



# FAUNA *of* AUSTRALIA

## 35. NATURAL HISTORY OF THE EUTHERIA

**P. J. JARMAN, A. K. LEE &  
L. S. HALL**

(with thanks for help to J.H. Calaby,  
G.M. McKay & M.M. Bryden)



## INTRODUCTION

Unlike the Australian metatherian species which are all indigenous, terrestrial and non-flying, the eutherians now found in the continent are a mixture of indigenous and exotic species. Among the latter are some intentionally and some accidentally introduced species, and marine as well as terrestrial and flying as well as non-flying species are abundantly represented. All the habitats occupied by metatherians also are occupied by eutherians. Eutherians more than cover the metatherian weight range of 5 g–100 kg, but the largest terrestrial eutherians (which are introduced species) are an order of magnitude heavier than the largest extant metatherians. Before the arrival of dingoes 4000 years ago, however, none of the indigenous fully terrestrial eutherians weighed more than a kilogram, while most of the exotic species weigh more than that.

The eutherians now represented in Australia are very diverse. They fall into major suites of species: Muridae; Chiroptera; marine mammals (whales, seals and dugong); introduced carnivores (Canidae and Felidae); introduced Leporidae (hares and rabbits); and introduced ungulates (Perissodactyla and Artiodactyla). In this chapter an attempt is made to compare and contrast the main features of the natural histories of these suites of species and, where appropriate, to comment on their resemblance to or difference from the metatherians.

## NATURAL HISTORY

### Ecology

Diet. The native rodents are predominantly omnivorous. The prevalence of items in their diet reflects seasonal availability. The diets of most species include a diversity of plant components (seeds, fruits, leaves, stems and roots). Insects and the fruiting bodies of endogenous fungi are important items for various species in some seasons (Watts & Aslin 1981; Strahan 1983).

A few species (for example, the Greater Stick-nest Rat, *Leporillus conditor*, the Broad-toothed Rat, *Mastacomys fuscus*, and the Swamp Rat, *Rattus lutreolus*) appear to be strict herbivores. The Water Rat, *Hydromys chrysogaster*, and the False Water Rat, *Xeromys myoides*, are carnivorous, feeding upon aquatic invertebrates and fishes.

The introduced *Rattus* species and the House Mouse, *Mus domesticus*, are omnivorous. In comparison to the Australian metatherians, the diets of the native rodents show a greater incident of seeds, corms and tubers. There are, however, no rodents that feed solely on terrestrial arthropods and few which include nectar, pollen and plant exudates in their diets (as do many metatherians). The absence of seed specialists, which are a conspicuous element in the rodent fauna of North America, is assumed to be a consequence of ants and birds pre-empting this resource (Morton 1979).

The Megachiroptera are frugivorous and/or nectarivorous. These food resources occur unpredictably; the timing of flowering and fruiting is irregular in many Australian forest trees. To find these foods, the bats move over hundreds of kilometres each year. Irregular flowering and fruiting also affect the bats' local density and behaviour. Some Megachiroptera show a preference for a particular food source, for example, the Little Red Flying-fox, *Pteropus scapulatus*, for the nectar of *Eucalyptus* species known as bloodwoods and turpentine (*Syncarpia*

species). The large number of species of fruiting and flowering trees fed on by each *Pteropus* species in Australia reflects the bats' need to be relatively unspecialised in choosing unpredictably productive food-species.

The Australian Microchiroptera are all insectivorous, although several are carnivorous as well. The Ghost Bat, *Macroderma gigas*, is largely carnivorous. The Large-footed Mouse-eared Bat, *Myotis adversus*, is known to catch fish, but is not an exclusive fish-eater. These bats tend to be opportunistic feeders, although gut and faecal analysis show that some have a preference for specific types of prey, such as moths or beetles. Several (for example, *Mormopterus* and *Nyctophilus* species) feed off the ground; others, such as *Nyctophilus* species, are foliage gleaners. Several can be found feeding around concentrations of insects, such as nuptial flights, mass hatchings and around street lights; they include *Chalinolobus*, *Miniopterus* and *Eptesicus* species. Australia lacks a sanguivorous (blood-feeding) bat comparable to the Neotropical vampires. The proportion of bats known to feed on ants and other non-flying insects in Australia is abnormally high.

The mysticete or baleen whales which pass through Australian waters are all basically krill-eaters or are planktivorous, but most also take some fish. Odontocete or toothed whales, porpoises and dolphins opportunistically take a wide range of prey, from squid and small fish up to other whales, seals and penguins. Otariid seals also take fishes and squid, hunting them in-shore. The phocid seals enjoy a greater range of diets, from krill (the Crab-eater Seal, *Lobodon carcinophagus*, is a krill specialist) to penguins and other seals (which are hunted by the Leopard Seal, *Hydrurga leptonyx*). More detail can be found in Chapters 48 to 53 and 56. The only sirenian in Australian waters, the Dugong, *Dugong dugon*, grazes unselectively on beds of marine grasses, as it does elsewhere in its Indo-Pacific range.

Diets of the introduced Eutheria are covered in their respective chapters. Most are generalists of their type; the formerly domestic animals take particularly catholic diets. This, in part, contributes to their ability to compete with native herbivores and may have been important in their becoming established in Australia. Establishment of those introduced mammals in many areas has led to extreme change, usually simplification, in the vegetation communities of those parts of Australia where they are dominant. Nevertheless, where several exotic herbivores now live sympatrically, dietary differences contribute to their ecological separation.

The metatherians and native eutherians fall into broadly different feeding niches. The metatherians are terrestrial carnivores, some highly specialised eaters of invertebrates, omnivores and medium to large herbivores. The native eutherians are marine carnivores, piscivores, molluscivores and crustacivores, aerial insectivores and nectarivore/frugivores and the rodents which eat combinations of seeds, vegetation and fungi. The only macroniche offering scope for competition was that using nectar, pollen and fruit, in which the highly mobile Megachiroptera might compete with the sedentary scansorial metatherians such as pygmy-possums, possums and gliders. With the introduction of eutherian carnivores and herbivores, eutherians and metatherians came into direct competition. The lack of dietary specialisation of the introduced species and lack of appropriate defences in the native plants or prey, however, probably has led to the success of the exotics, rather than any general 'superiority' of eutherians in dietary competition with metatherians.

Macroniches and Habitats. The Australian rodents are even more conservative than the Australian metatherians in diversity of lifestyles. Genera of Australian rodents occupy only seven of the 53 macroniches which characterise mammals (Eisenberg 1981, Table 35.1), that is, less than half of the number of

macroniches occupied by genera of Australian metatherians. More than half of the rodent genera are semi-fossorial. There are no completely fossorial, termite-eating or terrestrial insectivorous and carnivorous rodents in Australia.

**Table 35.1** Macroniches of Australian murid rodent genera arranged in order of mean body length of genera. (Macroniches after Eisenberg, 1981; mean body lengths after Strahan, 1983). 1. *Rattus lutreolus*; 2. *R. fuscipes*; 3. not known, extrapolated from Menzies & Dennis (1979) 4. all *Rattus* other than (1) and (2) (includes the two introduced species).

MACRONICHE	GENERA	MEAN BODY LENGTH (mm)
Arboreal frugivore/omnivore	<i>Uromys, Mesembriomys</i>	285
Semiaquatic crustacivore/piscivore	<i>Hydromys, Xeromys</i>	210
Terrestrial herbivore/browser	<i>Leporillus</i>	205
Semifossorial herbivore/grazer	<i>Mastacomys, Rattus</i> (1)	165
Semifossorial fungivore/omnivore	<i>Rattus</i> (2)	165
Arboreal herbivore/browser	<i>Melomys, Pogonomys</i> (3)	145
Semifossorial herbivore/granivore	<i>Zyromys, Notomys, Conilurus, Pseudomys, Leggadina, Rattus</i> (4), <i>Mus</i>	115

Terrestrial and semi-fossorial rodents occur throughout Australia. The arboreal species tend to be concentrated in the forests and woodlands in the northern third of the continent. Species densities today tend to be highest towards the northern margins of Australia and are least in inland New South Wales and South Australia. Sub-fossil deposits, however, suggest that this is a recent pattern and that rodent faunas from arid communities were formerly at least as rich as those of tropical communities today (see Chapter 47). The overall distribution of arboreal, terrestrial and semifossorial rodents today broadly resembles that of metatherians using the same substrata for activity. Unlike the metatherians, however, there are no fully arboreal rodent species in the temperate forests of southern Australia, but there are proportionally more species of rodents in heathlands. There is, however, no aquatic metatherian equivalent of the Water Rat.

Bats can be classified according to their roosting-site preferences. These roost sites reflect both physical (protection) and physiological needs of bats during daylight hours. The categories of roost sites for the Megachiroptera are: hanging in trees in the open (*Pteropus* camps); in dense vegetation (*Syconycteris*, *Macroglossus* and *Nyctimene* species); rocky overhangs, boulder piles and dense vegetation (*Dobsonia* species).

The Microchiroptera generally are classified as tree- or cave-dwellers, with several species utilising both refuge types. Tree-dwellers occupy hollow limbs and trunks or roost under sheets of bark. A number of these species also will roost in buildings. Cave-dwelling species select caves with particular microclimatic features. Alternative sites within caves are in areas with a domed ceiling which collects warm air. In winter, several species undergo periods of torpor in caves which have been selected for their low (10–12°C) temperatures. The Australian Megachiroptera occupy the volant frugivore, frugivore/nectarivore or nectarivore niches. The Microchiroptera occupy the volant, aerial insectivore and foliage-gleaner/insectivore niches (Eisenberg 1981, Table 35.2), while perhaps adding a volant/scansorial or even volant/terrestrial set of macroniches to those suggested by Eisenberg.

**Table 35.2** Macroniches of Australian bats (after Eisenberg, 1981)

MACRONICHE	GENERA	MEAN HEAD/BODY LENGTH (mm)
Volant frugivore/nectarivore	<i>Pteropus, Dobsonia, Nyctimene</i>	225
Volant nectarivore	<i>Syconycteris, Macroglossus</i>	55
Volant carnivore/insectivore	<i>Macroderma</i>	115
Volant insectivore/piscivore	<i>Myotis</i>	54
Volant insectivore	<i>Rhinolophus, Rhinonycteris, Hipposideros, Taphozous, Saccolaimus, Miniopterus, Chalinolobus, Scoteanax, Scotorepens, Pipistrellus, Falsistrellus, Eptesicus, Chaerephon, Mormopterus, Myctinomus, Murina</i>	60
Volant insectivore/voliage-gleaner	<i>Nyctophilus</i>	52
Volant insectivore/arachnivore	<i>Phoniscus</i>	55

**Table 35.3** Macroniches of Australian marine mammals (after Eisenberg, 1981.)

MACRONICHE	GENERA	MEAN HEAD/BODY LENGTH (m)
<b>A. Whales</b>		
Aquatic planktonivore	<i>Eubalaena, Balaenoptera, Caperea, Megaptera</i>	15
Aquatic molluscivore (mainly squid)	<i>Physeter, Mesoplodon, Hyperoodon, Grampus</i>	7
Aquatic piscivore/molluscivore (fish more than squid)	<i>Pseudorca, Lagenorhynchus, Delphinus, Turstrops, Stenella, Lagenodelphis</i>	2.5
Aquatic molluscivore/piscivore (squid more than fish)	<i>Kogia, Ziphius, Globicephala</i>	5
Aquatic carnivore	<i>Orcinus</i>	7
Aquatic ?piscivore	<i>Tasmacetus, Steno, Sousa</i>	3
Aquatic piscivore/?crustacivore	<i>Orcaella</i>	2
Aquatic ?molluscivore/crustacivore/piscivore	<i>Neophocoena</i>	1.5
<b>B. Pinnipeds</b>		
Aquatic planktonivore (krill)	<i>Lobodon</i>	2.5
Aquatic molluscivore/piscivore (squid more than fish)	<i>Mirounga, Ommatophoca</i>	3.5
Aquatic molluscivore/piscivore/crustacivore (squid, fish, lobsters & octopus)	<i>Arctocephalus</i>	2
Aquatic piscivore/molluscivore	<i>Neophoca, Leptonychotes</i>	2.5
Aquatic carnivore/planktonivore (mammals, birds and krill)	<i>Hydrurga</i>	3
<b>C. Sirenians</b>		
Aquatic herbivore	<i>Dugong</i>	4

The mysticete (baleen) whales all fall within the niche of pelagic, migratory plankton-feeders (Table 35.3, Eisenberg's aquatic planktonivore) and the odontocete (toothed) whales within the niches of pelagic or in-shore pursuers of

medium to large prey (aquatic carnivore and aquatic piscivore/molluscivore), niches they share with otariid seals. None of the whales use beaches for breeding, although several mysticetes once entered sheltered bays to give birth and care for the young calves. The phocid seals are diverse in feeding niches, some, for example, the Crab-eater Seal taking krill (aquatic molluscivore/crustacivore), others taking squid and fish (aquatic piscivore) and the Leopard Seal preying on other seals and penguins (aquatic carnivore). Most hunt and feed around the edges of, or under, pack ice. Otariids and phocids are largely separated geographically, most phocids ranging south of, and otariids north of, the Antarctic Convergence. The Southern Elephant Seal, *Mirounga leonina*, is an exception, being a phocid which ranges north of the Convergence. It shares the otariids' need for isolated beaches to haul out on for breeding, while the other phocids use ice.

