the body surface is a basic mammalian activity and marsupials share many grooming behaviours with other mammals. The relatively unspecialised forepaw is used extensively in grooming. It is mobile and has some grasping ability in most species. Also used are the tongue, teeth and hind foot. Much grooming is performed in a sitting position and generally occurs in bouts, particularly at the beginning of the daily activity period or after feeding. Grooming of the head is stereotyped and similar in many species. The forepaws are wiped repeatedly along the side of the head from behind the ears to the tip of the snout where the paws are licked (Fig. 18.5a). This behaviour serves a cleaning function and spreads saliva and secretions of the glands of the mouth region over the whole head, an important focus of sniffing in social interactions (Russell 1985).

The forepaws comb fur wherever they can reach and hold the pouch, scrotum and tail for cleaning with tongue and teeth. Although the movement is similar to that in many other mammals, the syndactylous digits of many marsupials make a particularly effective comb. The hind foot scratches behind the head, the ears and shoulders and is usually used when the animal is sitting (Fig. 18.5b).

Pouch cleaning is one of the few grooming behaviours peculiar to marsupials. The pouch is held open with the forepaws and the snout inserted while the female sits or stands. The long tail of macropodoids requires a specific grooming position – the animal stands or sits with its tail forward between its legs where it can be reached easily (Fig. 18.5c). This is a common resting position in many smaller macropodoids and the birth position in some species.

Some grooming movements have become especially stereotyped and function as visual signals, for example scratching, licking and biting the chest in various displays of kangaroos (Kaufmann 1974a; Croft 1981a, 1981b).

Use of Dens, Nests; Thermoregulation

An important role of behaviour is to keep an animal within the range of environmental conditions where its body functions most efficiently. The most important responses to extremes of temperature include construction and use of a nest, den, burrow or shelter, selection of sheltered habitat, changes in daily activity pattern and such behaviours as huddling, licking and torpor to increase or decrease heat loss or gain.

When they are not active, most small marsupials use some form of enclosed shelter which protects them from predators and extremes of temperature. Pre-existing structures may be used: tree hollows by many arboreal species, (Menkhorst 1984); hollow logs on the ground used by the Numbat (Christensen *et al*. 1984); and deep cracks in the soil used by small dasyurids such as planigales and dunnarts (Morton 1978b, 1978d; Denny 1982). Constructed shelters are either nests in thick vegetation or burrows. Burrows provide an environment with stable air temperature and high humidity and are used by many small desert-dwelling dasyurids, the Bilby (Johnson & Johnson 1983), the Numbat (Christensen *et al*. 1984) and the wombats (McIlroy 1973; Wells 1978a). The latter are the largest marsupials to construct a shelter. Nests in thick vegetation may be a hollowed out chamber in thick grass, as used by some peramelids (Gordon 1974) and many small macropodoids (Russell 1984). Elaborate nests or dreys, which involve carrying and placing of nest material,

A

Figure 18.5 **A**, Grooming: face washing by the Honey Possum (*Tarsipes rostratus*). As in other marsupials, the unspecialised forelimbs are used in grooming the head. They are wiped repeatedly along the side of the head from behind the ears to the tip of the snout and then licked. As well as grooming, this behaviour spreads saliva and other glandular secretions over the head.

B

B, Sitting Tail Forward: This position is adopted by many species during grooming, especially to groom the hind feet and tail and also to use the hind feet to scratch the head and neck.

C

C, Pouch Cleaning: Red Kangaroo (*Macropus rufus*) female. While the female stands or sits the pouch is held open with the forepaws, her snout is inserted into the pouch to lick the inner surface or a young in the pouch. (© ABRS) [K. Hollis]

are constructed by the Common Ringtail Possum, *Pseudocheirus peregrinus*, when no tree hollows are available. The Brush-tailed Bettong, *Bettongia penicillata*, uses its tail to carry nest material and shelters in a cavity within a clump of fibrous material placed at the base of a dense shrub (Christensen & Leftwich 1980). Many species collect and carry material to line a hollow or burrow, for example the Brush-tailed Phascogale, *Phascogale tapoatafa*, (Cuttle 1978a) and the Brown Antechinus (Settle & Croft 1982a).

The larger kangaroos select appropriate shelter such as dense vegetation for a windbreak against cold wind or shade from the sun. For animals in rocky habitats, such as the Common Wallaroo, the Scaly-tailed Possum, *Wyulda squamicaudata*, and the Rock Ringtail Possum, *Petropseudes dahli*, caves are a particularly effective shelter (Dawson & Denny 1969). Daily activity patterns may change to avoid extreme environmental conditions. Kangaroos feed more at night and less during daylight in summer (Croft 1981a, 1981b). The diurnal Numbat retreats to a hollow log during the hottest part of the day in summer (Christensen *et al*. 1984).

A good example of specific behaviour to reduce heat gain is the tail forward sitting posture adopted by the Red Kangaroo in extremely hot conditions; the body is used to shade the large surface area of the tail (Russell & Harrop 1976). Licking of the vascularised region of the forearms helps promote heat loss at times of extreme heat stress (Needham, Dawson & Hales 1974).

Huddling is a specific behaviour to reduce heat loss and is described in many small marsupials, including species of *Sminthopsis*, *Acrobates*, *Petaurus* and *Tarsipes* (Morton 1978d; Frey & Fleming 1984a; Russell 1986). At least two, often many more, animals huddle in a tight cluster in a nest during inactive periods. Fleming (1980) has shown for the Sugar Glider, *Petaurus breviceps*, that the energy savings from huddling are considerable.

Torpor is an important energy saving measure when food is restricted and cold environmental conditions occur. Animals allow their body temperature to fall and become inactive, generally curled up as if asleep. Short term torpor probably occurs at some time in most small marsupials; it is known in dasyurids (Wallis 1982), petaurids (Fleming 1980), the Feathertail Glider (Frey & Fleming 1984a) and the Honey Possum (Wooller *et al*. 1981). The Mountain Pygmy-possum appears to be a true hibernator (Fleming 1985b) and can enter deep torpor for long periods in winter which it spends in a nest below the snow of its alpine environment (Mansergh 1984b). The nest is of particular protective significance to a torpid animal.

Feeding and Hunting

Among the wide variety of dietary specialisations found in the Metatheria, the most important distinction which influences feeding behaviour is that between foods of plant and animal origin. Only two aspects of feeding behaviour have been studied in any detail: the selection of food and the catching and eating of prey by carnivores.

Foods of plant origin are usually stationary. The important aspects of feeding behaviour are the location and selection of appropriate items. Herbivores such as the Yellow-footed Rock-wallaby, *Petrogale xanthopus*, the Common Wallaroo, the Red Kangaroo, and the Common Ringtail Possum are highly selective. The proportions of items in the diet differ from their relative availability in the habitat (Ellis *et al*. 1977; Copley & Robinson 1983; Pahl 1984). As well as particular species, foliage of specific ages may be chosen, as in *Pseudocheirus*. The feeding of petaurids such as the Sugar Glider, the Yellow-bellied Glider, *Petaurus australis*, and Leadbeater's Possum, *Gymnobelideus leadbeateri*, may involve chewing holes in the bark of particular *Eucalyptus* species to obtain carbohydrate rich sap (Smith 1982a; R. Russell 1984). Some very precise sensory discriminations and learning of preferences, locations and foraging skills must be involved; however, this is a little known area.

The characteristics, behaviour and relative size of the prey are important in determining the type of hunting and killing behaviour shown by carnivorous marsupials (including insectivores). All prey capture involves movements with the functions of orientation and approach, seizing and killing the prey. Species such as the Kowari, *Dasyuroides byrnei*, *Planigale* species and the Brush-tailed Phascogale, *Phascogale tapoatafa*, catch insects simply by picking up the insect and eating it or pinning it with a paw then picking it up and holding it until it stops wriggling (Hutson 1975; Andrew & Settle 1982; Cuttle 1982a). Larger prey, once firmly grasped, generally is despatched by a well-directed killing bite to the head or neck. Some of the larger, more specialised carnivorous marsupials, such as the Eastern Quoll, *Dasyurus viverrinus*, have evolved stalking behaviour and aimed bites like those of eutherian carnivores of similar size, such as cats (Pellis & Nelson 1984). Much of this skilled, highly

co-ordinated behaviour must be learned by a young animal. Play in young marsupial carnivores such as *Dasyurus* species is an important avenue for learning the skills of predators, as it is in eutherians (Croft 1982).

Learning

The ratio of brain weight to body weight for marsupials is generally low in comparison with eutherians of similar size, except for insectivores and edentates. Small relative brain size suggests reduced capacity to store and process information and, thus, no great development of learning capacity (Jerison 1973; Eisenberg 1981). No general statement about the learning ability of the Metatheria is possible as yet. The few experiments which have been done were criticised by Kirkby (1977) on the basis of poor experimental design, small number of subjects and use of immature animals. Most experiments tested the Virginia Opossum. This is not a field of research which has seen a high level of activity in Australia. Many experiments have tested animals on visual learning tasks which may not be appropriate for nocturnal animals which may rely more on smell and hearing. The Metatheria, as the Eutheria, are expected to show a range of learning capabilities related to diet, habitat and mode of life.

BEHAVIOUR AND SOCIAL ORGANISATION

Social organisation may be described in a general way by such measures as group size, mating system and pattern of dispersion. Fundamental to this is the way in which individuals interact and how such interactions form the consistent pattern which is the social organisation characteristic of a species. Social interactions consist of a series of acts which allow the exchange of information about the physiological or behavioural state of the individual. Such communication utilises many sensory modes. Social behaviour may be divided conveniently into Communication, Non-Agonistic Behaviour, Agonistic Behaviour (which includes threat, defence, attack and submission), Reproductive and Parental Behaviour.

Communication

Chemical communication is of considerable significance in all marsupials (see reviews by Biggins 1984; Croft 1982; Russell 1985). Marsupials have extensive olfactory sensory areas. Several varieties of skin glands produce odours and many behaviours are directed towards deposition and detection of odours. Important sources of odours are urine, faeces and the products of a variety of skin glands, particularly glands of the mouth, chin, pouch and sternum. One to three pairs of paracloacal glands open into the cloaca and produce a pungent secretion which is deposited separately or with urine and faeces. Odours are deposited passively or actively by rubbing mouth, chin, sternum or cloaca on objects in the environment, often with stereotyped behaviour such as cloacal dragging, sternal rubbing and 'chesting' (Fig. 18.6). Exploratory sniffing of the environment or encountered animals is an obvious part of the behaviour of all species. The most common form of social interaction involves sniffing, especially a nose-to-nose approach when animals meet (Fig. 18.7a). Active and passive substratum marking may serve to identify an exclusive territory. More generally, it probably allows an animal to recognise an area by smell and to distinguish the familiar from the unfamiliar.

