FAUNA *of* AUSTRALIA

25. THYLACOMYIDAE

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Bilby–*Macrotis lagotis* [F. Knight/ANPWS]

DEFINITION AND GENERAL DESCRIPTION

The family Thylacomyidae is a distinctive member of the bandicoot superfamily Perameloidea and is represented by two species, the Greater Bilby, *Macrotis lagotis*, and the Lesser Bilby, *M. leucura*. The Greater Bilby is separated from the Lesser Bilby by its greater size: head and body length 290–550 mm versus 200–270 mm; tail 200–290 mm versus 120–170 mm; and weight 600–2500 g versus 311–435 g respectively (see Table 25.1). The dorsal pelage of the Greater Bilby is blue-grey with two variably developed fawn hip stripes. The tail is black around the full circumference of the proximal third, contrasting conspicuously with the pure white distal portion, which has an increasingly long dorsal crest. The Lesser Bilby displays a delicate greyish tan above, described by Spencer (1896c) as fawn-grey and lacks the pure black proximal portion in the tail. Rather, as its specific name implies, the tail is white throughout, although a narrow band of slate to black hairs is present on the proximal third of the length. Finlayson (1935a) noted that the Greater Bilby lacks the strong smell of the Lesser Bilby. The skull of the Lesser Bilby is distinguished from the Greater Bilby by its smaller size (basal length 60-66 mm versus 73–104 mm; [Troughton 1932; Finlayson 1935a]), the more inflated and smoother tympanic bullae (Spencer 1896c), the absence of a fused sagittal crest in old males and the distinctly more cuspidate character in the crowns in the unworn molars (Finlayson 1935a).

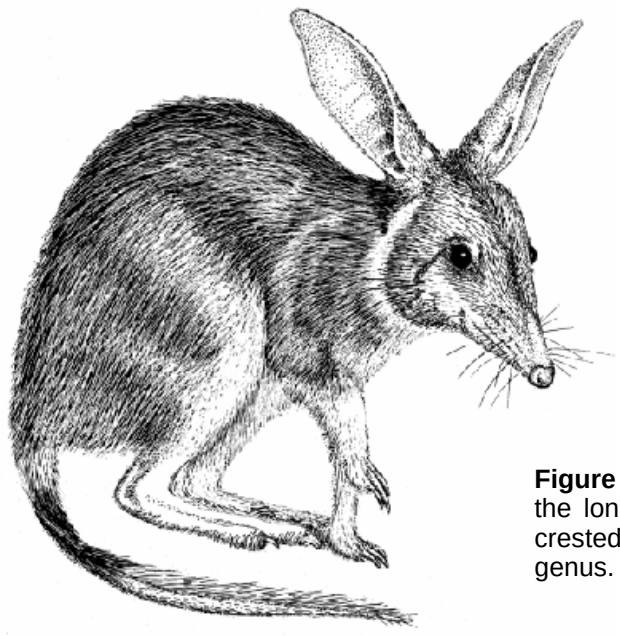

Figure 25.1 A male Bilby showing the long ears, pointed snout and crested tail which characterise the genus. (© ABRS) [H. Heinrich]

Both species differ from the other perameloids in their conspicuously long ears, which reach past the tip of the snout and the long tail, which is 50–66% of the body length and which bears a conspicuous terminal white crest. They differ from the central Australian Pig-footed Bandicoot, *Chaeropus ecaudatus* (presumed extinct) by the presence of three, rather than two, strongly clawed toes on the manus and a well-developed fifth toe on the pes. The skull is distinguished from other perameloids by the absence of a functional metaconule, enlarged and pyriform alisphenoid tympanic wings and strongly crescentic molar rows which merge anteriorly with a very gradually tapering rostrum.

Spencer (1896c) and Thomas (1887a) both stated that the Greater Bilby possesses no backward extension of the rhinarium as a rhinal callus which is conspicuous in the Lesser Bilby. Finlayson (1932b), in contrast, found this character to be variable in extent among twelve specimens collected from north-eastern South Australia. He also observed that despite Thomas' (1887a) claim, the British Museum Catalogue of 1888 depicted the Lesser Bilby with the callous '... distinctly indicated'.