The Dugong, *Dugong dugon*, is Australia's only marine, herbivorous mammal (aquatic herbivore) and the only marine mammal regularly found in shallow, tropical waters.

The niches of the introduced eutherians (Table 35.4) have been described in the Family chapters. The introduced Dingo and feral dog, *Canis familiaris*, the European Red Fox, *Vulpes vulpes*, and the feral cat, *Felis catus*, provide a suite of cursorial, stalking and pouncing carnivores, able to hunt in most terrestrial habitats and capable of taking most terrestrial vertebrate prey up to about 25 kg. The introduced eutherian herbivores (other than rodents) similarly form a suite of generalised terrestrial herbivores (terrestrial herbivore/grazers and terrestrial herbivore/browsers) ranging 1–1000 kg; but, unlike the introduced carnivores, none is ubiquitous. They occur in all habitats in all regions of Australia, often several species at a time. Sympatric species tend to be separated partially by diet; otherwise there is considerable separation by habitat preference. The Water Buffalo, *Bubalus bubalis*, and the Pig, *Sus scrofa*, are associated with wetlands; Dromedarys, *Camelus dromedarius*, generally termed camels, prefer arid shrublands; goats, horses and donkeys readily occupy hill country; hares prefer modified native or introduced grasslands with patchy ground cover; and rabbits require water and stable soils in which to burrow.

**Table 35.4** Macroniches of the introduced eutherians in Australia, other than rodents. (Macroniches after Eisenberg, 1981.)

MACRONICHE	GENERA	MEAN HEAD/ BODY LENGTH (m)
Semifossorial herbivore/grazer	<i>Oryctolagus</i>	0.4
Terrestrial herbivore/grazer/browser	<i>Lepus, Equus, Camelus, Dama, Cervus, Axis, Bos, Bubalus, Capra</i>	2
Terrestrial omnivore	<i>Homo, Sus</i>	1.5
Terrestrial carnivore	<i>Felis, Canis, Vulpes</i>	0.7

Most macroniches of the native eutherians, therefore, are complementary to those of the metatherians, while those of the introduced species overlap those of some native metatherians.

### Life Histories of Eutherians

The expression of life-history traits which influence reproductive rates differs markedly between groups of Australian rodents. The old endemics typically have small litters, long gestation and lactation periods and mature late (Tables 35.5 & 6). The young are precocial at birth, often with erupted incisors and conspicuous hair follicles, and are transported clinging to a teat. By contrast, the *Rattus* species tend to have larger litters, shorter gestation and lactation periods,

early maturity and relatively altricial young. Even among the *Rattus* species, the Swamp Rat, the Bush Rat (*R. fuscipes*), the Cape York Rat (*R. leucopus*), and the Pale Field-rat (*R. tunneyi*) tend to have lower reproductive rates than the Dusky Rat (*R. colletti*), the Long-haired Rat (*R. villosissimus*), and the Canefield Rat (*R. sordidus*), and the introduced Black Rat (*R. rattus*) and the Brown Rat (*R. norvegicus*), inappropriately termed the old and new endemics by Yom-Tov (1985) (Baverstock, Gelder & Jahnke 1983b). Most of the rodents have reproductive rates higher than equivalent-sized metatherians due to their production of larger, more frequent litters and shorter generation times. This is especially true of the endemic *Rattus* and peridomestic rodents.

**Table 35.5** Ranges of some life history traits of Australian rodents. Sources: Lee *et al.* 1981; Strahan, 1983; Watts & Aslin, 1981; Yom-Tov, 1985. <sup>1</sup>*Conilurus, Hydromys, Leggadina, Leporillus, Mastacomys, Melomys, Mesembriomys, Notomys, Pogonomys, Pseudomys, Uromys, Zyzomys*; <sup>2</sup>*Rattus fuscipes, R. leucopus, R. lutreolus, R. tunneyi*; <sup>3</sup>*R. colletti, R. sordidus, R. villosissimus*; <sup>4</sup>*R. rattus, R. norvegicus, Mus domesticus*.

GROUP	NO. OF SPECIES	BODY MASS (g)	USUAL LITTER SIZES	GESTATION (d)	LACTATION (d)	AGE AT FIRST PARTURITION (m)
old endemics <sup>1</sup>	39	10–606	2–5	28–44	20–42	2–12
<i>Rattus fuscipes</i> group <sup>2</sup>	4	76–125	3–5	21–25	21–31	1.25–3
<i>Rattus sordidus</i> group <sup>3</sup>	3	61–125	6–7	20–27	20–21	1.25–2.25
feral murids <sup>4</sup>	3	17–320	6–9	19–22	18–20	1.5–3.5

The central Australian rodents breed aseasonally in the periods of plant growth which follow irregular rainfall. Rodents inhabiting the more mesic margins of the continent tend to breed in specific seasons. In the north, most litters are produced late in the wet season and early in the dry season (March–June), while in the south breeding often is confined to the warmer months (November–March).

In contrast to the short-lived, fast-breeding, Australian rodents, the bats are typically long-lived, with a low reproductive potential. At birth, the Megachiroptera are furred and have open eyes; in contrast, the Microchiroptera are naked and their eyes closed. Bats grow rapidly. Adult proportions are attained by 6 weeks in the Microchiroptera and approximately 3 months in flying foxes. The Microchiroptera give birth, highly predictably, in early summer, but the Megachiroptera produce young over an extended period from late spring to summer. Most bats give birth to a single young (in contrast to the small, terrestrial, dasyurid insectivores), but several vespertilionids give birth to twins. Most females do not breed until 2 years old (again in contrast to the small dasyurids). Reproduction in males of some species is socially delayed.

The majority of bats form nursery colonies, some of which are spectacular and can consist of hundreds of thousands of individuals. Juvenile mortality is high in both Megachiroptera and Microchiroptera, but survivors live for about 20 years. Large maternity colonies replace at least 20 % of the population yearly with no noticeable effect on the population's numbers. Mortality factors in bats are not well known. Megachiroptera are hunted by carpet snakes and eagles and in some areas human-induced mortality can be heavy. The Microchiroptera are predated by snakes, lizards and dasyurids. Foxes, owls and hawks are severe predators around the entrance to bat roosts, particularly maternity sites in caves. Australia has no specialist bat-predators (comparable to the bat-hawks of Africa and Asia).



The life histories of Australian marine mammals are characterised by medium to long gestations (but not outstandingly long for the sizes of the animals); highly seasonal birth of single, precocial young; variable degrees of parental care; long growth to maturity; physiologically and socially delayed maturation in males of the many heteromorphic species; and potentially long lives.

Both phocid and otariid females mate soon after giving birth; the blastocyst remains unimplanted for some months before gestation resumes. As in many other species which must congregate seasonally in restricted, protected sites to give birth (as do many cave-breeding bats, for example), this synchronisation of birth and mating allows some males to monopolise females at the only time when they are predictably sedentary. These species tend to be highly heteromorphic.

The young of dugong, mysticete and odontocete whales, which are born at sea, are highly precocious and able to swim at birth. Those of otariid and phocid seals, which are born on shore or ice, are less precocious. They need several days to become furred, open-eyed and mobile on land, but weeks or months before they learn to swim. Otariid young are suckled for ~12 months, but phocid pups for only 2–4 weeks; they then live on accumulated fat before taking to the water and hunting independently several weeks later.

Whales and pinnipeds (especially phocids) produce milk which is outstandingly rich in fat and low in water, but protein and carbohydrate concentrations are comparable to those of rodents and terrestrial carnivores.

Puberty in female mysticete whales may vary with population size, since in exploited species age at puberty is said to have fallen as populations were reduced. Most whales mature at 4–6 years. Phocid females mature at 2–4 years (6 years in elephant seals) and otariids at 4–6 years. Males of most species mature 1–4 years after the females. Whales, dugong, phocid and otariid seals have potential longevities of 20–50 years.

The exotic carnivores are characterised by early maturity and birth of only one or two large litters a year. Female foxes, cats and feral dogs can give birth when 1 year old, but dingoes rarely do so before their second year. Dingoes and foxes usually produce one litter a year (in late winter or spring); cats may give birth then and also in late summer; feral dogs may breed aseasonally. Each species bears three to five young in a litter. Survival of young is highly variable, depending on prey availability in that season and locality. Longevity is low in foxes (usually up to 4 years in the wild), but 12 years in feral cats and dingoes. Life history traits of these introduced carnivores converge (in age at maturity, litter sizes and numbers of litters a year except the cat which has two litters a year) with the metatherian Thylacine, Tasmanian Devil and the quolls. Their life histories do not seem to confer any obvious competitive advantages upon the introduced carnivores.

Australia's exotic, large, eutherian herbivores show two life history strategies. The larger species, horse, donkey, camel, deer and cattle, have long gestations (180–400 days) and lactation times (5–12 months); moderate times to maturity (2–4 years) in females; physiological and social delay of maturity in males (2–4 years more than their females); nearly always a single young at a birth; 1–2 year inter-birth intervals; and life spans of 12–20 years. By contrast, feral goats and pigs mature very young (6–12 months in female goats and 12–18 months in sows); produce more than one young (twins in goats; four to six piglets) after short gestations (150 days in goats, 115 in pigs); and have short lactations (2–3 months). Both pig and goat females breed before reaching maximal body size. The pig and goat, therefore, appear to have a greater potential than the other large eutherian herbivores for rapid increase.

The leporids obviously have an even greater potential for increase, having many litters of several young in a prolonged breeding season. Female rabbits from early litters are able to breed in their first year. Not surprisingly, these potentials for increases have been reflected historically in the rapid spread of hares and rabbits and the fast spread of pigs and goats, but a much slower spread of species such as deer and buffalo. Among metatherians, only some bandicoots such as the Northern and Southern Brown Bandicoot, *Isoodon macrourus* and *I. obesulus*, match the rabbit's fecundity. Leporids are taken by many native and exotic predators.

Hominid life history is outstanding for the time taken to maturity, socially delayed onset of reproduction (especially in males) in many societies, extremely long but variable lactation (up to 4 years) and, consequently, variable but long inter-birth interval and extreme potential longevity (threescore years and ten according to one authority). Hominids and the exotic large herbivores in Australia are virtually free of predators (except crocodiles) when adults, although dingoes may prey on young.

### Interspecific Interactions

Dispersal and pollination of plants. Fungal sporocarps are included in the diet of a variety of rodents from mesic habitats and these rodents may play a significant role in the dispersal of the fungal spores. In this they resemble metatherian potoroids. Similarly, in the rainforest of northeastern Queensland the White-tailed Rat, *Uromys caudimaculatus*, collects the large seeds of rainforest trees and those which escape its predation may be dispersed over short distances. The Bush Rat collects the seeds of *Macrozamia* species into caches near their burrows and may use these seeds as a food resource. Some seeds, however, escape predation and as a result are dispersed from the parent plant. The Large Rock-rat, *Zyomys woodwardi*, similarly disperses the woody seeds of *Terminalia carpentariae*, *Canarium australianum* and other plants in northern Australia (Begg & Dunlop 1980). Other native rodents may have dispersed *Santalum* seeds in central and western Australia. Potoroids and the Mountain Pigmy-possum, *Burramys parvus*, are known to cache seeds, but do not collect such woody or large seeds as do these rodents.