Auditory communication varies in importance. Some species produce a very limited range of sounds. For others, an extensive repertoire of vocalisations is an important part of social behaviour. The nature of auditory communication is related to habitat and social organisation. The variety of vocalisations appears to be least in the large terrestrial herbivores. In the large kangaroos, the Red

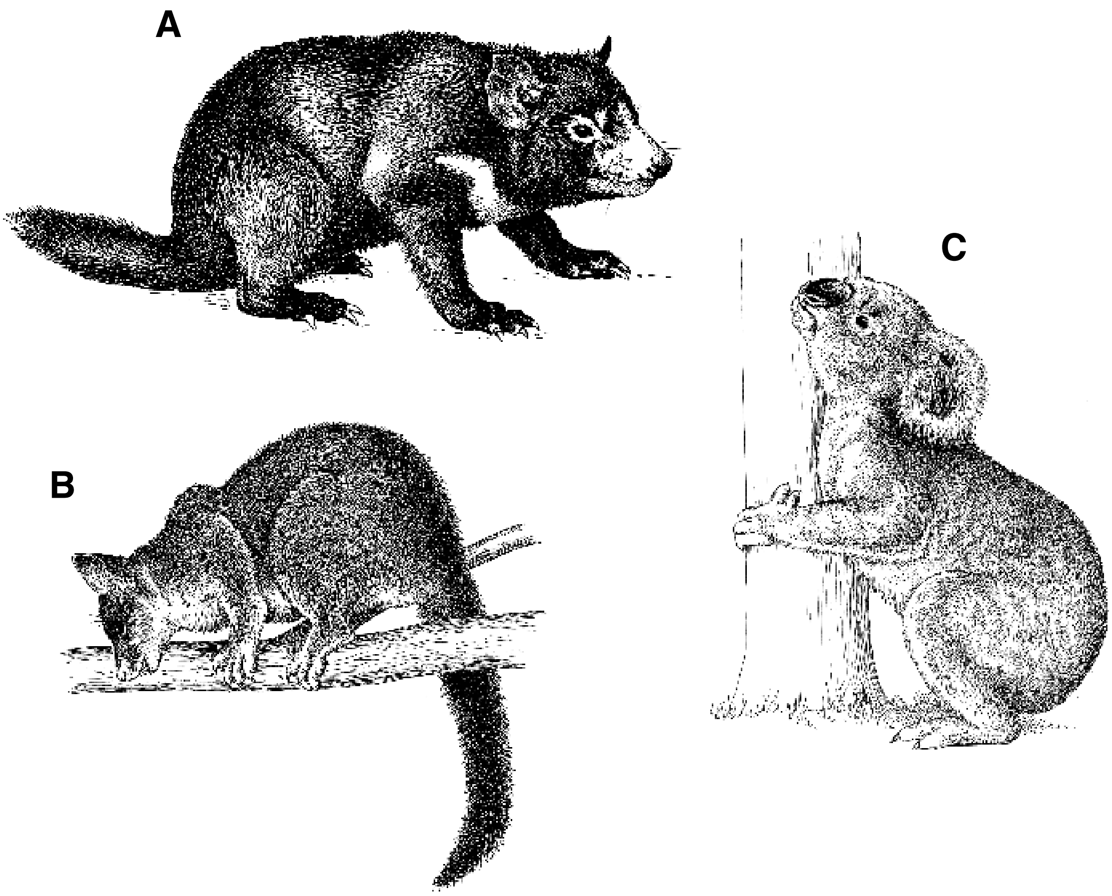


Figure 18.6 Chemical Communication: various forms of active substratum marking; **A**, Cloacal Dragging. The anogenital area is dragged across the substratum. Cloacal dragging occurs in most dasyurids, but is most prolonged and stereotyped in Tasmanian Devils. (After Eisenberg, Collins & Wemmer 1975 or Russell 1985); **B**, Chinning. Marking by male Common Brushtail Possums, usually used on smaller branches in trees. He rubs the branch with the glandular area of the chin and the corner of the mouth. (From photographs by J.W. Winter, from Russell 1985); **C**, Chesting. Marking by male Koalas, the sternal glandular area is rubbed on the base of a tree. Similar marking also is performed by Common Brushtail Possums (After Smith 1980b) (© ABRS) [K. Hollis]

Kangaroo and the Common Wallaroo, Croft (1981a, 1981b) found vocal behaviour limited to male 'clucking' in sexual following, an aggressively voiced 'Ha' sound, and mother-young contact calls (soft clucking by the mother and a loud coughing by the young). These are relatively quiet sounds operative over short distances. When an alarmed animal begins to hop, a louder-than-usual thump is made with the hind feet for the first few steps and this 'alarm-thump' is an additional auditory signal.

The dasyurids have repertoires of five to eight sounds. The larger species, *Dasyurus* species and the Tasmanian Devil, produce sounds audible at a considerable distance (Eisenberg, Collins & Wemmer 1975). In addition to the mother-young contact calls and male sexual following calls of kangaroos, there is a range of calls of increasing intensity produced in agonistic contexts, male and female mate attraction calls and various twittering calls produced in novel or stressful situations (Croft 1982). The greatest variety of calls is produced by some of the arboreal phalangeroids (Biggins 1984). Extensive repertoires have been described for the Yellow-bellied Glider (Kavanagh & Rohan Jones 1982; R. Russell 1984) and the Common Brushtail Possum (Winter 1975, quoted by E. Russell 1984). Some of these sounds are complex and audible over large distances.

A

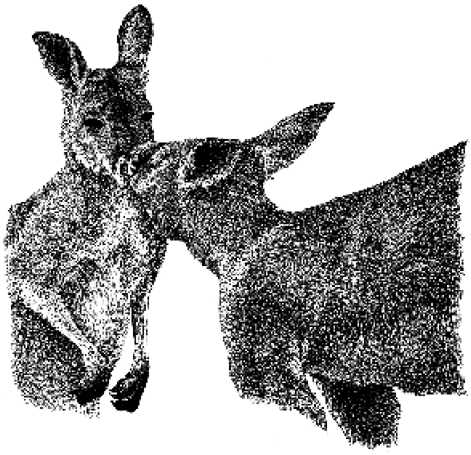
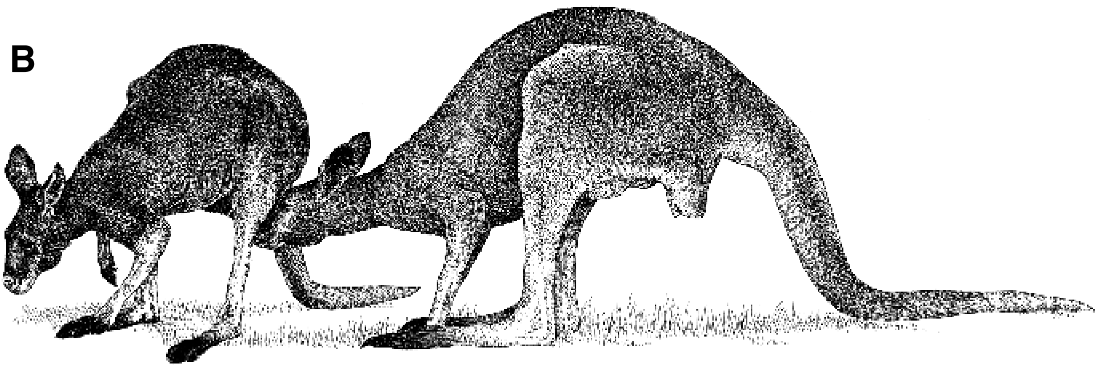


Figure 18.7 Non-agonistic Social Interactions: Sniffing. **A**, Nose-to-nose sniffing by two Red Kangaroos (*Macropus rufus*): by far the most common social interaction in marsupials and an introduction to many other interactions; **B**, Sexual Checking of a Female by a Male Kangaroo. Adult males smell the pouch and cloaca of all females they encounter and remain to follow any female approaching oestrus. (After Russell 1985) (© ABRS) [K. Hollis]

B



Visual signals are not highly developed except in species such as the larger kangaroos which are more active by day. Information conveyed by visual signals is most often about the motivational state of the sender, whether friendly or unfriendly, likely to attack or flee, and may be reinforced by auditory or olfactory signals. As in other mammals (Eisenberg 1981), the usual form of visual signal is some modification of body posture, emphasising size and offensive weapons in the case of threat or hiding these in the case of submission.

Most species show some form of threat posture in which the body is held upright, tail and head extended, ears erect and the gaze directed at the opponent. This posture is usually quadrupedal, but is often bipedal in kangaroos. The mouth may be open, with lips retracted exposing the teeth. A threatened animal may respond by abandoning its own threat posture or by turning aside or moving away with no further modification of body posture. It also may assume a submissive posture in which the body is hunched low to the ground and the head turned aside, often with ears folded. In the extreme case, a prostrate, belly-up appeasement posture is adopted (see reviews by Croft 1982; Russell 1984). The dark brush tail of many species (Tasmanian Devil, *Phascogale* species, *Trichosurus* species), patterns of stripes (Striped Possum, *Dactylopsila trivirgata*, *Petaurus* species, Honey Possum) and the lighter ventral surface of most species all serve to make body positions more visible at night.

The most complex and specialised visual displays occur in the larger macropodids in agonistic contests between males. The various upright threat postures are seen most commonly and contain elements that resemble the behaviour of fighting males (Fig. 18.8). Several other visual threat displays have been described (Kaufmann 1974a; Croft 1981a, 1981b) (Fig. 18.9).

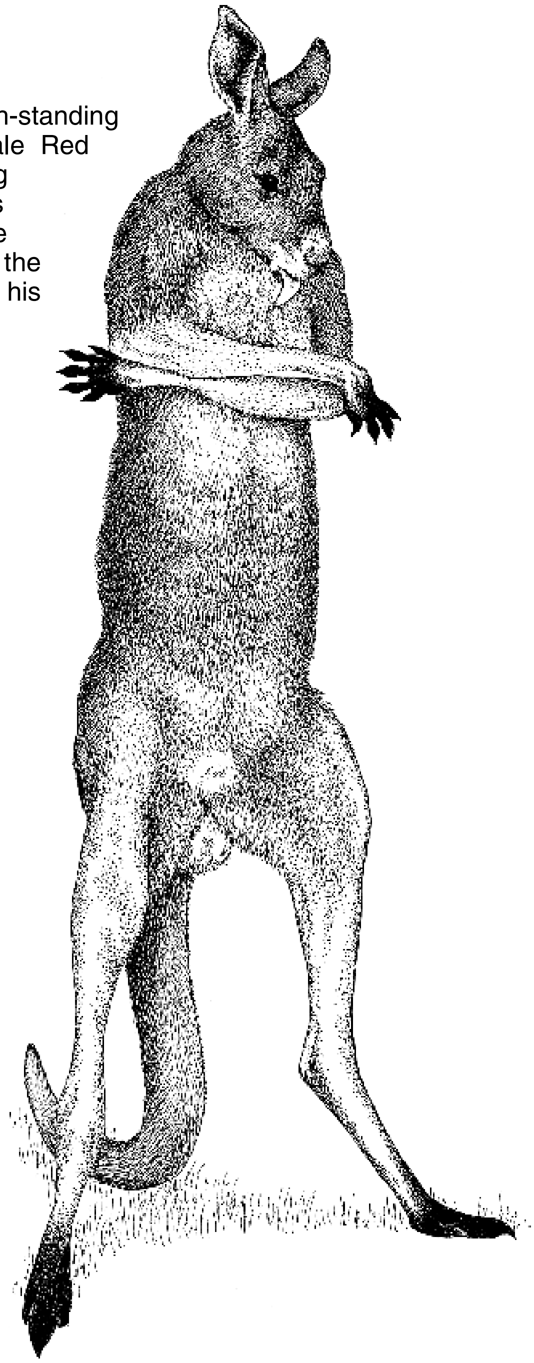


Figure 18.8 Visual Display. High-standing threat display of large adult male Red Kangaroo *Macropus rufus*. Using his tail for support, he stands erect, moving his head from side to side, licking and biting the glandular sternal area and his forelimbs which may be held crossed. (Based on Sharman & Calaby 1974) (© ABRS)
[K. Hollis]