HISTORY OF DISCOVERY

Reid (1837) described the Greater Bilby from a skin and skull of an old female collected by A. Gordon from Swan River in Western Australia. The holotype skin and skull are registered in the British Museum BM No. 55.12.24.68 (skin) and BM No. 50.11.22.31 (skull) (Tate 1948). Initially, Reid (1837) wrongly located the specimen from 'Van Diemen's Land' (Tasmania) where the species has not existed in historic times. He at first placed the species within *Perameles*, but proposed the subgenus *Macrotis* to mark the distinction between it and other species of *Perameles*. During the subsequent 84 years, various authors used three different generic names and no fewer than 10 different spellings for them. Reasons for suppressing and erecting the genera varied from consideration that a name was preoccupied to the rather fantastic reason by Gould (1863) that the '... term *Macrotis* was objectionable from its similarity to the specific name'.

Troughton (1932) finally clarified the situation and after reviewing 19 publications dating from Reid's (1837) description, identified *Macrotis* as the valid name. Confusion remained for a further 29 years, with *Thalacomys* being used into the 1960s (Finlayson 1961). Stabilisation was finally reached in favour of *Macrotis* following Ride's (1970) work.

The Lesser Bilby was originally described by Oldfield Thomas as *Peregale leucura* from a single specimen among a collection of mammals forwarded to the British Museum by J. Beazley of Adelaide (Thomas 1887a). At the time, Beazley was taxidermist in the South Australian Museum (Jones 1923). The exact locality was not recorded by Beazley, but Thomas (1887a) noted that other specimens in the collection were either '...North Australian species...' or had been '...obtained in the neighbourhood of Adelaide itself'. Jones (1923) considered that it came from northern South Australia.

The specimen was a young male still with its '...milk premolar' and well preserved in spirit (Thomas 1887a).

A further five specimens collected 'about forty miles to the north-east of Charlotte Waters' were sent by the then telegraph operator P. Byrne to Baldwin Spencer who described them as *Peregale minor* (Spencer, 1896)c on the basis of skull measurements and length of the molars. Forty miles north-east of Charlotte Waters places the collection locality at approximately 20°40'S; 135°12'E in sand dune country of the Simpson Desert in the Northern Territory.

A further three specimens labelled 'Barrow Creek, 1901' are in the Museum of Victoria. Parker (1973) questioned the validity of the locality on the basis of the absence of apparently suitable habitat for some considerable distance. Further evidence for this conclusion came from Spencer & Gillen's (1912: 396) account of their expedition through central Australia in 1901. Spencer's remarks on the fauna are sparse throughout the two volumes with the exception of their stay at Barrow Creek. Considerable detail is given of this period including the comment that '...the only mammal of any value that the women brought in was the rabbit bandicoot (*Peregale lagotis*)'. He discussed *Macrotis leucura* and obliquely mentioned his recently described *Peregale minor*, but made no comment about

specimens from Barrow Creek, something he would almost certainly have done had he secured specimens there. It seems likely that the three 1901 specimens also were taken by Byrne and inadvertently labelled Barrow Creek.

Le Souef (1930) reported the collection of a further specimen of the White-tailed Rabbit Bandicoot *Thalacomys leucurus* in 1924 by an expedition undertaken by Dr. G. Horn. Finlayson (1935a) noted that this specimen was collected at Mungeranie in South Australia (28°01'S; 138°40'E).

A valuable series of twelve specimens from which he described *Thalacomys minor* var. *miselius* was collected by H.H. Finlayson near Cooncherie (Finlayson 1935a). These were the last to be collected alive and represent only the fifth occasion that the species has been so collected. The most recent record is a skull of indeterminate age taken by P. Hanisch in 1967 from a Wedge-tailed Eagle (*Aquila audax*) nest among sand dunes in the Simpson Desert of the Northern Territory at approximately 24°30'S; 134°55'E (specimen record Northern Territory Museum).