All of the flying foxes (*Pteropus* species) and blossom-bats (*Macroglossus* and *Syconycteris* species) carry large quantities of pollen in their fur and around the muzzle as a result of feeding on blossoms and may be important vectors in pollination. This is particularly noticeable when flying foxes feed on eucalypts where they crawl all over the inflorescences. Several eucalypts have their maximum output of nectar at night and produce their inflorescence on the upper, outer extremities. This suggests a long relationship with nocturnal, flying pollinators. The fruit eaten by flying foxes and tube-nosed bats (*Nyctimene* species) provides nutrients to the bats in return for seed dispersal. As the largest flying, fruit-eating mammals, flying foxes have the ability to carry large seeds over great distances. The only exclusively nectarivorous marsupial, the Honey Possum, *Tarsipes rostratus*, is found in an area where no nectar-eating bats occur.

Mixed colonies. Roosting sites are often shared by several species of bats. In flying fox camps, the Black Flying-fox, *Pteropus alecto*, the Grey-headed Flying-fox, *P. poliocephalus*, and the Little Red Flying-fox, *P. scapulatus*, regularly occur together. In such camps, the latter species tends to segregate, while the other two may mix. Cave-dwelling bats often share roosts, with up to four species occurring together. Such roosts often reflect a similarly needed micro-climate (for example, high humidity) or the scarcity of roost sites. Tree-dwelling bats occasionally share their roost site, but due to the restricted size of the roost only one or two additional species are involved.

Several species of bats regularly roost in the same cave or mine as the carnivorous, bat-eating Ghost Bat. Examples are: the Yellow-lipped Eptesicus, (*Eptesicus douglasorum*), Dusky Horseshoe-bat, (*Hipposideros ater*), Hill's Sheath-tail Bat, (*Taphozous hilli*), and the Orange Horseshoe-bat, (*Rhinonycteris aurantius*). These species usually roost in areas separate from *M. gigas*, but the tell-tale presence of wings under feeding roosts indicate that these bats frequently fall prey to the Ghost Bat.

Like some of the bats, the otariid seals may have mixed-species breeding colonies on safe beaches, sometimes shared with elephant seals.

### **Predator-prey interactions.**

When Australian rodents 'plague' or erupt, predators, including the Barn Owl, Letter-winged, Black-shouldered and Black Kites, Dingo, fox, cat, Ghost-bat and snakes, are attracted to the eruptions. These are most conspicuous in the arid centre of Australia, in the wheat belt and in the cane fields of the North-East. During eruptions, predators may feed almost exclusively on the plaguing species, giving some relief from predation to alternative prey species, including small dasyurids; but this protection may be removed abruptly when the plague collapses.

Predator-prey interactions within the Australian marine mammals include predation by Leopard Seals (*Hydrurga leptonyx*) upon the young of both otariid and other phocid seals and predation by Killer Whales, *Orcinus orca*, upon the young of other whales as well as the young and adults of many phocid and otariid seals.

Predator-prey interactions also occur among Australian terrestrial carnivores. Dingoes kill both cats and foxes. Substantial dingo populations may limit the distribution of foxes and have been a major reason for the slow speed of fox populations into much of northern Australia. The role of dingoes in eradicating some metatherian carnivores from mainland Australia is equivocal, as is that of foxes and cats more recently in reducing the range of larger dasyurids. These carnivores certainly prey upon native rodents and metatherians (as well as other native vertebrates), but it is still impossible to evaluate the significance of their impact. These three introduced carnivores prey heavily upon the exotic leporids, especially rabbits. Dense fox, cat or dingo populations, supported by abundant rabbits, may have had a great impact upon more vulnerable native species. Some native raptors rely heavily upon rabbits as prey.

Dingoes appear to influence the abundance of the larger kangaroos and emus (Caughley *et al.* 1980) and to affect the reproductive success of the Swamp Wallaby (Robertshaw & Harden 1986) and Eastern Grey Kangaroo (P.J. Jarman personal observation). With the Aborigines, they may have constrained populations of Koalas (Strahan & Martin 1982).

Impact on indigenous herbivores. Introduced rodents have been blamed for the demise of endemic rodent species, but evidence for this is contentious. The House Mouse tends to make temporary use of heathlands occupied by endemic rodents following fire and in late autumn. This species and the Black Rat are often found in communities from which one or more native species have disappeared; under these circumstances they show little overlap in habitat with the remaining native rodents (Braithwaite, Cockburn & Lee 1978).

Rabbits and hares may have had a direct impact upon metatherian small herbivores through competition for food, shelter or burrows. Rabbits took over Burrowing Bettong and Bilby burrows. In captivity, buck rabbits have killed bettongs (J.H. Calaby personal communication). The major impact of these and other exotic Eutheria upon communities of native animals, however, probably has come through their alteration of plant communities and the environment.

Although not all the changes have been detrimental to all native species, the trend has been towards simplification of the structure of plant communities, reduction in cover, reduction in species diversity and disturbance to surface soil structure. The larger macropodids tend to avoid sheep and cattle when feeding in the same paddocks (Andrew & Lange 1986).

**Table 35.6** Constants for allometric relationships for the life history traits (LHT) of Australian rodents ( $LHT = aM^b$ ); only relationships derived from significant regressions are included. Source of data: Yom-Tov (1985); M = material body mass. LHT examined: litter size, gestation length, lactation length, age at weaning, age at maturity.

LHT	GROUP	a	b
Litter size	old endemics	2.00	-0.14
Gestation (d)	old endemics	40.50	0.06
	<i>Rattus &amp; Mus</i>	24.38	0.05
Age at maturity (m)	old endemics	7.20	0.21

### Diseases and Parasites

Australian native rodents rarely have been implicated as vectors of disease. A notable exception is the Canefield Rat which, along with the introduced Black Rat, harbours *Leptospira*, the causative agent of Weil's Disease. This disease was prevalent among cane-cutters when sugar cane was harvested by hand. Leptospirosis, in fact, is widely distributed among native and introduced eutherians. Bubonic plague in Sydney in the 19th Century presumably was borne by introduced rats and their fleas. Scrub typhus has been recorded from northern Australia.

A characteristic feature of both Megachiroptera and Microchiroptera is the presence of wingless flies (Family Nycteribiidae) which live their whole life cycle either on the body or in the roosts of bats. Another ectoparasitic fly (Family Streblidae) is found on the Microchiroptera. Both these ectoparasites have small, flattened bodies which allow them to move readily through dense pelage, press themselves close to the host's body or hide in the narrow crevices within the roost. Their integuments are generally well sclerotised and streamlined by setae or combs that aid in locomotion, reduce abrasive damage and facilitate escape if caught while the host is grooming (Marshall 1982). The only food ingested by nycteribiids and streblids is the host's blood which is imbibed directly. These ectoparasites have three larval instars within the adult female and pupate in the roost. The adult flies are found mainly on the host. A number of other ectoparasites, such as ticks, fleas and mites, also are found on bats.

The internal environment provided by bats has been widely exploited by invertebrates. A large number of protozoans have been recorded in bats, but little is known of their occurrence in Australian bats. Nematodes and cestodes have invaded the intestine, bladder, body cavity and circulatory system of many bat species. Possibly the best account of the life history of a bat nematode is the study on *Toxocara pteropodis* (Ascaridoidea) in Australian flying foxes by Prociv (1983b; see Chapter 37).

In countries where rabies occurs, bats are always found to be rabies-positive. Fortunately, rabies does not (yet) occur in Australia. Flying foxes carry antibodies for Ross River Virus, but are not regarded as a reservoir.

There is nothing peculiarly Australian about the diseases and parasites of the marine mammals. Parasites and pathology of seals were reviewed by King (1983b). Whales, like the seals, carry typical mammalian pathogens. They suffer from trematodes which invade the head sinuses. Some people consider that these contribute to the disorientation which leads to whales stranding in shallow

water. Unlike other marine mammals, whales may carry barnacles and isopods in the genus *Cyamus* (misleadingly called 'whale lice') which cling to the whale's hair.

All the marine mammals may suffer loss of parts of fins and flippers from attack by sharks and killer whales. Small inshore whales (for example, the Bottlenose Dolphin, *Tursiops truncatus*) and the Dugong frequently carry large scars from the propellers of power-boats.

The introduced eutherian carnivores carry a rich parasitic fauna and suffer many diseases; these are detailed in Chapter 54 and 55. Domestic dogs and cats which come in contact with their wild counterparts readily contract their diseases. The role of the Dingo and domestic dog in maintaining *Echinococcus granulosus* (hydatid cysts), the cat's harbouring of *Toxoplasma gondii* and the potential of all three species to transmit rabies (particularly the fox), are the most serious aspects of this group's impact on human health.

The leporids provide an interesting example of closely related species which differ profoundly in their susceptibility to a disease. Rabbits are highly sensitive to the *Myxoma* virus, while hares are naturally immune to it. Myxomatosis provides a good example of a disease which plays a large part in the population limitation of a species and is often held up as a glowing example of biological control, although it exemplifies lost opportunities and mismanagement. Mosquitoes and rabbit fleas are vectors of the virus.

The exotic, eutherian, large herbivores suffer many of the diseases known from their domestic counterparts in Europe and are reservoirs and vectors for many pathogens. Bovine tuberculosis is harboured by feral cattle, buffalos and pigs; brucellosis is harboured by cattle and the buffalo. Like the exotic carnivores and rabies, these exotic herbivores would act as carriers if currently exotic diseases such as rinderpest or foot-and-mouth disease became established in Australia.

There are strong similarities at the ordinal level between the metatherians and Australian eutherians in the types of parasites they carry, although there are differences at the level of genus or family. Relatively few of the parasites introduced with exotic eutherians have come to affect metatherians, although liver flukes and hydatid cysts are exceptions. Many of the blood-sucking and freely mobile invertebrates (mosquitoes, flies, ticks and leeches, for example) native to Australia have had no difficulty in using exotic eutherians, including humans.

## BEHAVIOUR

Activity scheduling. The bats and rodents, the majority of Australian terrestrial eutherian species, are crepuscularly and nocturnally active. It is worth noting that several important activities, especially courtship, mother-young interactions and grooming, are largely scheduled for the 'inactive' diurnal phase. At the other extreme, hominids are diurnally active. The leporids, canids and felids are partly diurnally, although predominantly nocturnally, active. The equids, camelids, suids, bovids and cervids, while nocturnally active, carry movement, feeding, drinking and social interactions well into daylight hours. Horses, in particular, spend relatively little of the daytime resting. The marine Eutheria, especially the great whales, may be mobile and actively feeding through the full 24 hours. Thus, while the bats and rats resemble the small metatherians in being nocturnally active and the leporids distribute their activities much as do the small macropodids and potoroids, the larger marine and terrestrial herbivorous eutherians are much more diurnally active than extant metatherians. There are seasonal variations in daily scheduling of activity in some species. The diurnally active species, in particular, tend to reduce activity in the middle of the day in hot and sunny conditions; in this they parallel the larger macropodids. Activity

schedules of many eutherian species reflect the seasonality of their breeding. Most microchiropteran bats in Australia may enter torpor for part of the day while roosting, but none of the rodents do so.

During the night, bats spend most of their time searching for food; the amount of time spent on the wing depends upon food abundance and foraging technique. Some insectivorous bats in North America and Africa avoid strong moonlight, staying on the roost or foraging in the shadow of trees. Strong winds or heavy rain at night also suppress bats' foraging activities.

Some microchiropteran bats (for example, *Miniopterus* species) regularly undergo periods of torpor, with reduced body temperature and metabolic rates, as a response to a reduction in insect numbers. This is common in areas of Australia where night temperatures drop below 10°C. No Australian rodent is known to enter torpor, although many small dasyurids, burramyids and one monotreme, the Echidna, do so.

The introduced American Grey Squirrel, *Sciurus carolinensis*, hibernates in parts of its native range, but was not recorded doing so in its introduced range in Australia. At least two Australian rodents, the Broad-toothed Rat and the Bush Rat, can remain active under snow, like many Palearctic and Nearctic rodents.

**Grooming.** The Australian eutherians are as dependent as are the metatherians upon grooming to keep the fur fit for insulation and reflectance and free of ectoparasites. Only the whales and dugong, with their reduction of fur, show little grooming. Phocid and, in particular, otariid seals groom themselves both in the water and ashore, especially when moulting. They use the claws of the fore- and hind flippers to scratch at their pelage, only occasionally using the teeth. Mother otariids groom young by licking and nibbling, as do terrestrial carnivores. Dogs, foxes and cats spend much time self-grooming. Cats are well known for their use of the licked back of a forepaw to wash otherwise unlickable parts of their heads. All use their paws, claws, teeth and tongues. These species exhibit much mutual grooming between parents and offspring, between littermates or, in dingoes, between pack members. The mother's licking of the perineum may be important for inducing defaecation and urination in neonates of these terrestrial carnivores, just as it is for metatherian macropodid pouch-young.