The only frequently observed form of active tactile communication is allogrooming, the grooming of one animal by another. Additionally, there are many forms of passive, non- agonistic contact between individuals which can be considered tactile communication in that they convey information about the behaviour of one individual to another. In this category must be included contact between a mother and her young in the pouch and between animals resting together in contact. In many of the smaller marsupials which give birth to several young, mothers and young or litter-mates may huddle in a nest or burrow. Unrelated individuals may also huddle, as in *Antechinus* species, the Feathertail Glider, *Sminthopsis* species and the Honey Possum (Morton 1978d; Frey & Fleming 1984a; Lee & Cockburn 1985; Russell 1986). Where there is a bonded social group (such as in the Yellow-bellied Glider, the Sugar Glider and Leadbeater's Possum), it is that group which huddles (R. Russell 1984; Henry & Suckling 1984; Smith 1984a). Huddling has an important thermoregulatory function, but any agonistic behaviour must be suspended for it to occur.

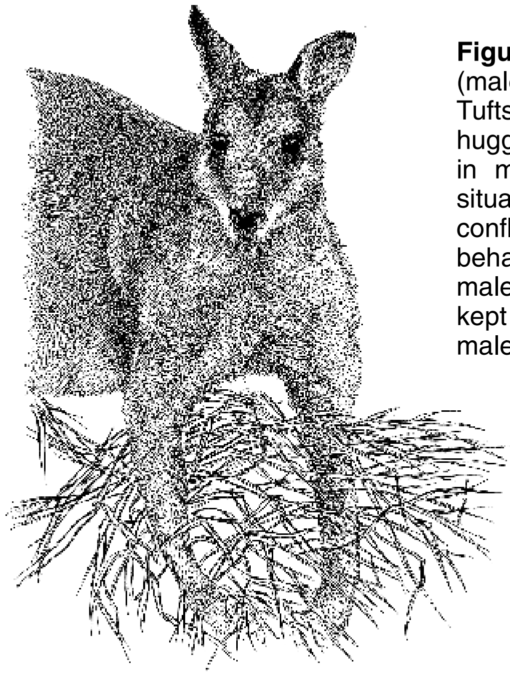


Figure 18.9 Visual Displays. Grass-pulling (male Agile Wallaby, *Macropus agilis*). Tufts of grass or bushes are picked up or hugged to the chest. Grass-pulling is seen in many species of *Macropus*, often in situations where elements of threat are in conflict with elements of fear or sexual behaviour, for example in subordinate males attracted to oestrous females but kept at a distance by a more dominant male. (© ABRS) [K. Hollis]

Studies of dasyurids in captivity did not record allogrooming in any context except between mother and offspring (see reviews by Croft 1982; Russell 1984). It may occur in huddled groups (as in the Honey Possum, Russell 1986), but has escaped observation. Allogrooming has been described between adults in many kangaroos, but is generally infrequent. In those species in which a few individuals form a stable social group, allogrooming is more frequent and, as Ganslosser (1979) suggested for the New Guinean tree-kangaroo, *Dendrolagus dorianus*, probably serves a bonding function within the group as in primates and birds. In species such as the Sugar Glider and the Yellow-bellied Glider, exchange of chemical stimuli and tactile communication are combined. Material from a scent gland in the dominant male is rubbed on to other members of the group, reinforcing the dominant-subordinate relationship.

Non-agonistic Interactions

The most important non-agonistic interactions in marsupials, as in many other mammals, are the various investigative sniffings which are a preface to most other social interactions. Initial approach and nose-nose sniffing, leading to sniffing of other regions of the body, are important for the recognition of individuals and sexual status. In group-living species, such as the New Guinean Tree-kangaroo and some of the arboreal petaurids, non-agonistic sniffing and allogrooming interactions are an important part of group cohesive behaviour. In territorial species, whether solitary or group-living, few non-agonistic responses to strangers occur. In the gregarious larger macropodids, tolerance of other individuals leads to a higher frequency of non-agonistic interactions, many of which are difficult to recognise as such. These generally involve one individual approaching another or a group, which is clearly aware of it. The animals become alert and sniff towards the approaching individual, but do no more than tolerate its presence close by.

Agonistic Interactions

Agonistic interactions involve threat, supplanting interactions or fighting. Passive supplanting involves no obvious threat other than a direct approach by one animal to another which moves away. In active supplanting, one individual performs an overt aggressive act which causes the other to retreat. The

aggressive act may be simply a visual threat display or involve physical attack by pushing (Fig. 18.10a), grabbing, hitting, biting, lunging or chasing. If the opponent does not retreat but threatens or attacks in return, then fighting ensues. The nature of fighting ranges from the generalised mammalian pattern of scrambling, or wrestling fights (seen in most marsupials, including didelphids, small dasyurids, peramelids and the Honey Possum), to the highly ritualised fights of the large kangaroos. The latter involves many different elements of threat, wrestling and kicking, in a complex sequence. Serious fights over resources are relatively rare in the large kangaroos, but there is a high incidence of play fighting and long 'boxing' contests between young males (Fig. 18.10b–d).

Agonistic interactions are important in establishing dominance relationships in a group or population. If the outcome of a competitive interaction between two animals is predictable at some practical level of certainty, then the animal likely to succeed is said to be dominant (Rowell 1974). Older or larger animals may be dominant in a group. A resident animal in its own home range may be dominant to an intruder. Once a dominance relationship is established, further contests between the individuals in question can be settled without expensive fights. For males, dominance is important for priority of access to females. In many marsupial species with promiscuous mating systems, most matings are performed by a relatively few dominant males.

Reproductive Behaviour

The necessary first phase of reproductive behaviour is for a male and female to be aware of each other such that when a female is in oestrus and ready to mate, at least one male is present. The behaviour involved in establishing contact between a male and a female approaching oestrus depends on the mating system of the species and whether breeding is seasonal or continuous.

The higher level of activity during the breeding season in both males and females in many species increases their chance of meeting (Lee *et al*. 1982). In addition, many species use mate-attracting calls, such as the high-pitched clicking sounds produced by some small dasyurids (Croft 1982). Male Koalas produce a loud bellowing call during the mating season, often in agonistic encounters, but also serving to advertise presence (Smith 1980a, 1980b). Females of continuously breeding species may be in oestrus at any time of year and males must monitor continuously the reproductive state of all females they meet. In the Red Kangaroo, an important part of a male's daily activity is to approach and sniff the cloaca of all females in the area where he is grazing (Croft 1981a) (Fig. 18.7b). If a female is approaching oestrus, then the male stays nearby and begins pre-mating following behaviour, usually interrupted by the other males which have also found her. The leading dominant male usually is able to assert his priority of access and remains in consort with the female until she reaches oestrus and he is able to mate. During this consort period, the male has to repel other males by threats and fighting.

Pre-mating behaviour is much the same as in all mammals. The male pursues the female, who moves away but not so fast as to escape entirely. The male may attempt to mount or to hold the female by the body or tail, but she moves away until ready to mate. In many marsupials, males produce a soft clicking vocalisation during pre-mating following.

In mating, the male mounts the female and with his forelimbs holds her anterior to his pelvis. Most dasyurid males engage in some form of biting or head-rubbing on the neck of the female. There are many differences between species in the minor elements of behaviour during courtship and mating (see reviews by Ewer 1968; Eisenberg 1981; Croft 1982; Russell 1984). The duration of copulation is variable. Many small dasyurids have a period of intromission of