Finlayson (1935a) questioned the distinction between *leucura* and *minor*, noting that Spencer's (1896c) specimen was older and with considerably more molar wear than Thomas' (1887a) young male. Finlayson's (1935b) series of nine skulls depicted a useful range of ages enabling comparison with both species. He concluded that the unworn molars in the Lesser Bilby as figured by Bensley (1903) corresponded exactly to the completely unworn molars in his own series. He further concluded that there are no features in the skull, manus, pes and dimensions of the Lesser Bilby which could not be closely matched with immature examples of his series (Finlayson 1932b). He thought the absence of the slate grey dorsum of the tail, the sole of the pes and under-fur in Lesser Bilbies was attributed to bleaching in spirit and wryly noted that he was proceeding with '...experiments on the synthesis of *Th. leucurus* from *Th. minor miselius* by photo oxidation'.

He considered that although *leucurus* (1887) had priority over *minor* (1897), it was inappropriate and misdescriptive, since the tail is not wholly white and should give way to Spencer's name, *minor*. Ride (1971) synonymised the two names and gave precedence to *leucura*.

Two species and three subspecies of the larger *Macrotis* have been described. Thomas (1905) established *Macrotis sagitta* on the basis of material from Killalpaninna, east of Lake Eyre in South Australia. He regarded it as a distinct species on the basis of smaller size, paler tone of the pelage and shorter black section of the tail. Jones (1923) erected *M. nigripes* from material collected near Ooldea, South Australia by A.G. Bolam on the basis that the manus and pes were black. He regarded the small palatine vacuities as diagnostic and that the strikingly small teeth, especially the molars, made it distinct from *M. sagitta*.

Troughton (1932) suppressed *Macrotis sagitta* and *M. nigripes* and relegated them to subspecific status, a view supported by Tate (1948).

Troughton (1932) also established an additional three subspecies, *Macrotis lagotis cambrica* from eastern New South Wales, *M. lagotis grandis* from south of Adelaide, South Australia and *M. lagotis interjecta* from Rawlinna in Western Australia. The former was distinguished from *M. lagotis sagitta* by its woollier fur, larger size and more fuscous coloration. The second was distinguished by its large size and relatively shorter ears; and the third by its smaller size and shorter and woollier fur than the nominate subspecies.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The Greater Bilby shows a pronounced sexual dimorphism. Males grow to more than twice the body weight of females (2500 g versus 1100 g) and are of considerably greater stature with head-body length 330–550 mm versus 290–300 mm. The male canines also are relatively larger than those of females. The snout is relatively long and pointed and shows a well developed rhinal callus (Figure 25.1). The long and rabbit-like ears gave rise to an earlier widespread common name of Rabbit-eared Bandicoot or simply Rabbit Bandicoot. The forelimbs are heavily built and together with the three stoutly clawed toes (and two unclawed toes), equip the animal with a formidable burrowing capability. The fur is very soft and silky to the touch. It varies in coloration between and within subspecies, but in general terms the dorsum of the body is clothed in ash-grey fur augmented to varying degrees with two fawn hip stripes. The ventrum is pure white to cream. The tail is clothed in body fur for the proximal 20% and the central 40% is sparsely haired underneath and covered with intensely black fur above. The terminal 40% is of pure white hair which develops a strong dorsal crest and ends in a spur or nail of unknown function.

Figure 25.2 The left hind foot of the Bilby showing the enlarged fourth digit and the pair of syndactylous digits. (© ABRS) [T. Cochran]

The hind limbs are gracile and loosely resemble those of macropodids with respect to the presence of syndactylous toes and an enlarged fourth digit (Fig. 25.2). Bilbies have been described as the most beautiful and graceful of the native mammals, but Finlayson (1935b) probably put it more accurately when he noted that the Bilby '... has carried a number of structural peculiarities to grotesque lengths yet manages to reconcile them all in a surprisingly harmonious, and even beautiful, whole'.