Bats are meticulous groomers and spend much of their non-flying, awake time cleaning their fur with their teeth, thumb and toes. The hind feet can reach most parts of the back, belly and head and the thumb claw is used to clean ears, lips and teeth. Most bats have prominent sebaceous glands on their muzzle and rub the secretions of these glands onto their wing and tail membranes. In comparison to some other eutherians, female bats do not spend much time grooming their young. Allogrooming is not a feature of the Chiroptera. To urinate and defaecate while hanging at the roost, bats invert themselves to be head-up. They also can urinate and defaecate while flying. In these ways they avoid fouling their fur.

Australian rodents are as clean as those elsewhere. They are ardent self-groomers, using fore- and hind paws, teeth and tongue to comb and lick the fur and skin. They will often manipulate and hold the coat with the forepaws while nibbling and licking at it. Grooming is often an important activity in the refuge and in the evening before the animal emerges to forage. Mothers groom their young with teeth and tongue. Allogrooming is common in some of the social species which nest communally, such as the Spinifex Hopping-mouse, *Notomys alexis* (Happold 1976a).

The introduced leporids are very like rodents in their grooming. Female rabbits, when about to give birth, groom out some of their own fur, using this to line the nest chamber. None of the introduced ungulates use their hooves in grooming, but are restricted to grooming with teeth and tongue. Many of them use objects, such as trees or rocks, to rub against and this may enable them to groom areas

like the neck, shoulders and rump which they otherwise have difficulty in reaching. Female ungulates groom the new-born vigorously and continue to do so, especially while it suckles, until near weaning. Grooming the perineum may stimulate the neonate to defaecate in some ungulate species. Horses (and sometimes camels) may roll in dry, dusty ground and some deer, cattle, buffalo and pigs (especially males) use wallows. What parts these actions play in maintenance of the skin and coat, rather than thermoregulation or social signalling has yet to be determined, but it is interesting that these actions occur in species which cannot scratch.

### Thermoregulatory Behaviour

The terrestrial eutherians in Australia strongly resemble the metatherians in their thermoregulatory behaviour. All Australian rodents spend their inactive daylight hours in natural, dug or rat-created burrows or crevices. Natural crevices include cracking clay soils, exfoliating rock, rock rubble and tree hollows. Some species build structures (the Greater Stick-nest Rat, *Leporillus conditor*, the Pebble-mound Mouse, *Pseudomys chapmani*, and *P. laborifex*). Many rodents build nests within their refuges. The flying foxes roost in trees and depend upon behavioural thermoregulation, using their extended wings to gather warmth from the sun, sheltering under wrapped wings in the rain or flapping their wings to cool themselves. By contrast, the microchiropteran bats shelter in above-ground sites, such as tree hollows, peeling bark or rock clefts, as well as caves (including mines) which provide protection from sun, wind and rain, as well as predators. Some Microchiroptera increase the temperature and humidity of their domed nursery caves by a period of active flight within the cave before leaving for the evening's feeding. In the Microchiroptera, huddling plays an important role in controlling temperature (and perhaps humidity), especially in nursery colonies. Some Australian rodents, such as *Notomys alexis*, also huddle (Happold 1976a; Lee, Fleming & Happold 1984), resembling in this behaviour some small Metatheria such as the Fat-tailed Dunnart, *Sminthopsis crassicaudata*.

Thermoregulatory behaviour in marine mammals while at sea is poorly known, but Australian pinnipeds can experience high radiant heat loads when ashore to breed. They then avoid heat-stress by wallowing and fanning themselves with their flippers. Several of the large, terrestrial eutherians, such as the Water Buffalo, feral cattle (bulls) and pigs (especially boars), wallow at least in part to keep cool. None of the smaller eutherians use wallows. All the larger terrestrial eutherians seek shade, usually under trees or shrubs, although goats will use caves and rock-shelters if available (and are said to oust rock-wallabies by doing so). Rabbits (but not hares), cats, foxes and dogs use self-dug or acquired burrows for daytime shelter.

Most of the terrestrial eutherians in Australia parallel the metatherians in avoiding high ambient temperatures and radiant heat by being nocturnally active, sheltering in the day in a burrow or other refuge or, if larger, by seeking shade. No extant metatherians wallow or fan themselves. Conversely, no larger eutherians in Australia cool themselves by spreading saliva as do the macropodids. All the introduced eutherians are substantially limited in their distribution, locally and continentally, by their need to drink free water.

### Feeding Behaviour

Australian eutherians display so vast a range of feeding styles that generalisations about feeding behaviour are difficult. The baleen whales probably are the best mammalian examples of species so large that they choose where to feed and then apply one feeding action without further selecting the individual food items. Nevertheless, sympatric baleen whale species do differ in

their duties, indicating differences either in selection of feeding sites, in feeding behaviour or in the effectiveness of the feeding apparatus resulting from differences in the length and arrangement of the baleen plates. The toothed whales and the pinnipeds take squid, fish, penguins and marine mammals by rapid pursuit. Species differ in specialisation of teeth, swimming speed, agility and diving ability; these indicate specific differences in hunting behaviour.

The large terrestrial eutherian herbivores are mainly dietary generalists (indeed, the feral pig is omnivorous) and tend to have large and seasonally changing foraging ranges. Like their counterparts elsewhere in the world, they tend to select stands of actively growing, low-fibre plants preferentially. This means that populations of several species utilise plant communities high on the soil catena and with ephemeral growth early in the productive season, retreating as growth slows towards lower catena levels with greater or more prolonged productivity. This behaviour parallels that of large macropodids. The behaviour involved in this selection of feeding habitat has been little studied.

Many large, terrestrial, eutherian herbivores feed in groups (buffalos, cattle, goats, camels, horses, donkeys and various deer). By responding to each other's alertness, group members are able to reduce the amount of time each spends in surveillance, thereby gaining extra feeding time. In this behaviour they match the large macropodids.

Mobility characterises the feeding behaviour of the fruit-bats Pteropodidae, which fly long distances (up to 20 km) in nightly search for flowering or fruiting trees and vines. Some populations also shift hundreds of kilometres seasonally, establishing temporary 'camps' or roosts near currently rich food-sources. Flying foxes will congregate in large numbers at an abundant food source, but when fruit and blossoms are sparse they forage solitarily. At a food tree, individual bats may defend a feeding territory. There is no metatherian counterpart to the volant mobility of these eutherian frugivores and nectarivores.

Some insectivorous bats also migrate to areas with predictably abundant communities of flying insects; others remain in a single home-range, but hibernate (or aestivate) at times of food scarcity. Likewise, insectivorous bats may congregate in areas of local insect abundance, but otherwise tend to forage solitarily, often flying around a repeated circuit. These bats hunt insects usually by fast aerial pursuit, but several Australian bats also catch insects by hovering and gleaning from foliage and even by landing and crawling over the substratum. Others such as *Rhinolophus* species capture prey by sallying (that is, waiting on a perch, then flying out to catch a passing insect); others such as *Miniopterus* species spend much of the night on the wing. All bats, however, have nocturnal roosts where they rest and groom between foraging flights. Ghost Bats have night feeding roosts where they return to consume their large prey. Hunting in the dark, both the avoidance of obstacles and the location and identification of prey is made possible by their supreme development of echolocation. Species of Australian Microchiroptera have been shown (Woodside & Taylor 1985; O'Neill & Taylor 1986) to have species-typical echolocatory emissions appropriate to their habitat (especially to the density of vegetation) and the type of insects they hunt.

Body mass and the frequency of the echolocation call used by a bat are inversely related. The high frequencies used by small bats are necessary to detect the small prey on which these bats feed. Conversely, only low frequencies are needed to detect large insects fed on by larger bats.

Fast-flying bats have 'louder' ultrasonic calls and they feed above the canopy of trees or in open spaces. They tend to have poor manoeuvrability and hence require stronger echoes from potential prey over greater distances so they can



change direction in time. Slow-flying bats which feed below the canopy in a 'cluttered' environment have faint calls and as a result need to be highly manoeuvrable. Several species of moths (including most of the Noctuidae) are sensitive to bat echolocation calls and are capable of taking evasive action when pursued by bats.

The odontocete (and perhaps some mysticete) whales and phocid seals use echolocation at least for navigation and possibly for detection of prey. Echolocation has yet to be demonstrated in metatherians, presumably because they neither fly nor swim.

The introduced, terrestrial, eutherian carnivores hunt prey by stalking and long pursuit (dog and Dingo), stalking and short pursuit (fox) or stalking and pouncing (fox and cat). Dingoes and feral dogs may hunt in packs and are more likely to scavenge carcasses than are foxes and cats. Foxes, however, will cache unconsumed prey and mark it with urine. The hunting behaviour of these introduced eutherians is generally similar to metatherian carnivores such as the Thylacine and *Dasyurus* species and the scavenging of dingoes may match that of the Tasmanian Devil, *Sarcophilus harrisii*. The suggestion has often been made that this similarity led to the eutherian carnivores ousting the metatherians in mainland Australia, a suggestion which cannot now be tested. The hunting behaviour of foxes and cats is the same as that of their European progenitors, allowing for differences in available prey. Dingoes, even when not hunting in a pack, will share food with pack members. All these eutherian carnivores carry food to young cubs in a den. The growing young to some extent are taught hunting techniques.

### Learning

Learning ability is hard to define and almost impossible to measure in a way that will allow comparison between animals of quite different habits and adaptations. There is a persistent hope that learning ability is reflected, coarsely if not finely, in brain size or morphology. Eutherians generally exceed metatherians of similar bodyweight in the size of their brains (Jerison 1973), but it is not self-evident that metatherians learn less well because of that. Within the eutherians present in Australia, however, there are some contrasts in relative brain-size. For their respective bodyweights, the flying foxes have larger brains than the insectivorous bats; the pinnipeds, cats, dogs and foxes (that is, the Carnivora) than the leporids, perissodactyls and artiodactyls; the odontocetes than the mysticete whales; and humans and some small odontocete whales have the largest relative brain sizes of all (Eisenberg 1981).

All the eutherian species depend upon learning to develop their behaviour. Learning gives individuals a flexibility in response to varying environments. Learning begins from birth, when teat-seeking and recognition of the mother must be learned quickly. Most young must learn to walk, swim or fly and learning is needed for the development of other motor skills. Some of this is revealed in play in which exploration of the environment, capture or manipulation of objects and fighting or courtship may all be practised. Extended parental care is often accompanied by learning by the juvenile, either through imitation of the parent, through the parent's provision of opportunities to repeat skills or through the practising of skills in a safe, guarded situation. Pinnipeds may teach their young to swim; cats, foxes and dogs may teach theirs to hunt and kill, in the case of cats by bringing live prey for the kittens to practice upon; and human parents or their surrogates, teach their offspring until well past physiological, sexual maturity, imparting knowledge, skills and attitudes. Whales, humans and dingoes learn the vocal communication of group members; most species learn to recognise individuals by their appearance or smell. Individuals of all species learn their local geography; the routes to food sources,

water or refuges; the boundaries; and the possible location of predators. Learning is a continuing part of every eutherian's behavioural response to its environment, potentially continuing all its life.

The eutherians in Australia happen to include some of the species whose learning has been best studied experimentally: the Brown Rat, House Mouse, Dog, Cat, small odontocetes such as the Bottlenose Dolphin, and humans. There is an extensive literature on learning in these species. Some, including humans, have been shown to be capable of learning how to learn.

## BEHAVIOUR AND SOCIAL ORGANISATION

### Intraspecific Communication

Forms of intraspecific communication in the Australian eutherian species parallel those in metatherians, but perhaps with more vocal and visual communication in the larger species. Communication serves to maintain contact between mother and young, between courting animals or between members of a social group; to identify individuals; to signal social or reproductive status; to indicate aggressive intent, dominance or submission; or to signal alertness to danger.