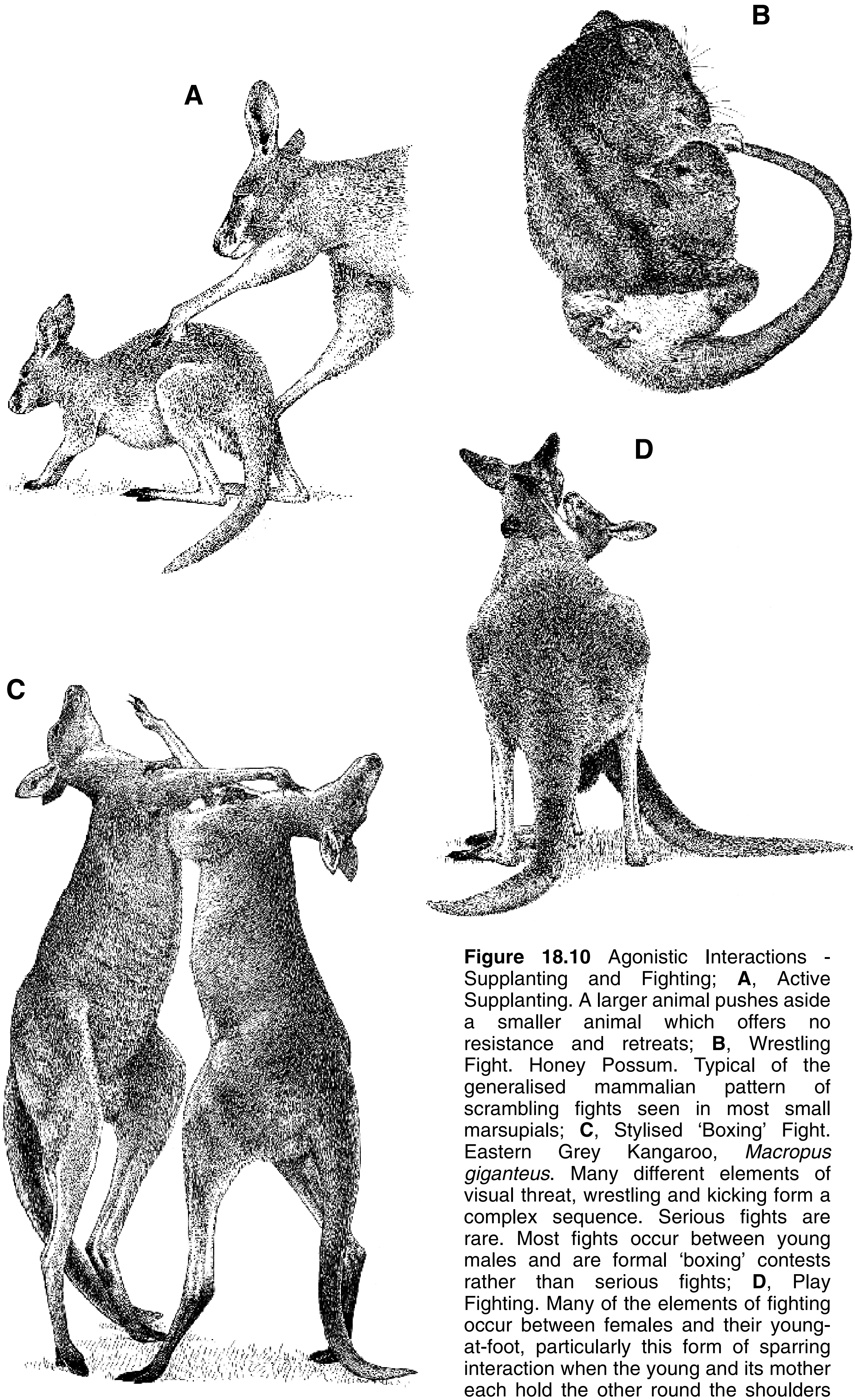


Figure 18.10 Agonistic Interactions - Supplanting and Fighting; **A**, Active Supplanting. A larger animal pushes aside a smaller animal which offers no resistance and retreats; **B**, Wrestling Fight. Honey Possum. Typical of the generalised mammalian pattern of scrambling fights seen in most small marsupials; **C**, Stylised 'Boxing' Fight. Eastern Grey Kangaroo, *Macropus giganteus*. Many different elements of visual threat, wrestling and kicking form a complex sequence. Serious fights are rare. Most fights occur between young males and are formal 'boxing' contests rather than serious fights; **D**, Play Fighting. Many of the elements of fighting occur between females and their young-at-foot, particularly this form of sparring interaction when the young and its mother each hold the other round the shoulders and grapple. (© ABRS) [K. Hollis]

several hours, with bouts of thrusting interspersed with periods of quiescence. In theperamelids, a series of brief intromissions at intervals of a few minutes occurs for up to 2 hours. Copulation in the macropodids may last for up to an hour with spaced bouts of thrusting. Similarly protracted copulation occurs in insectivores, but in most other eutherians it is short, although many intromissions may occur. Both Ewer (1968) and Eisenberg (1981) have speculated that this conservative pattern of long intromission may occur in species which copulate where predation is unimportant.

Birth

Because the marsupial young at birth is so small, undeveloped and fragile, the mother must behave in such a way as to give the young the best possible chance to reach the pouch and attach to a teat. Precise control of timing and pattern of behaviour at birth is very important. The young is very small relative to its mother, but makes its way from the external opening of the birth canal to the pouch without active assistance from the mother. It travels to the pouch over the mother's fur within a few minutes by alternate crawling movements of its forelimbs, grasping the fur with the clawed digits. The female's behaviour changes in the 24 hours before birth: she may become more or less active. In some species, there is a period of intensive pouch cleaning. A specific birth position, variable among the species, is adopted. Most macropodids adopt a sitting position with the tail forward between the legs, a common grooming position. The grey kangaroos, *Macropus giganteus* and *M. fuliginosus*, however, stand with the tail in its usual position. The Northern Brown Bandicoot, *Isoodon macrourus*, lies on one side with one hindleg raised. The Kowari, *Dasyuroides byrnei*, stands with its head curled tightly beneath its body towards the cloaca, which is held 20–30 mm from the ground by the tail. Of prime importance is that the birth position should be adopted at the right time and maintained until the young have attached to the teats on the abdomen or in the pouch. During birth, the female may lick amniotic fluid from near the vulva and from her abdomen where the young has crawled.

How the young finds its way to the pouch is not certain. At the time of birth, the olfactory epithelium is well developed, as is innervation of the tongue, jaws and snout (Hill & Hill 1955; Walker & Rose 1981; Hughes & Hall 1984). This supports suggestions that olfactory cues are important in navigation (Hill & Hill 1955; Tyndale-Biscoe 1973) and that tactile cues also could be involved. Cannon *et al*. (1976) suggested that gravitational cues are important, but the variability of birth positions casts some doubt on this.

Parental Behaviour

Male marsupials play no part in the rearing of young except for the few group-living or monogamous species where the male / female association persists after mating. Litter size and type of pouch are important factors in determining the pattern of maternal care (see Russell 1982, for review).

The pattern in most species with reduced or absent pouches is similar and found in most dasyurids and some didelphids. At first, the young are attached firmly and continuously to the teat and carried on the abdomen of the female. As soon as they develop the ability to open the mouth and release the teat, they are no longer carried, but left in a nest. At this stage, the young have little fur, their eyes are closed and their ability to maintain body temperature is not fully developed. Their mother forages alone and returns periodically to suckle her young, keeping them warm by huddling. When their eyes open and they become well furred and able to regulate body temperature, they begin to leave the nest, following their mother or riding on her back.

In many species with well-developed pouches and multiple young, the young are carried in the pouch until after they begin to release the teat. They are not left in a nest by their mother until they have some fur and their eyes are open. Development then proceeds as outlined above. This pattern applies to a wide range of species and genera, including those of the Tasmanian Devil, *Perameles*, *Isoodon*, *Pseudocheirus*, *Petaurus* and the Honey Possum.

The third pattern is seen in species which have a large pouch in which a single young remains until it is well furred and its eyes are open. When the young first begins to leave the pouch it is not left in a nest, but continues to return to the pouch and is transported by its mother. Characteristic of this pattern is a period (from one to several weeks, depending on species) in which the young spends more frequent and longer periods out of the pouch, until finally it no longer returns. When the young permanently leaves the pouch, it generally follows its mother at least until it is weaned. In some species an unweaned young may be left behind in a refuge if the mother has to travel a long way to food or water. This pattern is seen in the Koala, the wombats, Brushtail Possums and all kangaroos.

The period of dependence from birth to weaning is related to body size (Russell 1982). Time from birth to weaning is from 2–3 months in small (< 50 g) species, to more than a year in the wombats and some of the larger macropodids (> 20 kg), including a period of 8–9 months in the pouch and at least 3–4 months as a young-at-foot before weaning.

When young are in the pouch, the main function of maternal behaviour is to keep the young and the pouch clean. The female does this by licking. When their young are left in a nest, females may become very aggressive towards intruders and in some species are probably territorial. When young have developed sufficiently to leave the nest, they may ride on the back of the female when she forages and, later, follow on foot. The young continue to share their mother's nest until weaning and in some species even afterwards (Lee & Cockburn 1985). Retrieval of separated young occurs in some species. In others, maternal response to distress calls by the young is to merely wait for them to catch up.

Interactions between females and their young are best known for the larger, more diurnal species, such as kangaroos in which the time from the first pouch exit to weaning is long. The first excursions from the pouch appear to be accidental: the young falls out when the pouch is relaxed during grooming (Russell 1973). Later, the young is tipped out sometimes by its mother and sometimes leaves voluntarily towards the end of pouch life. In species in which embryonic diapause occurs, the pouch suddenly becomes smaller and tighter just before birth, preventing re-entry by the previous young (Rose 1986b; Sharman & Calaby 1964). When no birth is imminent, the factors determining the end of pouch life is unclear. There is close association of a female and her young between permanent pouch exit and weaning. The young continues to feed from the pouch and initiates the episodes of suckling, generally importuning its resting mother by pushing at her pouch with its head and forelimbs until she stands. There is close coordination of behaviour, with the young largely responsible for staying in touch with its mother. Females groom young and the young groom themselves and their mothers. This is the most frequent form of allogrooming seen in marsupials. Weaning results largely from lack of co-operation by the mother.

During association with its mother, the young learns to interact with its environment and with other animals. Most young marsupials exhibit some form of play. Young dasyurids usually engage in rough and tumble play not unlike that of carnivorous eutherians. R. Russell (1984) describes wrestling play in the Yellow-bellied Glider and Russell (1986) observed wrestling play in young

Honey Possums. In the solitary young of macropodids, play-fighting between mother and young is common (Fig. 18.10d). Exaggerated fast hopping around the mother is another form of play (Croft 1981a).

Social Organisation

Social organisation is the pattern of all social relationships which exist among members of a population. In practice, these relationships are expressed in behaviour which can be observed in the field, such as the pattern of dispersion, group size and composition and mating system. Although there are few detailed field studies of social behaviour and social organisation of marsupials, some information about the major variables of social organisation is available for many species (see reviews by Russell 1984; Lee & Cockburn 1985).

The most obvious manifestation of the social organisation of a species is the distribution of individuals in space. The area in which an animal normally lives is its home range. A home range from which conspecifics are excluded is a territory. The normal unit of dispersion in the population, the 'social unit', may be a single animal (or female with dependent juveniles), a pair (male and female) or a group. Animals of a pair or stable group share the same home range, although they may move independently within it. Groups which have a stable composition and persist in time are very different from the unstable groups seen in gregarious species. In these, although most animals are seen usually in the company of others, the members change constantly.

Another important feature of social organisation is the mating system, the social relationships which determine which male mates with which female. Three types of mating system are found in marsupials: monogamy, a prolonged association and essentially exclusive mating between a male and female; polygyny, a prolonged association and essentially exclusive mating between a male and two or more females; and, promiscuity, no prolonged association between a male and female, multiple matings by members of at least one sex.

Since social organisation is so variable interspecifically, any classification is necessarily very general, but some of the more common patterns may be distinguished. Four of these are listed below with examples. It must be stressed that social organisation within a species is not invariant and may vary according to population density or resource availability.

1. The social unit is a single individual which lives in a home range which overlaps, but does not coincide, with that of several other individuals. Part of the home range, such as a den or nest, may be exclusive to the individual. The mating system is promiscuous, with males moving over the range of many females. Examples are: many small (<1 kg) short-lived insectivorous species, including many species of the American family Didelphidae (Charles-Dominique 1983); peramelids such as the Northern Brown Bandicoot, *Isoodon macrourus*; dasyurids such as species of *Antechinus*, *Planigale* and *Sminthopsis*; the Honey Possum; and some small forest-living macropodoids such as the Rufous Bettong, *Aepyprymnus rufescens*, the Red-necked Pademelon, *Thylogale thetis* and the Parma Wallaby, *Macropus parma*.

2. The social unit is a cohesive stable group (often a family group) which shares a common home range, generally an exclusive territory. The few well-documented examples are medium-sized (100–600 g) phalangeroid exudate-feeder / insectivores such as Leadbeater's Possum, the Yellow-bellied Glider and the Sugar Glider.

Leadbeater's Possum units contain only one adult female and from one to three adult males plus sub-adults and juveniles. Only one male is reproductively active and the mating system is monogamous (Smith 1984b). In Victoria, Yellow-bellied Glider groups contain one male, one female and juveniles with a

monogamous mating system (Craig 1985), but in north Queensland groups with more than one adult breeding female occur (R. Russell 1984). Groups of Sugar Gliders are larger. More than one adult male and several breeding females comprise each group. The dominant male probably does most of the mating (Henry & Suckling 1984). Defence of resources which an individual could not perform, such as shared dens and special sap trees, may be an important function of the group.

3. The social unit is the individual. A male's home range overlaps the home range (or territory) of one or a small number of females with whom he has an exclusive mating relationship. The male may be territorial or dominant to other males in the area. Examples include the Common Brushtail Possum, the Mountain Brushtail Possum, *Trichosurus caninus*, the Koala and the Greater Glider.

Although one male and one or a few females have an exclusive mating relationship and live in the same area, this is a very different social situation from that of the cohesive group which shares a den and exhibits a wide range of social grooming and marking interactions. In the Greater Glider, a territorial male may overlap with one or two females. He occasionally visits them or shares a den with one or other of them. The females appear to avoid contact with each other, although their home ranges overlap to some extent (Henry 1984). In the Mountain Brushtail Possum, the relationship is almost exclusively monogamous (How 1981). This pattern appears to be favoured particularly by those arboreal folivores that are not very mobile over large distances, but whose specific food tree requirements necessitate dispersal.

4. The social unit is an unstable association of gregarious individuals. Many larger members of the family Macropodidae are found more often in the company of conspecifics than alone, generally in a small group which has no fixed composition. Examples are the wallaroos, wallabies and kangaroos (Antilopine Wallaroo, *Macropus antilopinus*, Agile Wallaby, *M. agilis*, Tammar Wallaby, Western Grey Kangaroo, Eastern Grey Kangaroo, Whiptail Wallaby, *M. parryi*, and Red Kangaroo).

In species of higher rainfall areas, populations are sedentary and loosely organised into a series of large groups or 'mobs' of mixed age and sex. They share a common home range which often is delineated by topographical boundaries. Mob home ranges can overlap extensively in areas where there is no topographical boundary. All members of a mob are not seen together at any time, but in smaller sub-groups. The Red Kangaroo, of arid Australia, is similarly gregarious, but home ranges are much larger (10 km^2 instead of 1 km^2). A local 'mob' is difficult to identify although most animals are sedentary at any one time. These gregarious species have a similar promiscuous mating system. Access to females is determined by a size-based male dominance hierarchy. The gregarious macropodids generally are larger species of more open habitat, including open forest.

The many small species of dasyurids, petaurids and burramyids which huddle in nests or tree hollows show apparent gregariousness or at least exhibit considerable social tolerance. The social organisation of only a few is known, but huddling appears to occur in conjunction with a variety of patterns of social organisation.

The full range of marsupial social organisation is probably not yet appreciated. Many species remain to be studied.

ECONOMIC SIGNIFICANCE

Economic and Cultural Significance

Australian ecosystems, the result of millions of years of evolution, support our lives and economy through interrelated ecological processes. Marsupials, the central element of the mammal fauna, are important components of these ecosystems and, consequently, are of great economic significance.

Marsupials can be economically significant either as assets or liabilities. As assets, they may have a direct value as a resource of saleable products or an indirect value through their importance to the culture and heritage of the community. As liabilities, they may be pests of agricultural production or human habitation. They may be perceived as a pest or a resource depending on their location, population density and the interests of the observer.

Marsupials can be direct economic assets when hunted. In the early days of European settlement, many species were the target. Today, on the mainland, commercial hunting is restricted to a few species of large kangaroo. Recreational hunting concentrates on birds and introduced mammalian pest species. In Tasmania, however, commercial and recreational hunting of marsupials is practised more widely, but there is disagreement in the community as to whether such hunting should continue.

There is more agreement on the cultural and heritage importance of marsupials. Some of the value of a species may be attributable to conventional beauty, for example the colours of the Yellow-footed Rock-wallaby, *Petrogale xanthopus*, or the grace of the Sugar Glider. In the past, these qualities have been the basis of the direct economic value of dead animals. Skins of the Yellow-footed Rock-wallaby were traded in large numbers because of their attractiveness. Today, importance as an asset is more likely to come through live marsupials. Species such as the Koala make a cash contribution to the economy through tourism.

In the past, marsupials had both direct and indirect value in the economy of Aboriginal Australians. With a few exceptions, this is not the case today. The Aboriginal community is increasingly part of the national economy and not reliant on traditional resources. Nevertheless, their rights under the law to use marsupials in a traditional manner remain. Cultural and heritage values of Aborigines, the totemic and sacred significance of places and things, include marsupials. The symbol of the kangaroo is, of course, of prime totemic significance for other Australians.

Species at risk of extinction have a particular cultural and heritage importance. Twenty- eight marsupials are in this category. Those which have not been seen for 50 years and which are thought to be extinct are marked with Ex in the following list from Ride & Wilson (1982):

Antechinus apicalis

Mountain Pygmy-possum *Burramys parvus*

Burrowing Bettong *Bettongia lesueur*

Brush-tailed Bettong *Bettongia penicillata* (& *tropica*)

Caloprymnus campestris (Ex)

Chaeropus ecaudatus (Ex)

Leadbeater's Possum *Gymnobelideus leadbeateri*

Lagorchestes asomatus (Ex)

Rufous Hare-wallaby *Lagorchestes hirsutus*

Lagorchestes leporides (Ex)

Banded Hare-wallaby *Lagostrophus fasciatus*

Northern Hairy-nosed Wombat *Lasiorhinus krefftii* (as *barnardi*)

Macropus greyi (Ex)

Bilby *Macrotis lagotis*

Lesser Bilby *Macrotis leucura* (Ex)

Numbat *Myrmecobius fasciatus*

Bridled Nail-tail Wallaby *Onychogalea fraenata*

Onychogalea lunata (Ex)

Western Barred Bandicoot *Perameles bougainville*

Perameles eremiana (Ex)

Proserpine Rock-wallaby *Petrogale persephone*

Red-tailed Phascogale *Phascogale calura*

Long-footed Potoroo *Potorous longipes*

Potorous platyops (Ex)

Julia Creek Dunnart *Sminthopsis douglasi*

Long-tailed Dunnart *Sminthopsis longicaudata*

Sandhill Dunnart *Sminthopsis psammophila*

Thylacine *Thylacinus cynocephalus* (Ex)

Although the community generally places considerable cultural importance on kangaroos, the perception of the significance and value of other marsupials varies greatly. Some sections regard all as sacrosanct, not to be killed or interfered with in any way. The fervour of this view varies with what may be called a cuddliness index, on which the Koala rates highly, but *Antechinus* species do not register. This is a form of 'speciesism', the attribution of superior status to one species over another. This term was developed to describe the way humans use animals for their own ends and do not allow them the right to live unmolested. This view is increasingly the basis of criticism of the way kangaroos are killed.

Agricultural Significance

At the focus of this issue of agricultural significance is the presence of kangaroos on land used for primary production. Whether marsupials really are pests in this situation is contentious. Generalised control mechanisms such as commercial hunting occur on a broad scale whereas agricultural damage is often localised in time and place. Based on the rationalisation that it is best to lower populations before they become pests, kangaroos are taken all year round and over a large area, but are only pests in local circumstances. For example, large numbers of kangaroos can be counted emerging from forest to graze on young wheat. They prefer to go through, rather than over, fences and, thus, may severely compromise attempts by graziers to fence other pests out of their land. During droughts, kangaroos undoubtedly compete with domestic stock for remnant pastures and water.

The controversy is further compounded because the problem is so subjective. Some graziers will tolerate more kangaroos than others. Their tolerance level also may be a function of the extent to which they have been encouraged to apply for licences to remove kangaroos from their properties.

Scientific Significance

Apart from their cultural significance to Australians, marsupials are of particular significance in a general scientific context. They are a major group of mammals which has evolved separately from eutherian mammals over the course of 100 million years. While the evolution and radiation of marsupials occurred in many places, most surviving families of marsupials are known only from Australia and New Guinea. They provide a compelling illustration of adaptive radiation and the parallel evolution of similar body forms by two long distinct lines of descent in different continents under similar selective pressures.

Medical and Veterinary Significance

Marsupials have had little direct economic impact on medical and veterinary science. At the time of white settlement, Australia had no ungulates and, consequently, was free of the diseases which affect domestic stock in other parts of the world. This assisted the invasion of Australia by hoofed animals, both domesticated and feral. In Africa, diseases such as trypanosomiasis and rinderpest placed limits on lands which could be colonised for the rearing of livestock. Marsupials do not appear to be likely reservoirs of exotic disease infection. Snowdon (1968) inoculated eight marsupial species with foot-and-mouth disease virus and exposed others to infected cattle. Although virus replication took place, it is considered unlikely that marsupials will play a significant role in the spread of foot- and-mouth disease under field conditions. During an outbreak of rinderpest in Western Australia in 1923, kangaroos and possums were inoculated and drenched with infected blood, but developed no clinical evidence of disease. Helminth parasites carried by marsupials are host-specific and generally incapable of infecting domestic stock.

In a few cases, marsupials may be a source of infection or disease important to human or domestic animal health. *Trichophyton mentagryphites*, the usual agent of the fungal infections found in macropodids and possums, produces only a mild lesion in the normal host whereas a severe infection has occurred frequently in people handling animals or untanned skins (Keep 1981). Similarly, hydatids (*Echinococcus granulosus*) in macropodids may have economic importance if they act as a source of re-infection and diminish the effectiveness of control programs intended to reduce the risk to human health. The strain of hydatids prevalent in domestic dogs and sheep is different to that in the feral cycle which operates in dingoes and kangaroos, so the two cycles may be independent (Kumaratilake & Thompson 1984). *Salmonella*, a human health hazard, has been found to be prevalent in captive macropodids (Samuel 1981). It contaminates kangaroo meat (Anderson, Crowder & Woodruff 1964) and the possibility exists of human infection.

Tuberculosis (*Mycobacterium bovis*) occurs in the Common Brushtail Possum in New Zealand (Ekdahl, Smith & Money 1970). There the disease has some economic significance and appears to compromise testing programs and attempts to eradicate tuberculosis from cattle. The same situation has not been reported in Australia.

Introductions, Naturalisation and Domestication

Introductions of exotic mammals to the Australian environment have profoundly affected marsupials. Rabbits, foxes and domestic stock such as sheep and cattle have altered drastically the habitat and pre-existing predator-prey relationships. The effect has been most profound on small and medium-sized kangaroos and bandicoots. Today, remnant populations linger on islands and areas of northern Australia where rabbits and predators such as the Fox, *Vulpes vulpes*, have been unable to penetrate. The islands of Shark Bay off the Western

Australian coast are especially important in this regard as they provide refuge for several species which were formerly widespread: the Banded Hare-wallaby, *Lagostrophus fasciatus*; the Western Barred Bandicoot, *Perameles bougainville*; and the Burrowing Bettong, *Bettongia lesueur.*

Some Australian marsupials have been introduced to other countries and become pests, for example the Common Brushtail Possum, the Red-necked Wallaby, *Macropus rufogriseus*, and the Tammar Wallaby, in New Zealand. Other species have become established in populations which do little harm: the Parma Wallaby, *Macropus parma*, and the Brush-tailed Rock-wallaby, *Petrogale penicillata*, in New Zealand and the Red-necked Wallaby in England.