Some of these functions are relevant only when two or more animals are together; others may apply when individuals are far apart. Some eutherian species have excelled at long-range communication, producing signals which carry great distances or persist a long time. Water is an excellent medium for carrying sound and some mysticete whales and phocid seals produce loud and far-carrying underwater calls. Those of Humpback Whales, *Megaptera novaeangliae*, have developed into complex songs, the form of which is sung in common by members of a 'clan' of migratory whales. Dingo packs howl in chorus, all members joining in. Vixens signal oestrus by loud, long-reaching calls. Rutting males of red and other deer roar or bellow in aggressive challenge (perhaps indicating their size by the pitch or volume of the sound). Although some of the arboreal metatherians, such as Koalas, Mountain Possums and Yellow-bellied Gliders, are loudly vocal, none of the terrestrial metatherians gives loud calls (except devils squabbling over a carcass or alarm squeals of bandicoots). Auditory communication is highly developed in bats and, in the Microchiroptera, contains forms and frequencies of calls different from those in echolocation. Many rodents have been shown to use ultrasonic calls, especially between mother and young (Happold 1976a; Watts 1976).

Visual communication is normally short-range and immediate, and is common and complex in the larger, diurnally active or social eutherians. In male-male aggression, it generally involves display (even exaggeration) of body size and of weapons (horns, antlers and teeth) or exhibiting preliminary steps towards fighting. In many eutherian species there are complementary signals of submission, usually involving reduction in apparent body size, hiding of weapons and withdrawal from fighting postures. The metatherian, larger macropodids have developed comparable postures and actions signalling aggression and submission. Body postures and movements are used by the larger eutherians, just as they are by the larger metatherians, to communicate between mother and young and between male and female in courtship and mating. Visual signalling is poorly recorded in bats and rodents, but is probably less important than other forms of communication, as it may be in small, dasyurid metatherians.

Olfaction in all the Australian eutherians except the whales, dugongs and phocid seals, plays an important role in individual (especially mother-young) recognition and in signalling an individual's dominance or reproductive status. The scent of a secretion can be sampled on the animal's body, but also can be

deposited, leaving a long-lasting trace remote from the individual that still serves the same signal function. Saliva, urine and faeces can carry signal smells. Males of large, terrestrial eutherians commonly smell or taste female urine in order to detect oestrus; male macropodids and some other metatherians do the same. Urine is used by eutherian terrestrial carnivores (dogs, foxes and tom cats) and many herbivores, including rodents, to mark territories or areas of dominance and to indicate the owner's status and presence even when the owner is elsewhere in the territory. Some species, horses, rabbits and dingoes for example, similarly may use faeces. Among metatherians, Common Wombats, *Vombatus ursinus*, and Tiger Quolls, *Dasyurus maculatus*, defaecate at repeatedly used sites, although the signal function of such behaviour is unproven. Male goats and some deer, like some metatherian macropodid males, may spray their own urine on themselves, enhancing their scent.

Eutherians have modified the secretion of skin glands to aid olfactory communication. These may either be widely dispersed over the body or concentrated in highly secretory areas. The latter may be invaginated to form a glandular sac and may have associated tufts or whiskers of hair which help disperse the scent. Table 34.7 lists the occurrence of such glandular areas in Australian eutherians. They are understandably absent in marine Eutheria, diverse and common in microchiropteran bats, carnivores and artiodactyls, but uncommon in perissodactyls and rodents. These glandular areas commonly occur around either the head (frontal, facial, pre-orbital and mental glands in particular) or the tail (anal, perineal and caudal glands) of the animals, reflecting their use in direct inter-individual communication, with animals positioned head-to-head or head-to-tail. Secretion from these glands may be deposited passively (for instance, that from the interdigital glands of sheep or goats) or actively wiped onto objects (for instance, that from chin glands of rabbits or pre-orbital glands of Hog Deer). They also may be rubbed onto other members of a social group. This may be the use made of the chest, throat or chin glands of highly social hopping mice (*Notomys* species) (Watts 1974b) and parallels the scent-marking that occurs within groups of metatherian Sugar Gliders, *Petaurus breviceps* (Schultze-Westrum 1965).

The Australian eutherians, then, contain mainly highly communicatory species. Some of their communications, such as the clan-shared song of humpback whales, the chorusing of dingo packs, the stench of a male goat or pig in full secretion or the combined sight, sound and smell of a rutting Red Deer stag, (even the languages of humans, so richly represented in Australia), impress us as more flamboyant than anything shown by metatherians. The only forms of communication which the eutherians and metatherians seem not to share are the specialised calls of the aerial bats and the marine whales and seals, ways of life not taken up by metatherians. All other differences are of degree, not kind.

### Non-agonistic Interactions

Non-agonistic interactions involve investigation of other animals' identity and reproductive or social status, parent-offspring interactions, interactions involved in communicating alarm and interactions within social groups, some of which contribute to group cohesion. Investigation has been described in the section on communicatory behaviour (above) and usually involves smelling, but also looking at and listening to, the investigated animal. Many of the larger eutherians can recognise each other by calls; these may be important for mothers relocating young in dense crèches of bats or otariids. Closer-range confirmation of identity almost always involves mutual nuzzling and face-sniffing, behaviour parallel to that of metatherians. Investigation of reproductive status of a female by a male often involves smelling or tasting urine or the genitalia, a closeness of investigation which is often repulsed by unwilling females. In the relatively complex, hierarchical male societies typical of the large and polygynous

eutherians, non-agonistic interactions involving recognition of and deference to differences in rank grade into agonistic interactions establishing or reinforcing those ranks. Thus, the relative positions and even the mutual orientations of two males in a herd of feral goats, for example, will be determined by subtle responses to each others' ranks. Such behaviour, too, is paralleled in the separation and mutual orientation of males in groups of some kangaroo species.

**Table 35.7** Skin glands found in genera of eutherian mammals in Australia. The glands listed are either invaginated or marked by tufts of scent-dispersing hairs. The secretions from the glands signal individual identity, social status or reproductive state.

FAMILY	GENUS	LOCATION OF GLAND
Pteropodidae	<i>Pteropus</i>	Scapular glands
Emballonuridae	<i>Taphozous</i>	Gular pouch
	<i>Saccolaimus</i>	Gular pouch
Hipposideridae	<i>Hipposideros</i>	Pre-anal & frontal glands
Rhinolophidae	<i>Rhinolophus</i>	Facial & axillary glands
Vespertilionidae	<i>Chalinolobus</i>	Head & muzzle glands
	<i>Eptesicus</i>	Head & muzzle glands
	<i>Scotorepens</i>	Head & muzzle glands
	<i>Scoteanax</i>	Head & muzzle glands
	<i>Pipistrellus</i>	Anal gland, head and muzzle glands
	<i>Myotis</i>	Anal gland, orbital gland
	<i>Nyctophilus</i>	Facial glands
Molossidae	<i>Nyctinomus</i>	Gular pouch
Leporidae	<i>Oryctolagus</i>	Chin, anal & inguinal glands
	<i>Lepus</i>	Chin, anal & inguinal glands
Muridae	<i>Notomys</i>	Chest, throat or chin gland
	<i>Conilurus</i>	Chin gland (?)
Canidae	<i>Canis</i>	Supra-caudal & anal glands
	<i>Vulpes</i>	Supra-caudal & anal glands
Cervidae	<i>Cervus</i>	Pre-orbital gland
	<i>Dama</i>	Interdigital & pre-orbital glands
	<i>Axis</i>	Interdigital glands
Bovidae	<i>Capra</i>	Interdigital & sub-caudal glands
	<i>Ovis</i>	Interdigital, pre-orbital & post-cornual glands
Suidae	<i>Sus</i>	Carpal, proctoideal (rectal), perineal, pre-orbital, mental, rhinarial & smegmal glands
Hominidae	<i>Homo</i>	Axillary & pubic tufts

Mutual grooming is seen more commonly among eutherian species than it is in metatherians (in which it is rare outside a mother-young pair). Many of the social eutherians indulge in long bouts of mutual grooming between adult or unrelated group members.

### Agonistic Interactions

The components of agonistic interactions have been presented in Chapter 18. Little need be said here except that the eutherians interact agonistically in just the same contexts as do metatherians. Agonistic interactions between females are generally low-level and uncommon except to protect a juvenile or the space around it in dense nursery groups of bats and sea-lions. Threats by males against females are rare, although females of many dimorphic species will defer to larger males at restricted sources of food, water or shelter. Threats by females against importunate males (especially small ones) are, however, common. The

commonest and most varied agonistic displays are those between males. Most species have a repertoire of pre-fight actions and postures which display the opponents' size, strength or weaponry and may include vocalisations. Males usually escalate through these displays before engaging in fighting. In eutherian species, the style of fighting ranges from rather unorganised 'scrambling' or wrestling in smaller species, such as the bats and rats, to highly organised clashes in those species which have well-differentiated weapons and shields (such as the otariids, bovids, cervids and suids). Fighting, to some extent, is adapted to the species' environment. Bats, for example, must usually fight in such a way that opponents do not fall to the ground. The species with exaggerated weapons tend to be the social, dimorphic species. Fighting is potentially lethal in all species and males engage in full-blown fighting infrequently, using less intense fighting or threats whenever possible. None of the metatherians have evolved the flamboyant cranial weaponry of horns and antlers present in some of the eutherians (some examples of which have been introduced to Australia) and only the carnivorous metatherians show some exaggeration of the canines in males, whereas males of some herbivorous eutherians, such as pigs, have enlarged canines. Those general differences apart, fighting in metatherians and eutherians is directly comparable in context and in appropriateness of mode.

### Reproductive Behaviour

Reproductive behaviour, as outlined in Chapter 18, involves a male or males becoming aware of a female's oestrus, the male inducing the female to allow mounting, thrusting and ejaculation and, in some species, behaviour involved in pre- or post-copulatory guarding by the male of the female. The diverse range of eutherians present in Australia displays a variety of forms of reproductive behaviour. Detection of a female's oestrous state has already been described. In many rodent, bat, canid, felid, suid and perhaps leporid species, females in or approaching oestrus may be abnormally active and mobile, increasing the probability of detection by males. In some otariid and cervid species, females in oestrus will approach dominant males and solicit their attention. Nevertheless, in most species a courting male must at the least attempt to halt a moving female in order to mount her. Male flying foxes display their genitalia at females in courtship. In most eutherians, the male mounts the female from behind with his abdomen resting on her back, the female supporting a large part of the male's weight. Bats mate (from behind) while both hang at the roost, accompanied by biting of the neck. Exceptions to this belly-to-back posture occur in odontocete and mysticete whales and humans. Copulation duration ranges from a few seconds in most rodents, bats, bovids and cervids, to 10–30 minutes in dogs and pigs. The patterning of duration has yet to be explained adaptively. None of the Australian native or introduced eutherians match the hour-long copulations of some metatherians. In some eutherians, a male may remain mounted after ejaculation and, after a refractory period, will resume thrusting to ejaculation once more. In others, the male dismounts, recovers and remounts (quite soon in bats); in yet others he mounts and ejaculates only once. In dogs and foxes the male dismounts, but remains 'tied' in intromission for a long time.

Most eutherian females are sexually receptive for one to a few hours, rarely for more than a day (flying fox females may be receptive for more than a day). During their receptivity, they will copulate one to a few times with one or more males. Most of the marine eutherians and the bats, canids, cervids and many of the rodents are strictly seasonal breeders, females beings receptive only once yearly. Several of the native rodents, all the introduced rodents, rabbits, hares, pigs, goats, feral cattle, feral horses, camels, cats and feral dogs (but not

dingoes) are far less seasonal; females come into oestrus either several times yearly or at any time of year. In these species, male inspection or courtship of females occurs during much or all of the year.

### Birth and Parental Behaviour

Eutherian young are much larger and more developed than metatherian young at birth; all weigh more than 1% of the mother's body weight (in Australia). Some are highly precocial at birth, able to move independently; others are altricial, unfurred, with shut eyes and relatively immobile. Precocial young are exemplified by the whales and dugongs; their young are born into the sea (tail-first in many whale species) and must swim or be guided to the surface soon after birth so as not to drown. Pinnipeds give birth on shore or on ice to young that are somewhat less precocious (and also may be born tail-first). Dugong may help the young to find the (pectoral) nipple; pinniped young are left to hunt the nipple unaided. Since the otariids and elephant seals give birth in large colonies and females do not isolate themselves during birth, young occasionally attempt to suck from cows other than their mothers. Cross-fostering sometimes occur if the foster-mother herself has a new-born calf. Within a few hours to a day, however, a firm mother/young bond is formed, after which a cow will repulse young other than her own.

Females of the group-living artiodactyl and perissodactyl, terrestrial herbivores may isolate themselves to give birth (especially deer), thereby avoiding problems of bonding failure. During birth, which takes time, the female is usually procumbent, on her brisket or partly on her side and physically stressed. The mother and neonate are vulnerable to predators, which may be avoided by her seeking cover or timing birth to occur at a low-risk time of day. The pig builds a farrowing nest. The female aids the neonate in finding the nipple by her posture or the splaying or lifting of a leg and by pushing the neonate in the right direction. Primiparae may exhibit such behaviour poorly. The sow lies on her side, exposing the row of teats within easy reach of the small piglets. Neonates have an innate teat-seeking behaviour. In most species, the female eats the afterbirth.

A characteristic feature of most species of bats is the formation of maternity colonies. These colonies can number from a few individuals to tens of thousands in the case of flying foxes and *Miniopterus* species. In some species, males are absent from these maternity groups. Birth occurs during the day and there are often other females in attendance (often sisters), sometimes grooming the mother (both Megachiroptera and Microchiroptera). Young are born (usually head-first) with mothers manoeuvring so that the wing or tail membrane can be used to catch the young as it is born. Females eat the placenta. Young seek and attach themselves to the axillary teats (with no help from the mother) and remain fairly immobile on the mother for their first few weeks. The age at which a young bat detaches from the mother comes when the young is too heavy to be carried by the flying mother. This occurs at about 1 week in the smaller Microchiroptera and up to 2 months in flying foxes. *Miniopterus* young may be left at night in a single crèche within the cave, young congregating in densities of up to 2000/m<sup>2</sup>. Flying fox mothers will deposit their young at a central crèche within the camp just before leaving for the night's foraging. Recognising individual young left at the roost among so many others (birth is synchronised in the maternity colonies) does not seem to be a problem; both auditory and olfactory cues are used. Young call at any moving bat and the female recognises the call of her own young, moves towards it and confirms its identity by smelling it. Nevertheless, cross-suckling does sometimes occur. Growth is rapid and the Microchiroptera attain adult size in 6 weeks. In the Megachiroptera (*Pteropus*), growth is completed by about 3 months. Prior to their first foraging, young bats stretch and flap their wings, while hanging at the roost. Young of

Microchiroptera are taken on their first foraging flight and taught to hunt by echolocation by their mothers. In contrast, flying fox young seem to have to learn to forage for themselves, attracted to a food source by the social calls of feeding bats.

The leporids contrast the rabbit (*Oryctolagus*), which gives birth in a specially prepared burrow and nest (lined with grass and fur), with the hare (*Lepus*), which gives birth merely under cover of vegetation. Rabbit young are unfurred and their eyes are closed. The mother spends brief periods of the day with them, lying on her side to give them access to the nipples. By contrast, hare neonates disperse soon after birth; each well-furred leveret, its eyes open, seeks a hiding place separate from its siblings and mother where it crouches motionless. The female returns to feed the leveret only once or a few times daily.

The introduced eutherian carnivores all give birth in a den to poorly furred young with closed eyes. The mother remains with the neonates for the first day before leaving them while she hunts. Dingo females may be fed at the den by other group members. The female of each species brings food to the maturing young. Fox and cat young may be brought live food items, which may be part of the young's education. Young of these species play, often at the entrance to the den, with their siblings and with any adults that are present. As they mature they are taken on excursions, then on full hunts, by the mother (or dingo pack members). All Australian rodents give birth to several altricial young at a time in a nest. The young of the old endemics attach to the mother's teats and remain attached while the mother moves, even outside the nest, until they are well furred. There are conspicuous differences in the early social development of the old endemics which reflect differences in sociality of the species (Table 35.5). For example, there is a longer period of maternal dependence and each developmental period is of longer duration in the highly social Spinifex Hopping-mouse, *Notomys alexis*, than in the solitary Desert Mouse, *Pseudomys desertor*, (Happold 1976a). Young of *N. alexis* experience social interactions with their fathers, older siblings, young of other litters and other adults in the nest, whereas female *Pseudomys desertor* nest alone with their litter. There is a high frequency of bonding behaviour in *N. alexis* at the time when bonds are breaking down between mother and offspring in *P. desertor*. The young of *Rattus* and *Mus* species do not attach to the mother's teats and are left in the nest when she forages.

Some of the outstanding features of birth and early development in the Australian eutherians include the extreme synchrony of birth in large maternal colonies of microchiropteran bats and otariid and elephant seals. In these species almost all females give birth within a period of a week or two. Flying foxes, despite breeding in similarly large colonies, extend this period of birth to several months. Both bats and pinnipeds combine auditory and olfactory cues in recognising their young in these aggregations. No metatherians breed in such large colonies. Birth in the eutherians is clearly a more stressful and risky process and many more eutherians than metatherians seek isolation or a nest in which to give birth. Isolation when a kangaroo joey is permanently leaving the pouch has been compared to isolation at birth in eutherian herbivores (Stuart-Dick 1988). Precociality in eutherian neonates is associated with fully marine mammals (whales and dugong) or highly mobile herbivores and with single young. Altriciality is typical of young born in nests or burrows and with litters of several young. Maternal care is highly variable and relatively unrelated to size. Elephant Seal females abandon their young 3 weeks after birth, while some megachiropteran bats and most large herbivores are still suckling their young after several months. Paternal care, which is most uncommon in Metatheria, is exhibited by a few Eutheria (horses, many murids, dingoes and humans, for example). Parental care in many carnivorous and insectivorous eutherians

include prolonged teaching of hunting methods, as in microchiropteran bats, pinnipeds, felids, canids and humans. Herbivorous eutherians tend not to display such teaching.

Parent-offspring behaviour in Australia eutherians covers much the same aspects as it does in metatherians: provision of food, warmth and shelter; retrieval, often in response to distress calls; protection from predators; grooming; play; and some teaching of skills (usually of food acquisition). Parental care may continue to full maturity of the offspring in many social eutherians (and even beyond in species some of whose young do not disperse), but its intensity declines and its form is likely to change towards little more than toleration of offspring.

### Social Organisation

Sociality. The eutherians in Australia show degrees of sociality from solitary to highly gregarious. Many of the solitary species are hunters: foxes, cats, ghost bats and other microchiropterans and some of the large whales. A few herbivores such as Brown Hares and many rodents also are essentially solitary. These species still need to associate with conspecifics to court, mate and rear their young. Many of them will come together with others when living at high density or sharing a limited resource. Foxes, at high density, will live in small groups of related females and a male, members of the group sharing a den. Nevertheless, group members usually hunt singly. Similarly, most of the gregarious species (those which are usually found in groups) contain classes of individuals which may be found alone or at least in smaller groups. Male feral pigs are often solitary. Female Red or Fallow Deer when about to give birth will go off alone. Female rabbits, depending on the status of the female, may dig a separate burrow inside a large warren or away from the warren in which to isolate themselves when they give birth.

Gregariousness tends to be associated with the use of a resource which is restricted in distribution or with behaviour which allows individuals to benefit by the close proximity of others. Since animals may use different resources at different stages of their daily activity cycle, individuals may be grouped for part of the day and dispersed solitarily or in smaller groups for the rest. Many microchiropteran bats congregate in huge groups in caves to shelter in the daytime, but disperse to hunt solitarily at night. Rabbits similarly share a warren, but feed as scattered individuals. Some native rodents, notably hopping-mice, share a nest, but forage alone. Feral cattle or buffalos graze in small groups, but gather in larger groups in shade or in waterholes. Flying foxes may either forage solitarily or gather in large numbers in a single tree that is fruiting or flowering prolifically. There are seasonal, as well as daily, variations in resource needs and, consequently, in sociality. Some species need special conditions in which to give birth, raise young or mate and these conditions affect their sociality. Otariid seals and some bats, for example, are highly gregarious when breeding because of the limited availability of the physically protected sites that they need.

Mammals may form groups for thermoregulatory reasons. Many microchiropteran bats roost in dense masses and some rodents, especially hopping-mice (*Notomys* species), nest communally, sleeping in huddles (Lee *et al.* 1984). By doing this, the mass of animals reduces the mutual surface area and cuts down heat loss. The temperature and humidity in the nursery-colony caves of some microchiropteran bats is maintained by the presence and activity of the bats. Horses, goats and sometimes cattle may give each other some mutual shade if they are forced to rest in the sun; adults commonly shade their young. Horses also may keep blood-sucking flies away from each other by standing parallel, head-to-tail and swishing their tails.



Sometimes the formation of groups allow animals to get food more efficiently or of a kind that would otherwise be unavailable. Dingoes hunt rats solitarily, but are likely to hunt adult wallabies or kangaroos in small groups. Some odontocete whales (such as the Bottlenose Dolphin and the Killer Whale) similarly hunt in groups at times.

Many of the larger eutherian herbivores may form groups for mutual protection against the risk of predation. If an animal is large and fast enough to run away from, or defend itself against, detected predators, then it can afford not to hide as long as it has a high probability of detecting an approaching predator. (Smaller species generally cannot depend on running and, therefore, have to hide and are usually solitary). One way of improving this probability is to live in company with other, alert individuals. Australia's feral eutherian herbivores evolved under the threat of predation; all the larger species feed and move in groups and show mutually communicated alertness. A very few (feral cattle, Water Buffalo and pigs) defend other group members against predators and the defended animals are usually relatives. A stallion also will defend mares and foals in his group against attack.

There are set limits, however, to the size that such groups can profitably reach. The benefits of being in a large group of alert animals may be outweighed by the disadvantages of having to compete with those animals for resources. Many species are found in bigger groups when using an abundant resource than when foraging for a scattered or limited resource. Animals which are resting are often more tolerant of the close proximity of others than they are when feeding: bats cluster in a cave in the day, but disperse to hunt at night; horses stand in the shade close together, but graze further apart. The resource which they need in the resting environment (the security of the bats' cave or the shade for horses) is more shareable than the food resources.

Some species or classes of animals defend access to resources. This can 'organise' the society and is discussed below.

Australian eutherians differ in degree of sociality from the metatherians. No metatherians form the huge aggregations of flying foxes or some insectivorous bats. In particular, no metatherians form the great nursery groupings formed by those same bats or by fur-seals, sea-lions and elephant seals. Lacking the metatherian pouch and transportable young, these flying and swimming mammals must find suitable, and often rare, protected sites at which to give birth and leave the young while the mother hunts. The large size of the nursery groups also may be a product of additional advantages gained by grouping (mutual protection against predators or control of the temperature and humidity in the caves used by some bats). The eutherian carnivores are generally as solitary as their metatherian counterparts. Dingoes, however, form bigger packs than were reported for thylacines. The larger eutherian herbivores form bigger herds than any extant metatherian herbivores, but eutherians the same size as the larger kangaroos and wallabies are no more social. Hares and rabbits (when feeding) are as solitary as the bettongs (which they match in size) and, like them, hide in burrows or squats under vegetation. The rodents forage as solitarily as most small dasyurid metatherians (their counterparts in size, but not diet); a few of them nest as gregariously as do some dasyurids.

Sociality, then, is an aspect of behaviour in which metatherians and eutherians can be seen to have responded very similarly to selective pressures.

### **Organisation and mating system**

Sociality is only one aspect of the organisation of a population. Individuals may behave differently towards other individuals according to their sex, age or social classes and these differences in behaviour can further organise the society. The ways in which males behave towards females, and towards other males which

might compete to mate with those females, are particularly influential. Male mating behaviour superimposes detailed organisation upon a society which already may be organised into groups by the animals' response to the dispersion of resources, risks of predation and by the offspring-rearing needs of females.

Eutherians display a rich variety of forms of social organisation and many are represented in Australia. The following is a simplified classification.

1. Solitary; ranges of any members may overlap. In this system, the least 'organised' society, individuals are usually found solitarily (except during courtship, mating and the rearing of dependent young) and live in home ranges which can overlap those of any other individuals. This apparent freedom of overlap of ranges, however, may reflect lack of detailed study of many species. This organisation seems to typify the solitary Lesser Wart-nosed Horseshoe-bat, *Hipposideros stenotus*, whose individuals, at least in dry country, roost separately and have foraging ranges which overlap. It is the common organisation among *Pseudomys* species in mesic habitats (Happold 1976a). Females in these species nest alone. This also is true of the Bush Rat and the Fawn-footed Melomys, *Melomys cervinipes*, in which individuals are solitary and male and female ranges overlap.