Similar transportations and releases of marsupials within Australia have been rare, for example, the release of the Koala on Kangaroo Island, although many species have been moved so that they can be established in zoos. Marsupials have not been domesticated. Common Brushtail Possums do live commensally in suburbia. Several species of kangaroos and wallabies are kept in fauna parks and zoos.

Breeding in captivity

A national objective of wildlife conservation and management should be to have colonies of all endangered species established as a safeguard against possible failures to manage adequately the natural habitat of the species. This is being done for a few species. Attempts are being made to establish colonies of endangered species such as the Bilby in Alice Springs and the Numbat in Western Australia.

Conservation and Control

A commonly stated objective of species conservation is to maintain populations which are sufficiently large as to be genetically stable in the long term. Ideally, this would mean managing populations and ecosystems to prescribed goals, but this is rarely, if ever, done. The variations in public perceptions greatly affect conservation measures taken for individual species.

Wildlife authorities usually begin conservation measures by assessing the distribution and abundance of animals, often with inadequate resources and techniques. Their scope to manage habitat, however, is limited to minor activities in reserves and national parks under their control. They are unable to create suitable habitat for a species throughout its range and populations are not manipulated towards prescribed goals. The primary conservation measure taken is to place restrictions on the number of animals that can be killed.

The effort and the extent of even these limited interventions depend on where the political process determines that the balance lies between economic assets and liabilities. Normally, larger animals with a higher cultural value, such as the Yellow-footed Rock-wallaby, will be regarded as a greater asset and receive more attention and, hence, funds from wildlife managers than smaller animals such as bandicoots, which are more threatened, but have lower status. Species which are both large and culturally significant receive the most funds. If species also are seen as pests, such as the Red and Grey Kangaroos, they receive most of the conservation, research and management effort.

Even though maintaining the distribution of native species on lands used for primary production requires decisions that may be economically unpalatable, from a conservation perspective they are essential to the long term survival of many species. Conservation of a species cannot depend alone on islands of reserved land. Active management is required on all forms of land tenure throughout the whole of a species range.

Management Practices

Surveying populations is the first step in their management. Techniques in common use for determining abundance and distribution of marsupials are: spotlight counts from vehicles and on foot; aerial surveys; capture, mark, release and recapture; measuring the dilution of marked animals in the total population; tracking animals carrying radio transmitters; faecal pellet counts; counting of signs and footprints in natural areas and specially prepared sand trays; nest hollow and burrow counts.

Managing populations, which means changing their distribution and abundance, is achieved most effectively in the long term by habitat alteration. Techniques include: varying vegetational successional stages by controlling fire frequency and stocking rates of domestic animals; logging intensity; slashing and application of seed and fertiliser.

Techniques for managing populations in the shorter term include: controlling hunting; restricting movements with fences; removing predators; and providing artificial water and trapping. The variety of traps depends on size of the species involved and ranges from small break back traps to large netting enclosures around water points.

Hunting

Hunting of marsupials can be considered in the categories of sport, pest control and commerce. Sport hunting often is associated closely with pest control where agriculturalists encourage amateur sport hunters to assist in the control of unwanted kangaroos on their properties. Small kangaroos, such as the Red-necked Wallaby and the Agile Wallaby, are taken for sport, pest control, crayfish bait and for dog food on properties that have working dogs. The larger kangaroos are also hunted for many of these reasons where a commercial industry is not permitted, such as in Victoria and the more intensively settled area of New South Wales. Apart from Tasmania, where the tradition is incorporated in law, much of this sporting and recreational hunting is illegal.

The industry based on commercial hunting of kangaroos was worth about $10 million per year in the early 1980s and quotas are set for the taking of approximately two million animals each year. The species concerned are given below (under Legislation). They are used for pet food, the skin trade and meat for human consumption in Australia and overseas.

Determining how many kangaroos should be taken each year has become a very complex procedure. The primary considerations are: the competing claims of agriculturalists wanting relief from their perceived problem; the need of the kangaroo industry for a stable supply of kangaroos so the industry can operate through good and bad seasons and can respond to pest control requests when needed; and the desire of kangaroo protection organisations to minimise the numbers of kangaroos killed. There is little biology in this procedure; the debate does not consider the relationship between the animals and their habitat. Although extensive aerial surveys have been conducted and there is no doubt that the proportion of the population taken is well within the short term sustainable harvest, the consequences of habitat change on populations are largely ignored.

The basic management question remains unaddressed: how many kangaroos should there be in Australia and where should they be located? Any answer needs to take into account current and proposed land uses in kangaroo habitat. It also would encourage Australian pastoralists to view kangaroos as a resource rather than pests. Kangaroos could be the most suitable grazing animals for much of Australia's rangelands where they evolved and probably are better adapted to survive than sheep or cattle. Kangaroos also appear to have less

deleterious effects on native pastures and soils and their numbers fluctuate with good and bad seasons. The meat is low in fat and cholesterol which makes it attractive to health conscious consumers. Thus they have the potential to complement current commercial grazing animals, but there are problems to be solved before this develops further. Meanwhile, the complexities and conflict will continue as long as the rationale of the kangaroo industry is a confused mix of sustained yield harvesting within a pest control operation.

Legislation

Legal authority for fauna (and land use) is vested in the State and Territory Governments and the Commonwealth where it controls a Territory. The Commonwealth controls the export of fauna, encourages the development of national policies on fauna and is responsible for fauna matters which might flow from international treaties such as the Convention on International Trade in Endangered Species of Flora and Fauna (CITES).

Fauna legislation of the States prevents killing, holding or interference with Australian native specimens or species. Fines are imposed upon people contravening these provisions. Special fines are allocated to further protect endangered species. Provision is made for interference with or killing of specimens for scientific purposes.

More general nature conservation legislation reserves the habitat of fauna as part of a conservation area network. The purpose is to protect ecosystems and ecological processes. Legislation, however, fails to protect habitat which is not included in reserves.

All marsupials are covered and protected by State and Territory fauna legislation. They may be taken and hunted under licence in some States on the basis that they are in numbers in excess of those that would ensure satisfactory survival and, in others, on the basis of mitigating agricultural damage. There is also legal variation between States over whether they can be shot for sporting purposes, as pests or used commercially. The sale of the larger kangaroos is legalised throughout Australia, but in Victoria, the Northern Territory and the Australia Capital Territory the hunting of kangaroos for commercial purposes is not permitted. At the national level, the Commonwealth Government permits kangaroo meat and skins to be exported in the name of controlling populations and mitigating the damage done to agricultural production. Licences also may be issued for special purposes such as scientific research although they are restricted, especially for endangered species.

The species of marsupials that are abundant and which are hunted for commercial purposes are the Red Kangaroo, the Eastern Grey Kangaroo, the Western Grey Kangaroo, the Common Wallaroo, the Whiptail Wallaby, the Red-necked Wallaby, the Agile Wallaby and the Swamp Wallaby. Further species that generally have a restricted range, but may be locally abundant, may be taken legally where their numbers are in pest proportions. They are the Black-striped Wallaby, *Macropus dorsalis*, the Tammar Wallaby, the Tasmanian Pademelon, *Thylogale billardierii* and the Common Brushtail Possum.

The wide variation in legal protection given to marsupials reflects the range in community attitudes towards wildlife and the lack of a national consensus on whether marsupials are pests, a resource to be utilised on a sustained basis or whether they should be protected totally. When they are utilised, there is no compulsion to take the full value. Often only skins are retrieved, leaving meat to waste. Some species are not utilised commercially at all and the many thousands that are shot are abandoned.

Codes of practice are emerging as another procedure which influences attitudes and behaviour towards marsupials. One, on the behaviour of people harvesting kangaroos has been developed and endorsed by the Council of Nature Conservation Ministers. It does not have any binding legal basis, but should assist in improving animal welfare standards. Others are being developed to set standards for killing and live capture of free living animals, capture techniques (traps, handling and restraint), holding, marking, release and transport of captured animals and euthanasia of animals.

The standards and sophistication of management vary greatly between species and areas. Monitoring of populations of some species, such as the large kangaroos, is proceeding at quite a sophisticated level using extensive aerial surveys. Others are largely ignored. Nowhere, however, are adequate measures made of changes to habitat or the consequences of change. Even for species that are so abundant that they are used commercially, it is essential to assess not only the resource and determine an annual cull, but also to measure changes to the refuge areas and other components of the animal's environment essential to reproduction.

Because plans of management for species do not contain this sort of detail, short term objectives are confused. Some species such as kangaroos are at the one time: pests subject to a harvest which is said to be sustainable, and; the object of major cultural attention with implicit (and often explicit) demands for total protection. Until there is wider debate and objectives are set in the context of changing habitat and land use, conservation, management and legislation will continue to be confused. Agreement must be reached in advance on what is to be accomplished and precise descriptions made on the density, distribution and economic use desirable for species.

LITERATURE CITED

Anderson, K., Crowder, E.F. & Woodruff, P. (1964). The isolation of Salmonellae from kangaroo meat sold as pet food. *Medical Journal of Australia* 2: 668–669

Andrew, D.L. & Settle, C.A. (1982). Observations on the behaviour of species of *Planigale* (Dasyuridae, Marsupialia) with particular reference to the narrow-nosed planigale (*Planigale tenuirostris*). Pp. 311–324 *in* Archer, M. (ed.) *Carnivorous Marsupials Vol. 1*. Royal Zoological Society of New South Wales : Sydney

Arundel, J.H., Barker, I.K. & Beveridge, I. (1977). Diseases of Marsupials. Pp. 141–154 *in* Stonehouse, B. & Gilmore, D. (eds) *The Biology of Marsupials*. MacMillan : London

Arundel, J.H., Beveridge, I. & Presidente, P.J.A. (1979). Parasites and pathological findings in enclosed and free-ranging populations of *Macropus rufus* (Desmarest) (Marsupialia) at Menindie, New South Wales. *Australian Wildlife Research* 6: 361–379

Biggins, J.G. (1984). Communication in possums: a review. Pp. 35–57 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Blackall, S. (1980). Diet of the Eastern Native-Cat, *Dasyurus viverrinus* (Shaw), in southern Tasmania. *Australian Wildlife Research* 7: 191–197

Bolliger, A. & Finckh, E.S. (1962). The prevalence of cryptococcosis in the koalas (*Phascolarctos cinereus*). *Medical Journal of Australia* 1: 545–547

Braithwaite, R.W. & Lee, A.K. (1979). A mammalian example of semelparity. *American Naturalist* 113: 151–155

Burton, J.D. (1981). Studies into aspects of lumpy jaw in macropods. Unpublished PhD Thesis, Melbourne University : Melbourne

Calaby, J.H. (1960). Observations on the Banded Ant-eater *Myrmecobius f. fasciatus* Waterhouse (Marsupialia), with particular reference to its food habits. *Proceedings of the Zoological Society of London* 135: 183–207

Callinan, R.B. & Kefford, B. (1981). Mortalities associated with herpes virus infection in captive macropods. *Journal of Wildlife Diseases* 17: 311–317

Cannon, J.R., Bakker, H.R., Bradshaw, S.D. & MacDonald, I.R. (1976). Gravity as the sole navigational aid to the newborn quokka. *Nature* 259: 42