2. Solitary; discrete ranges. Surprisingly few eutherians live solitarily in ranges which are defended, excluding other members of the population (except during courtship, mating and rearing young). This organisation, however, usually is seen in feral cats, foxes at low density and Leopard Seals.

3. Pairs. Species in which the male and female form a bonded pair for longer than just the breeding season include the stick-nest rats (*Leporillus* species) and many human societies. The pair of stick-nest rats occupy and defend a stick-nest, but do not necessarily defend a foraging range away from it. Dingoes at low density may live as life-long pairs. Crab-eater and Ross Seals form pairs for the length of the breeding season, although at other times the former is gregarious and the latter solitary.

4. Female groups; polygyny. In many eutherian species, females can be found in groups. This presents an opportunity for males to prevent other males having access to these females. If the grouping of females is persistent, one male (sometimes more) may attach himself to the group, excluding other males from the group. This 'ownership' by a single male has led to such female groups sometimes being called harems. The term is misleading, since the females may remain together regardless of the presence or absence of the male, who is thus seen not to cause their grouping, but simply exploits it. If the female group is impermanent, females coming together and parting at will and frequently, there is no single group to which a male may become attached. In such species, males are likely to achieve polygyny (mating with several females, to the exclusion of some other males) either by holding a territory from which other males are excluded or by a system of roving dominance.

4a. Persistent female group with one male; separate bachelor male groups. This organisation, characterised by the presence of only one adult male with a group of females, is found in feral horses, camels and the Large-footed Mouse-eared Bat, *Myotis adversus*. Feral horse mares live in bands of unrelated females. Each band is accompanied by one stallion, who drives away other males and tries to capture other females to add to his band (which can justifiably be called a harem). Occasionally, more than one stallion lives with the group. Males without harems live solitarily or, more usually, associate in smaller groups of open (that means, changeable) membership. Stallions without harems challenge harem-holders, attempting to take over their groups and also try to capture and tend young mares at puberty. Camel females live in permanent groups accompanied by one male, who drives away other males who live solitarily or in small bachelor groups. Female groups, however, are not always accompanied by

a male and the accompanying male may sometimes change. Female groups also may join temporarily with other groups. A *Myotis adversus* male defends a territory within the roosting area (in a cave) and holds a harem of females within the territory for the duration of the breeding season (Dwyer 1970c).

4b. Persistent female group, with one breeding male, but subordinate males tolerated in the group. Some males who live with persistent groups of females tolerate other males which remain subordinate and do not court or mate females. Such organization characterises *Pseudomys* species (except the Desert Mouse, *Pseudomys desertor*) in xeric environments and hopping-mice, *Notomys* species. Spinifex Hopping-mouse, *Notomys alexis*, groups may defend a group-territory, all members taking part in territorial defence (Happold 1976a). Rabbit females live in persistent groups, each centred on warren systems (a cluster of burrows) and accompanied by one or a few males. One of these bucks is dominant and defends the area around the warren. The other males may remain within the warren as long as they accept his dominance. A similar kind of organisation is seen in dingo packs; subordinate males defer to the dominant dog who is the only breeding male in the group. Like the hopping-mice and the rabbits, dingo females and subordinate males may join in defence of the group's range. In each of these species there is a hierarchy among females as well, which determines the individual female's probability of breeding.

4c. Persistent female kin groups. In a few species, the groups of females are known to consist of related females, either mother and daughters or sisters. Although, in some respects, these groups are no different from any other fixed-membership female groups, it does also make altruism adaptive in certain circumstances. Thus, vixens in high-density populations may fail to disperse at puberty, remaining with their mother, just as dingo bitches regularly do. In such groups it is usual for only one female to breed. If more than one whelps, the dominant female kills the subordinate's pups. The subordinate females join in feeding (and rarely suckling) the dominant's young, to whom they are, of course, closely related. While groups of vixens usually are courted by only one dog fox, dingo packs may contain several males, one of which is dominant and mates. Groups of *Tursiops* species may consist of groups of related females with accompanying males. Sub-groups of females in feral cattle and water buffalo herds also may be kin.

5. Female groups; male territoriality. In many species, males do not remain permanently with one group of females; instead they defend an area containing resources which females require, thereby gaining access to the females coming to use those resources. The breeding-season organisation of fur-seals (*Arctocephalus* species), sea-lions (*Neophoca* species) and elephant seals (*Mirounga* species) provides one example. Males of these species haul out on the few, traditionally used breeding beaches many weeks before females arrive. There is intense competition among males to establish territories on the beaches. By the time females arrive, the areas of beach most favoured by females for giving birth have a mosaic of territories established on them. Subordinate males, or those who have been unable to gain territories, are driven off these beaches or to the periphery. Once females arrive, they choose a site on the beach at which to give birth and thus place themselves within a territory. Although males may try to limit their movements, females are able to move between territories. Elephant seal dominant males may sometimes tolerate subordinate males within their territories and a few matings are lost to these subordinates who steal a mating while the dominant is engaged in mating.

The *Pteropus* flying foxes appear to have a similar organization within the camp. Males compete for territorial control of branches, using their established dominance in that territory to prevent other males from reaching the females who roost within it. The organisation of *Myotis adversus* described above (4a) possibly is similar. In these bats and pinnipeds, the resource sought by females, a

safe site for breeding, is spatially limited, making their use of it predictable. Their society, however, is not organised by the territoriality of males when they are away from breeding sites.

Male feral pigs and sperm whales establish territories, defending areas against other adult males. They then associate with females which pass through these territories while feeding, inspecting them and courting any which are in oestrus. Such territories are much larger than those of otariid seals on their breeding beaches or flying foxes in camps. Red and Fallow Deer (and possibly other species) in Australia have societies which are organised by male territoriality, at least during the rut. As the rut approaches, the more dominant males in the population mark out territories by the use of scent marks, visual displays and calls. Males fight vigorously, sometimes lethally, for possession of territories. Females form impermanent groups which wander through the territories where, during the rut, they are inspected and courted by the males. A male, especially of Red Deer, may try to hold together a group of females, but he rarely establishes long-term control over them. Fallow Deer in some places in Europe have been reported forming 'leks', concentrations of very small territories to which oestrus females come to be mated.

6. Non-persistent female groups; non-territorial males. Several species of large eutherians in Australia usually live in groups whose membership changes as individuals join or leave it. (Nevertheless, there may be sub-group units, often of related females, which tend to remain together). In some of these, many adult males can be found within the group, there being a hierarchy amongst them which determines each male's probability of undisturbed courtship and mating of oestrus females. Neither the whole group nor any of the males defend a territory. Examples are feral cattle, Water Buffalo, goat and Chital. The dominant males are usually the oldest and largest, but in Chital an adult male's status also is determined by his current stage of antler growth. Some male cattle and water buffalo may become solitary.

Social organisation: general comments. Although most of the smaller eutherians are solitary and most of the larger species are gregarious, there are some rodents and bats which form groups and many of the largest whales form, at best, very small groups. Grouping can be seen as an adaptive response to several different aspects of the individuals' needs for resources, protection from predators, thermoregulation or contact with conspecifics. In some species groups are flexible, temporary aggregations of animals; in others, the group members live together almost permanently.

The social systems found in metatherians also are found in eutherians. Eutherians, however, emphasise territoriality rather more than do the extant terrestrial metatherians. Kin-grouping, with defence of the group's range, is present in some metatherians as well as eutherians.

## **ECONOMIC AND CULTURAL SIGNIFICANCE**

Because of their size, number of species and the popular, dismissive view of 'rats and bats', the native rodents and bats have not achieved the status allotted metatherians as important members of Australian ecosystems or vertebrate communities. They are, nevertheless, significant components of the fauna of the continent, contributing 21 % and 25 % of endemic, terrestrial, mammalian species. Australia's rich fauna of marine mammals is perhaps even less popularly appreciated, despite their former economic importance. By contrast, the introduced eutherians have a readily appreciated importance either as pests, for commerce, for sport-hunting or for their impact on communities of native plants and wildlife. The cultural and economic importance of Australian eutherians are summarised in Table 35.8.

### Economic pests

Of the rodents, the House Mouse undoubtedly has caused most economic loss, primarily through damage to stored grain, but also to growing cereal crops (a form of damage which it shares with several native species and which is aggravated by its ability to 'plague'). Certain of the native species, such as the Grassland Melomys, *Melomys burtoni*, and the Canefield Rat, cause substantial damage in sugarcane fields by gnawing through the outer rind of the cane and exposing the sap to bacteria which reduces the sugar content (McDougall 1944b). Two native species, the Bush Rat and the Pale Field-rat, *Rattus tunneyi*, have proved a pest in silviculture. Bush Rats may ringbark pine seedlings while the Pale Field-rat burrows to feed on the roots of hoop pine (*Araucaria cunninghamii*). The economic importance of rodents in harbouring and transmitting diseases in Australia has been covered above.

During periods of poor flowering and fruiting of native vegetation, flying foxes can cause severe losses in orchards. This is particularly so for North-Eastern New South Wales and South-Eastern Queensland where three species of flying foxes are found. Crops damaged by flying foxes include stone fruit, bananas, citrus, pomes and many of the newly established tropical fruits such as lychees. After many attempts to control flying foxes (some techniques being quite barbaric), recent studies have shown that netting is the most satisfactory method of protecting a crop from flying foxes.

The leporids, once established, quickly became considerable pasture pests, the extent of the later eruption of rabbits eclipsing that of the earlier hares. They damaged pasture, crops and structures (by rabbits burrowing).

Hares were controlled by shooting and driving, while rabbits were shot, driven, trapped and poisoned. Poisons used include arsenic and strychnine, often distributed by poison-carts which left a trail of poison baits that attracted and killed many other animals including native wildlife. Between the 1920s and 1950s, control was labour-intensive and involved fencing, trapping, ferreting and digging rabbits out of warrens. The release of myxoma virus reduced rabbits considerably and they were briefly of little relevance as a pest in many areas. The respite was brief. Rabbits now are controlled by much more sophisticated and less widely harmful poisons (especially sodium monofluoroacetate in carrot bait-trails and anticoagulants), by warren-ripping or exploding, clearing or harbour and by gassing in warrens. Myxomatosis continues to play a useful part in their control in some areas and research is still conducted on ways of making the disease more effective. More money and effort is expended on rabbit control than on any of the other exotic mammals in Australia. They are one of the worst exotic pests in areas conserved for wildlife, especially when they support populations of exotic carnivores such as foxes and cats.

The exotic eutherian carnivores can cause considerable economic damage. Dingoes were such heavy predators on non-shepherded sheep that they were vigorously hunted from, and fenced out of, sheep-rearing areas. They are less effective predators of cattle and have been tolerated to varying extents in cattle rangelands in inland Australia. The dingo-fences, which form a nearly continuous barrier between sheep-raising areas of the southern States and dingo-occupied cattle country or unstocked lands to the north and north-east, are the world's largest structures built to control wildlife. Thylacines, because of their attacks on sheep, were viewed in the same fashion in Tasmania and were similarly hunted and poisoned. Foxes were widely held to be predators of newly born lambs, but the evidence is equivocal. They and cats were supposed to be predators which might control rabbits. During the eruption of rabbits, opinions were divided as to whether foxes should be preserved to control rabbits or eliminated because they took lambs. In either case, nothing effective was done. Dingoes now are controlled by combinations of fencing, trapping and poisoning.