Charles-Dominique, P. (1983). Ecology and social adaptations in didelphid marsupials: comparisons with eutherians of similar ecology. Pp. 395–422 *in* Eisenberg, J.F. & Kleiman, D.G. (eds) *Advances in the Study of Mammalian Behaviour. American Society of Mammalogists, Special Publication* No. 7

Christensen, P. & Leftwich, T. (1980). Observations on the nest-building habits of the brush-tailed rat-kangaroo or woylie (*Bettongia penicillata*). *Journal of the Royal Society of Western Australia* 63: 33–38

Christensen, P., Maisey, K. & Perry, D.H. (1984). Radio-tracking the Numbat, *Myrmecobius fasciatus*, in the Perup Forest of Western Australia. *Australian Wildlife Research* 11: 275–288

Copley, P.B. & Robinson, A.C. (1983). Studies on the yellow-footed rock-wallaby, *Petrogale xanthopus* Gray (Marsupialia: Macropodidae). II. Diet. *Australian Wildlife Research* 10: 63–76

Corbett, L.K. (1975). Geographic distribution and habitat of the marsupial mole, *Notoryctes typhlops*. *Australian Mammalogy* 1: 375–378

Craig, S.A. (1985). Social organization, reproduction and feeding behaviour of a population of yellow-bellied gliders, *Petaurus australis* (Marsupialia: Petauridae). *Australian Wildlife Research* 12: 1–18

Croft, D.B. (1981a). Behaviour of red kangaroos, *Macropus rufus* (Desmarest 1922), in northwestern New South Wales, Australia. *Australian Mammalogy* 4: 5–58

Croft, D.B. (1981b). Social behaviour of the euro, *Macropus robustus* (Gould), in the Australian arid zone. *Australian Wildlife Research* 8: 13–49

Croft, D.B. (1982). Communication in the Dasyuridae (Marsupialia): a review. Pp. 291–309 *in* Archer, M. (ed.) *Carnivorous Marsupials Vol. 1*. Royal Zoological Society of New South Wales : Sydney

Cuttle, P. (1978). The behaviour in captivity of the dasyurid marsupial *Phascogale tapoatafa* (Meyer). Unpublished MSc Thesis, Monash University : Melbourne

Cuttle, P. (1982a). A preliminary report on aspects of the behaviour of the dasyurid marsupial *Phascogale tapoatafa*. Pp. 325–332 *in* Archer, M. (ed.) *Carnivorous Marsupials Vol. 1*. Royal Zoological Society of New South Wales : Sydney

Dawson, T.J. & Denny, M.J.S. (1969). A bioclimatological comparison of the summer day microenvironments of two species of arid zone kangaroos. *Ecology* 50: 328–332

Denny, M.J.S. (1982). Review of planigale (Dasyuridae, Marsupialia) ecology. Pp. 131–138 *in* Archer, M. (ed.) *Carnivorous Marsupials Vol. 1*. Royal Zoological Society of New South Wales : Sydney

Dickman, C.R. (1984). Competition and co-existence among the small marsupials of Australia and New Guinea. *Acta Zoologica Fennica* 172: 27–31

Dickman, C.R. (1986b). Niche compression: two tests of a hypothesis using narrowly sympatric predator species. *Australian Journal of Ecology* 11: 121–134

Eisenberg, J.F. (1981) *The Mammalian Radiations*. University of Chicago Press : Chicago xx 610 pp.

Eisenberg, J.F., Collins, L.R. & Wemmer, C. (1975). Communication in the Tasmanian devil (*Sarcophilus harrisii*) and a survey of auditory communication in the Marsupialia. *Zeitschrift für Tierpsychologie* 37: 379–399

Ekdahl, M.O., Smith, B.L. & Money, D.F.L. (1970). Tuberculosis in some wild and feral animals in New Zealand. *New Zealand Veterinary Journal* 18: 44–45

Ellis, B.A., Russell, E.M., Dawson, T.J. & Harrop, C.J.F. (1977). Seasonal changes in diet preferences of free-ranging red kangaroos, euros and sheep in western New South Wales. *Australian Wildlife Research* 4: 127–144

Ewer, R.F. (1968b). *The Ethology of Mammals*. Logos Press : London 418 pp.

Fleming, M.R. (1980). Thermoregulation and torpor in the sugar glider, *Petaurus breviceps* (Marsupialia: Petauridae). *Australian Journal of Zoology* 28: 521–534

Fleming, M.R. (1985b). The thermal physiology of the mountain pygmy-possum *Burramys parvus* (Marsupialia: Burramyidae). *Australian Mammalogy* 8: 79–90

Fleming, M.R. & Frey, H. (1984). Aspects of the natural history of feathertail gliders (*Acrobates pygmaeus*) in Victoria. Pp. 403–408 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Fox, B.J. (1981). Niche parameters and species richness. *Ecology* 62: 1415–1425

Frey, H. & Fleming, M.R. (1984a). Thermoregulatory behaviour of free-ranging feathertail gliders *Acrobates pygmaeus* (Marsupialia: Burramyidae) in Victoria. Pp. 393–401 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Friend, J.A. & Burrows, R.G. (1983). Bringing up young numbats. *SWANS* 13(1): 3–9

Ganslosser, U. (1979). Soziale Kommunikation, Gruppenleben, Spiel und Jugendverhalten des Doria Baumkänguruhs (*Dendrolagus dorianus* Ramsay 1833). *Zeitschrift für Säugetierkunde* 44: 137–153

Godsell, J. (1982). The population ecology of the eastern quoll *Dasyurus viverrinus* (Dasyuridae, Marsupialia), in southern Tasmania. Pp. 199–207 *in* Archer, M. (ed.) *Carnivorous Marsupials Vol. 1*. Royal Zoological Society of New South Wales : Sydney

Goldingay, R.L. (1984). Photoperiodic control of diel activity in the sugar glider (*Petaurus breviceps*). Pp. 385–391 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Gordon, G. (1974). Movements and activity of the short-nosed bandicoot *Isoodon macrourus* Gould (Marsupialia). *Mammalia* 38: 405–431

Guiler, E.R. (1970a). Observations on the Tasmanian Devil, *Sarcophilus harrisii* (Marsupialia: Dasyuridae). I. Numbers, home range, movements and food in two populations. *Australian Journal of Zoology* 18: 49–62

Guiler, E.R. (1971b). Food of the potoroo (Marsupialia, Macropodidae). *Journal of Mammalogy* 52: 232-234

Hall, S. (1980a). The diets of two coexisting species of *Antechinus* (Marsupialia: Dasyuridae). *Australian Wildlife Research* 7: 365–378

Hall, S. (1980b). Diel activity of three small mammals coexisting in forest in southern Victoria. *Australian Mammalogy* 3: 67–79

Heinsohn, G.E. (1966). Ecology and reproduction of the Tasmanian bandicoots (*Perameles gunnii* and *Isoodon obesulus*). *University of California Publications in Zoology* 80: 1–107

Henry, S.R. (1984). Social organisation of the greater glider (*Petauroides volans*) in Victoria. Pp. 221-228 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Henry, S.R. & Craig, S.A. (1984). Diet, ranging behaviour and social organisation of the yellow-bellied glider (*Petaurus australis* Shaw) in Victoria. Pp. 331-341 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Henry, S.R. & Suckling, G. (1984). A review of the ecology of the sugar glider (*Petaurus breviceps*). Pp. 355–358 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Hill, J.P. & Hill, W.C.O. (1955). The growth stages of the pouch young of the native cat (*Dasyurus viverrinus*), together with observations on the anatomy of the newborn young. *Transactions of the Zoological Society of London* 28: 349–453

How, R.A. (1981). Population parameters of two congeneric possums *Trichosurus* spp. in north-eastern New South Wales. *Australian Journal of Zoology* 29: 205–215

Hughes, R.L. & Hall, L.S. (1984). Embryonic development in the common brushtail possum *Trichosurus vulpecula*. Pp. 197–212 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Hutson, G.D. (1975). Sequences of prey-catching behaviour in the brush-tailed marsupial rat (*Dasyuroides byrnei*). *Zeitschrift für Tierpsychologie* 39: 39–60

Jerison, H.J. (1973). *Evolution of the Brain and Intelligence*. Academic Press : New York xiv 482 pp.

Johnson, C.N. & Johnson, K.A. (1983). Behaviour of the bilby, *Macrotis lagotis* (Reid), (Marsupialia: Thylacomyidae) in captivity. *Australian Wildlife Research* 10: 77–87

Johnson, K.A. (1980a). Diet of the bilby, *Macrotis lagotis*, in the western desert region of central Australia. *Bulletin of the Australian Mammal Society* 6: 46–47

Johnson, P.M. & Strahan, R. (1982). A further description of the Musky Rat-Kangaroo, *Hysiprymnodon moschatus* Ramsay, 1876 (Marsupialia, Potoroidae), with notes on its biology. *Australian Zoologist* 21: 27-46

Kaufmann, J.H. (1974a). Social ethology of the whiptail wallaby, *Macropus parryi*, in north-eastern New South Wales. *Animal Behaviour* 22: 281–369

Kavanagh, R.P. & Rohan-Jones, W.G. (1982). Calling behaviour of the yellow-bellied glider, *Petaurus australis* Shaw (Marsupialia, Petauridae). *Australian Mammalogy* 5: 95–111

Keep, J.M. (1981). Wildlife diseases of the Pacific basin. Pp. 8–12 *in* Fowler, M. (ed.) *Wildlife Diseases of the Pacific Basin and Other Countries*. Proceedings of the 4th International Conference of the Wildlife Disease Association, Sydney. Wildlife Diseases Association : California

Kerle, J.A. (1984c). Variation in the ecology of *Trichosurus*: its adaptive significance. Pp. 115–128 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Kerr, A., Whalley, J.M. & Poole, W.E. (1981). Herpes virus neutralising antibody in grey kangaroos. *Australian Veterinary Journal* 57: 347–348

Kinnear, J.E., Cockson, A., Christensen, P. & Main, A.R. (1979). The nutritional biology of the ruminants and ruminant-like mammals - a new approach. *Comparative Biochemistry and Physiology* 64A: 357–365

Kirkby, R.J. (1977). Learning and problem-solving behaviour in marsupials. Pp. 193–208 *in* Stonehouse, B. & Gilmore, D. (eds) *The Biology of Marsupials*. Macmillan : London

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

Lee, A.K. & Cockburn, A. (1985). *Evolutionary Ecology of Marsupials*. Cambridge University Press : Cambridge viii 274 pp.