**Table 35.8** Economic importance of eutherian mammals in Australia.

NEGATIVE EFFECTS				
		Reservoir of disease	Agricultural pest	Miscellaneous nuisance
Rodents		Commensals can transmit bubonic plague ( <i>R. rattus</i> ) & leptospirosis	Native & exotic species; in wheat, sugarcane, rice, sunflower and stored products	Exotics (mainly) as household pests. <i>Hydromys</i> may damage irrigation banks, fishing nets
Megachiroptera		-	In some seasons bats eat orchard fruits	Complaints of noise and smell near camps
Microchiroptera		-	-	Roost in houses
Whales		-	-	-
Pinnipeds		-	-	May damage fishing nets
Canids & Felids		Hydatid cysts, <i>Toxoplasma</i> and rabies (potentially)	Predators of stock and poultry	Kill conserved native animals
Leporids		-	Destructive of pasture, crops, orchard & plantation trees	Rabbit burrows may erode soil and under ine buildings and roads
Perissodactyls & Artiodactyls		Carry many diseases of stock	Competitors for pasture and water	Damage fences. Cause erosion. Alter native plant communities from fresh wetlands to desert habitats
POSITIVE EFFECTS				
	Exploitation	Sport hunting	Aesthetic etc.	Miscellaneous
Rodents	<i>Hydromys</i> for skins. Some natives have potential as pets or as experimental animals	-	-	Conservation value
Megachiroptera	Taken for meat in neighbouring countries	Crab pot bait	Camps & flights are wildlife spectacle	Crucial pollinators & seed dispersers
Microchiroptera	Guano used as fertilizer	-	Flights & cave roost are wildlife spectacle	Sensitive to insecticides. Main nocturnal insectivore
Whales	Formerly for oil, meat	-	Wildlife spectacle	Captive display of small species
Pinnipeds	Formerly for pelts	-	Wildlife spectacle	Minor captive display
Canids & Felids	Fox pelts	Fox; formerly dingo	Chorusing of dingoes	-
Leporids	Formerly heavily, now lightly, for pelts, fur & meat	Formerly shot or used for coursing (hares)	-	-
Perissodactyls & Artiodactyls	Venison; others for pet food. Some capture for domestication or export	Deer, pig, goat, water buffalo hunted for trophies	Feral horses and camels admired by a few tourists, making their eradication difficult	-

The exotic artiodactyls and perissodactyls were either released domestic stock (horse, cattle, goat, donkey, camel, pig, Water Buffalo, Banteng) or introduced for sport (deer species). With the exception of deer, for which the environmental impact remains unassessed, these exotic herbivore species all contribute to the ecological disturbance of the area they occupy. This is usually detrimental to the conservation of communities of native wildlife. Control is usually by mustering or shooting from helicopters. Feral pigs also are trapped and poisoned or caught with the aid of dogs.

### Exploitable Resources

In contrast to the metatherians, where pelts from a large range of species were harvested during the 19th century and the first third of the 20th, the only terrestrial native eutherian harvested for pelts was the Water Rat (which, like the Platypus and most other aquatic mammals, has a fine, dense underfur).

The large accumulations of bat guano in caves, generally as the result of a maternity roost, are a rich source of nitrates. In many overseas countries, guano deposits have been mined for fertiliser. This was tried on a small scale in Australia, but did not prosper. Bat guano was mined near Rockhampton during World War I to extract nitrates for gunpowder.

Marine mammals played a crucial role in providing the first major exports from the fledgling British colony in the late 18th and early 19th Century. Mysticete whales, Dugongs and Elephant Seals were killed for oil. Fur-seals and sea-lions were killed in large numbers for their pelts. Whaling and sealing led to exploration of the southern coast of the continent and industries based on them supported the early settlement of Bass Strait and South Australian islands. Initially, whaling was shore-based, often taking females entering bays to calve. Similarly, seals were taken on their breeding grounds. Such exploitation quickly exterminated local populations. Bay-whaling and sealing rarely lasted at any one site for more than 30 years. Pelagic hunting of baleen and sperm whales started later and persisted longer; the last whaling station (Cheynes Beach, W.A.) closed in 1978. Whales now are rigorously protected in Australian waters, as are most pinnipeds; some seals still are killed when they are thought to be interfering with the interests of fishermen. Dugong continue to be hunted for food by Aborigines and Islanders.

Rabbits and hares supported industries based on their meat and pelts. The demise of rabbits through myxomatosis in the 1950s and 1960s released mobile chillers which were then used for kangaroo harvesting. The prolific export of rabbits from Australia to Britain in the 19th Century destroyed the British indigenous rabbit industry. Other introduced eutherians have formed the basis for industries exploiting their meat or skins. Feral horses once were widely mustered for stock horses or army remounts. Camels and Water Buffalo occasionally are captured for live export. There is an industry based on domestic Water Buffalo in the Northern Territory. Feral goats with appropriate traits are captured to breed mohair of kashmir varieties. Deer, pigs, and sometimes, Water Buffalo and horses are slaughtered for human consumption; most of the feral ungulates are shot or slaughtered for pet food. In this respect they share the commercial fate of the largest kangaroo species.

Flying foxes have proved to be useful models in biomedical research and regularly are used in studies on skin cancer, optic and auditory systems, reproduction and parasitology. The Microchiroptera also have been used in biomedical research, particularly in studies on blood flow where their thin wings allow for the direct observation of flowing blood within vessels. A few of the native rodents, especially the Spinifex Hopping-mouse, have proved easy to maintain in captivity. They are used as pets and in teaching, especially where schools wish pupils to learn natural history by watching Australian, rather than exotic, animals.

### Sport

Foxes, hares, rabbits and several species of deer were introduced for sport in the 19th Century, when 'acclimatisation' of exotic species was strongly endorsed by the ruling class. Foxes and Red Deer were hunted with packs of hounds by mounted sportsmen and women. Both species were initially 'boxed' or 'carted', that is, they were recaptured alive and kept to be released and hunted again.

Hares were used for coursing greyhounds or whippets, bets being laid on which dog would catch the hare. Hares and rabbits also were hunted on foot, with guns, and this was a popular form of social hunting. Landowners at first prided themselves on the 'sport' they could offer guests on rabbit or hare-drives. Once these species became agricultural pests, their value for sport diminished. Of this list, only the various deer species retain much value for sport. For the same reason, feral pigs, Water Buffalo and goats are hunted for sport, while feral horses, donkeys and camels (which provide no recognised trophies) are not.

### **Tourism, Conservation and Cultural Values**

The Megachiroptera are the major nocturnal pollinators of Australia's hardwood forests, particularly along the eastern coast. They also are responsible for the dispersal of seeds over large distances, making them potentially very important in transporting plants between isolated remnants of rainforest. The Microchiroptera are the predominant nocturnal insectivores. Each bat can consume 20 – 30 % of its body mass in insects each night. Most species eat moths and beetles, some of which have been shown to be agricultural pests.

In several localities overseas, and now in Australia, the evening emergence of large numbers of bats from their daytime roost has become a tourist attraction. The daytime camps of flying foxes are a popular attraction for tourists from North America and Europe where all bats are small and secretive.

Small odontocetes in the wild have become a tourist attraction at Shark Bay in Western Australia; their capture for display in 'dolphinariums' is restricted in some states.

### **Medical and Veterinary Significance**

While the bats, native rodents and marine mammals are of relatively little medical and veterinary significance (see Economic and Cultural Significance), the introduced rodents and eutherians are of very considerable veterinary and some medical importance. Veterinary importance arises from the fact that feral artiodactyls and perissodactyls are conspecific with domestic stock and thus able to harbour and transmit their diseases. So great is the risk of this occurring that contingency plans exist for the attempted local eradication of populations of some feral species (especially pigs) in the event of an outbreak of exotic communicable disease. The prospects for success in such operations are at present poor. More emphasis, therefore, must be placed upon monitoring and limiting their populations before disease occurs. That the larger feral stock can be controlled adequately by a combination of fencing, shooting and mustering has been amply shown in the Brucellosis and Tuberculosis Eradication Campaign in the Northern Territory.

Medical problems from exotic eutherians are no different to those in other continents. Humans suffer infrequently from diseases harboured by stock and most risk in Australia comes from domestic rather than feral stock. Q-fever has been associated with abattoirs. Hunters should be aware, however, of the minor health risks of handling (but not generally of eating well-cooked) feral stock. The feral counterparts of human commensals, dogs, cats, house mice and Black and Norway Rats, give more cause for concern as these species can serve as vectors or reservoirs of a number of zoonoses (some of which are given above).

The use of some native eutherians in biomedical research has been mentioned above (see Economic and Cultural Significance).



### Introduction, Naturalisation and Domestication

None of Australia's marine or terrestrial native eutherian species has been introduced, as a feral animal, to any other country nor have there been introductions of any of these species within Australia. In these respects the native eutherians contrast with the metatherians.

On the other hand, Australia has gained all her medium and large, and three of her small, terrestrial eutherians by human introduction. The three small species are the three rodents which are common commensals of human in Europe, the House Mouse, and the Black and Brown Rat. The Pacific Rat, *Rattus exulans*, although present on two northern offshore islands, is absent from mainland Australia (Watts & Aslin 1981). In the Polynesian Pacific this rat (the Kiore of New Zealand) is thought to have been spread deliberately by humans (Wodzicki & Taylor 1984).

Almost all of the domestic stock brought to Australia established feral populations, with the exception of sheep. While typical European breeds of stock were introduced to, and escaped from, the settlements in southern Australia, tropical breeds or species, such as Water Buffalo, Banteng and Timor ponies were brought to the ill-fated settlements in the tropical north where they now have substantial feral populations. A few species, such as the South American camelids, failed to become established, as did some species of deer which were introduced for release to the wild. Six species of deer successfully established wild populations: Fallow Deer, Chital, Hog Deer, Rusa, Sambar and Red Deer. The first of these, the Asian Chital, was introduced in 1803; most were brought to Australia from Europe in the heydays of the Acclimatisation Societies between 1850 and 1890 (Frith 1973).

The acclimatisation movement also introduced the European Rabbit, Brown Hare, European Red Fox and several game birds for hunting. Most were initially introduced to Victoria where they were released or escaped to the wild. They then spread to most suitable habitats in the rest of Australia (Rolls 1969; Jarman 1986a, 1986b).

Cats and dogs quickly escaped from domestication. Cats may even have reached Australia from wrecked Dutch trading ships before British settlement. While cats have spread to the whole of mainland Australia and many of its coastal islands, feral dogs have spread less far. This may be because of competition from the already established Dingo, which had arrived in Australia with humans about 4000 years ago. The range of the Dingo has been greatly reduced in sub-tropical Australia as settlers killed it in grazing country. In several places, especially near towns, feral domestic dogs have replaced the Dingo and are as much of a pest. Dingoes and feral dogs interbreed readily. It is interesting that neither mongooses nor ferrets have established wild populations in Australia.

The purposefully or accidentally introduced eutherians have had a profound effect on most Australian ecosystems, altering the soils, the structure and floristics of the vegetation and the animal communities.

### Breeding in Captivity

A variety of native rodents have been successfully bred in captivity. Several of the highly social desert rodents, such as the Spinifex Hopping-mouse, breed so readily that they have become established as pet and laboratory animals. Research was carried out by CSIRO Division of Wildlife Research into the feasibility of breeding and raising Water Rats, *Hydromys chrysogaster*, in captivity for fur production.

Given appropriate facilities all the Megachiroptera breed readily in captivity. Flying foxes have been bred by a number of institutes and zoos in Australia, as well as several overseas zoos. Among the Microchiroptera, the Ghost Bat has

been bred in captivity and, due to its IUCN-rating as rare and vulnerable, several breeding colonies are being established to maintain a gene pool and for possible release into the wild. Although many of the vespertilionids have been kept successfully few species actually have bred in captivity (Hall 1982a; Humphrey-Smith 1982). The most successful captive breeding has been of *Nyctophilus* species (Ryan 1963a; Phillips 1984). None of the Australian hipposiderids or rhinolophids has been bred in captivity.

Few of the marine mammals are kept in captivity and fewer still breed there.

All the feral eutherians breed readily in captivity. Some species of feral stock are captured for re-domestication.

### Conservation, Control and Legislation

The endemic eutherians generally are conserved and protected as fully by law as are the metatherians. There are, however, exceptions. Bats are protected in all Australian states except Queensland where the four *Pteropus* species currently are listed as unprotected fauna. Protection of flying foxes in Queensland was removed as a result of political lobbying by fruit-growers. Hopefully, flying foxes will be returned to the protected fauna list when a scientifically based management program is established.

In all States permits can be obtained allowing control measures to be taken against native species which are pests. Under such permits flying foxes are controlled in other States, rodents are poisoned in cane fields, roosts of vespertilionid and molossid bats are removed from roofs, and sea-lions are shot on commercial fishing grounds.

All native eutherians are conserved in national parks and other forms of reserves. Some abandoned mines and tunnels outside national parks specifically have been protected by law to conserve the colonies of bats which they contain. Australia supports international conventions conserving whales and Antarctic seals. Some States have placed limits on the capture and display of marine mammals in oceanaria.

Few of the introduced eutherians enjoy any legal protection even in national parks. Exceptions to this are dingoes in the Northern Territory and deer in some States. The control of all mammal pests is subject to laws regarding cruelty to animals and the use of poisons and firearms. In most States, landowners are obliged by law to attempt to control those mammals which are declared noxious.

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