Lee, A.K., Woolley, P. & Braithwaite, R.W. (1982). Life history strategies of dasyurid marsupials. Pp. 1–11 *in* Archer, M. (ed.) *Carnivorous Marsupials*. Royal Zoological Society of New South Wales : Sydney Vol. 1

Lyne, A.G. (1981). Activity rhythms in the marsupials *Isoodon macrourus* and *Perameles nasuta* in captivity. *Australian Journal of Zoology* 29: 821–838

Mansergh, I.M. (1984b). Ecological studies and conservation of *Burramys parvus*. Pp. 545–552 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Martin, R.W. (1981). Age-specific fertility in three populations of the Koala, *Phascolarctos cinereus* (Goldfuss) in Victoria. *Australian Wildlife Research* 8: 275-283

Martin, R.W. & Lee, A.K. (1984). The koala, *Phascolarctos cinereus*; the largest marsupial folivore. Pp. 463–467 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

McIlroy, J.C. (1973). Aspects of the ecology of the common wombat *Vombatus ursinus* (Shaw 1800). Unpubl. Ph.D. Thesis, Canberra : Australian National University xvi 285 pp.

McLennan, D.G. (1984). The feeding behaviour and activity patterns of the brushtail possum, *Trichosurus vulpecula*, in an open eucalypt woodland in southeast Queensland. Pp. 155–161 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Menkhorst, P.W. (1984). The application of nest boxes in research and management of possums and gliders. Pp. 517–525 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Millar, J.S. (1977). Adaptive features of mammalian reproduction. *Evolution* 31: 370–386

Millar, J.S. (1981). Pre-partum reproductive characteristics of eutherian mammals. *Evolution* 35: 1149–1163

Morton, S.R. (1978a). Torpor and nest-sharing in free-living *Sminthopsis crassicaudata* (Marsupialia) and *Mus musculus* (Rodentia). *Journal of Mammalogy* 59: 569–575

Morton, S.R. (1978b). An ecological study of *Sminthopsis crassicaudata* (Marsupialia : Dasyuridae). I. Distribution, study areas and methods. *Australian Wildlife Research* 5: 151-162 [63]

Morton, S.R. (1978d). An ecological study of *Sminthopsis crassicaudata* (Marsupialia: Dasyuridae). III. Reproduction and life history. *Australian Wildlife Research* 5: 183–211

Morton, S.R. (1979). Diversity of desert-dwelling mammals: a comparison of Australia and North America. *Journal of Mammalogy* 60: 253–264

Morton, S.R. (1982). Dasyurid marsupials of the Australian arid zone: an ecological review. Pp. 117–130 *in* Archer, M. (ed.) *Carnivorous Marsupials*. Royal Zoological Society of New South Wales : Sydney Vol. 1

Needham, A.D., Dawson, T.J. & Hales, J.R.S. (1974). Forelimb blood flow and saliva spreading in the thermoregulation of the red kangaroo, *Megaleia rufa*. *Comparative Biochemistry and Physiology* 49A: 555–565

O'Reilly, H.M., Armstrong, S. & Coleman, G.J. (1984). Response to variations in lighting schedules on the circadian activity rhythms of *Sminthopsis macroura froggatti* (Marsupialia: Dasyuridae). *Australian Mammalogy* 7: 89–99

Ovington, J.D. (1978). *Australia's Endangered Species*. Cassell : Sydney 183 pp.

Pahl, L. (1984). Diet preference, diet composition and population density of the ringtail possum (*Pseudocheirus peregrinus cooki*) in several plant communities in southern Victoria. Pp. 253-260 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Pellis, S.M. & Nelson, J.E. (1984). Some aspects of predatory behaviour of the quoll, *Dasyurus viverrinus* (Marsupialia: Dasyuridae). *Australian Mammalogy* 7: 5–15

Pianka, E.R. & Schall, J.A. (1981). Species densities of Australian vertebrates. Pp. 1675–1694 *in* Keast, A. (ed.) *Ecological Biogeography in Australia*. Junk : The Hague Vol. 2

Procter-Gray, E. (1984). Dietary ecology of the coppery brushtail possum, green ringtail possum and Lumholtz's tree-kangaroo in north Queensland. Pp. 129–135 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Ride, W.D.L. & Wilson G.R. (1982). Australian animals at risk. Pp. 27–44 *in* Groves, R.H. & Ride, W.D.L. (eds) *Species at Risk: Research in Australia*. Australian Academy of Sciences : Canberra

Rose, R.W. (1986b). The control of pouch vacation in the Tasmanian bettong, *Bettongia gaimardi*. *Australian Journal of Zoology* 34: 485-492

Rourke, J. & Weins, D. (1977). Convergent floral evolution in South African and Australian Proteaceae and its possible bearing on pollination by non-flying mammals. *Annals of the Missouri Botanical Garden* 64: 1–71

Rowell, T.E. (1974). The concept of social dominance. *Behavioural Biology* 11: 131–154

Russell, E.M. (1973). Mother-young relations and early behavioural development in the marsupials *Macropus eugenii* and *Megaleia rufa*. *Zeitschrift für Tierpsychologie* 33: 163–203

Russell, E.M. (1982). Patterns of parental care and parental investment in marsupials. *Biological Reviews of the Cambridge Philosophical Society* 57: 423–486

Russell, E.M. (1984). Social behaviour and social organization of marsupials. *Mammal Review* 14: 101–154

Russell, E.M. (1985). The Metatherians - Order Marsupialia. Pp.45–104 *in* Brown, R.E. & Macdonald, D.W. (eds) *Social Odours in Mammals*. Oxford University Press : Oxford

Russell, E.M. (1986). Observations on the behaviour of the honey possum *Tarsipes rostratus* (Marsupialia: Tarsipedidae) in captivity. *Australian Journal of Zoology Supplementary Series* 121: 1–63

Russell, E.M. & Harrop, C.J.F. (1976). The behaviour of red kangaroos (*Megaleia rufa*) on hot summer days. *Zeitschrift für Tierpsychologie* 40: 396–426

Russell, R. (1984). Social behaviour of the yellow-bellied glider *Petaurus australis* in north Queensland. Pp. 343–353 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Samuel, J.L. (1981). Salmonella in macropods. Pp. 61–63 *in* Fowler, M.E. (ed.) *Wildlife Diseases of the Pacific Basin and other Countries*. Proceedings of the 4th International Conference of the Wildlife Disease Association, Sydney. Wildlife Diseases Association : California

Settle, G.A. & Croft, D.B. (1982a). Maternal behaviour of *Antechinus stuartii* (Dasyuridae, Marsupialia) in captivity. Pp. 365–381 *in* Archer, M. (ed.) *Carnivorous Marsupials*. Royal Zoological Society of New South Wales : Sydney Vol. 1

Sharman, G.B. & Calaby, J.H. (1964). Reproductive behaviour in the red kangaroo, *Megaleia rufa*, in captivity. *CSIRO Wildlife Research* 9: 58–85

Smith, A.P. (1982a). Diet and feeding strategies of the marsupial sugar glider in temperate Australia. *Journal of Animal Ecology* 51: 149–166

Smith, A.P. (1982b). Is the striped possum (*Dactylopsila trivirgata*; Marsupialia, Petauridae) an arboreal anteater? *Australian Mammalogy* 5: 229–234

Smith, A.P. (1984a). Diet of Leadbeaters possum, *Gymnobelideus leadbeateri* (Marsupialia). *Australian Wildlife Research* 11: 265–273

Smith, A.P. (1984b). Demographic consequences of reproduction, dispersal and social interaction in a population of Leadbeaters possum (*Gymnobelideus leadbeateri*). Pp. 359-373 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Smith, A.P. & Lee, A.K. (1984). The evolution of strategies for survival and reproduction in possums and gliders. Pp. 17–33 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Smith, A.P. & Russell, R. (1982). Diet of the yellow-bellied glider *Petaurus australis* (Marsupialia : Petauridae) in north Queensland. *Australian Mammalogy* 5: 41-45

Smith, M. (1980a). Behaviour of the koala, *Phascolarctos cinereus* Goldfuss, in captivity. III. Vocalisations. *Australian Wildlife Research* 7: 13–34

Smith, M. (1980b). Behaviour of the koala, *Phascolarctos cinereus* Goldfuss, in captivity. IV. Scent-marking. *Australian Wildlife Research* 7: 13–34

Snowdon, W.A. (1968). The susceptibility of some Australian fauna to infection with foot and mouth disease virus. *Australian Journal of Experimental Biology and Medical Science* 46: 667–687

Statham, H.L. (1982). *Antechinus stuartii* (Dasyuridae: Marsupialia) diet and food availability at Petroi, northeastern New South Wales. Pp. 151–163 *in* Archer, M. (ed.) *Carnivorous Marsupials*. Royal Zoological Society of New South Wales : Sydney Vol. 1

Stodart, E. (1977). Breeding and behaviour of Australian bandicoots. Pp. 179–191 *in* Stonehouse, B. & Gilmore, D. (eds) *The Biology of Marsupials*. Macmillan : London

Stoddart, D.M. & Braithwaite, R.W. (1979). A strategy for utilization of regenerating heathland habitat by the brown bandicoot (*Isoodon obesulus*; Marsupialia, Peramelidae). *Journal of Animal Ecology* 48: 165–179

Turner, V. (1982). Marsupials as pollinators in Australia. Pp. 55–66 *in* Armstrong, J.A., Powell, J.M. & Richards, A.J. (eds) *Pollination and Evolution*. Royal Botanic Gardens : Sydney

Turner, V. (1984a). *Banksia* pollen as a source of protein in the diet of two Australian marsupials, *Cercartetus nanus* and *Tarsipes rostratus*. *Oikos* 43: 53–61

Turner, V. (1984b). *Eucalyptus* pollen in the diet of the feathertail glider, *Acrobates pygmaeus* (Marsupialia : Burramyidae). *Australian Wildlife Research* 11: 77-81

Tyndale-Biscoe, C.H. (1973). *Life of Marsupials*. Edward Arnold : London viii 254 pp.

Tyndale-Biscoe, C.H. (1979a). Ecology of small marsupials. Pp. 343–379 *in* Stoddart, D.M. (ed.) *Ecology of Small Mammals*. Chapman Hall : London

Walker, M.T. & Rose, R. (1981). Prenatal development after diapause in the marsupial *Macropus rufogriseus*. *Australian Journal of Zoology* 29: 167–187

Wallis, R.L. (1982). Adaptation to low environmental temperatures in the carnivorous marsupials. Pp. 285–290 *in* Archer, M. (ed.) *Carnivorous Marsupials*. Royal Zoological Society of New South Wales : Sydney Vol. 1

Webber, C.E. & Whalley, J.M. (1978). Widespread occurrence of neutralising antibodies to herpes virus from a parma wallaby. *Australian Journal of Experimental Biology and Medical Science* 56: 351–357

Wells, R.T. (1978a). Field observations of the hairy-nosed wombat [*Lasiorhinus latifrons* (Owen)]. *Australian Wildlife Research* 5: 299-303

Winter, J.W. (1975). The behaviour and social organization of the brush-tail possum (*Trichosurus vulpecula*: Kerr). Unpublished PhD Thesis, University of Queensland : St Lucia 388 pp.

Wooller, R.D., Renfree, M.B., Russell, E.M., Dunning, A., Green, S.W. & Duncan, P. (1981). Seasonal changes in a population of the nectar-feeding marsupial *Tarsipes spencerae* (Marsupialia: Tarsipedidae). *Journal of Zoology , London* 195: 267–279