The Lesser Bilby is essentially a diminutive Bilby of much paler coloration. The fur is exceedingly fine, soft and silky and, in Finlayson's (1932b) series of summer skins, shows no guard hairs.

On the dorsal surface the basal three-fifths of the hair shafts are a medium slate colour, merging distally into a subterminal band of very pale grey and ending in a bright chestnut tan tip. The fluffy nature of the fur tips enables the subterminal grey band to greatly reduce the richness of the external colour and from a little distance the general fur colour is a delicate cinereus tan (Finlayson 1932b).

The ventral surface is pure white externally and very pale slate basally, although some individuals possess entirely white fur in the mid-ventral areas. The colour of the sides is like that of the back and merges imperceptibly with the ventrum. The muzzle, anterior from about the mystical vibrissae, differs from the rest of the body in having adpressed short silvery hairs.

The ear is pale flesh-coloured in the conch, but distally is prominently dappled with slate or black. Externally at the base it is clothed with tan tipped hairs, but for the distal 80% is sparsely covered with short adpressed iron-grey or silvery hairs.

The forelimb is white and the palm of the manus pink and naked except for a narrow tract of hairs at its centre. The femoral portion of the hind limb is covered with body hairs, but the tibial portion is almost naked. The pes, which is exceedingly slender and delicate, is uniformly white above. Below, it is hairy except for the calcaneal and interdigital pads and variously coloured pale slate or white.

The proximal fifth of the tail is clothed above and below with body fur and the distal two-fifths bears on the upper surface a beautiful crest of progressively lengthening pure white opaque hairs. The central two-fifths is short-haired on all surfaces, the dorsum having a narrow band of pale slate hairs bordered on either side by fawn. The underside of the tail is white and short haired in its entire length.

The linear dimensions of the sexes are similar in adult forms, but males are considerably more bulky. Finlayson (1935a) gave the following range of measurements for freshly killed specimens: head and body 241–250 mm (male), 247–250 mm (female); tail 1550–167 mm (male), 142 mm (female); weight 362–435 g (male), 310–312 g (female).

Skeletal System

The Bilby is polyprotodont with the dental formula I 5/3 C 1/1 PM 3/3 M 4/4 (Jones 1924: 153).

The incisors are small and sharp. The canines are large, (Fig. 25.3) relatively larger than in any other bandicoot genus. In males, the canines vary in length from 10.3–7.3 mm and in females measure 5.2–3.3 mm. This pronounced sexual dimorphism appears to have a basis in the use of canines in threat display (see below). There is a substantial space (diastema) between the canines and premolars. The premolars are compressed teeth with a single row of three sharp tubercles, the middle of which is longest.

McCracken (unpublished data) noted that the hypoconid and ectoconid have been added to the basic ancestral tribosphenic arrangement of the lower molars and this enhances the squaring-off effect. The hypocone is absent in the upper molars and the metacone occupies a similar position. The upper molars are squared off by the extreme lingual positioning of the metacone and by the presence in M^{1-3} of a much enlarged and longitudinally elongate stylar cusp.

The structure of the skull is illustrated in Fig. 25.3. The vertebral formula is as follows (McCracken unpublished data): seven cervical, 11 thoracic, eight lumbar and 20 sacral and caudal. McCracken (personal communication) had difficulty in defining the division between the sacral and caudal vertebrae. There are thirteen ribs two of which are floating and eleven articulate with the thoracic vertebrae. The digital formula of the forelimb is, in relation to digital size, III > II > IV > V > I. Digits I and V are clawless, but the others are well developed and terminate in strong recurved claws. The hind limb has a digital formula of IV > V > II, III and is much larger than the forelimb.

Locomotion

The Bilby moves with a stiff-legged cantering gait in which the forelimbs are placed on the ground, one slightly forward of the other, and the hind legs are brought forward together to be put down in front of the forelimbs. The gait

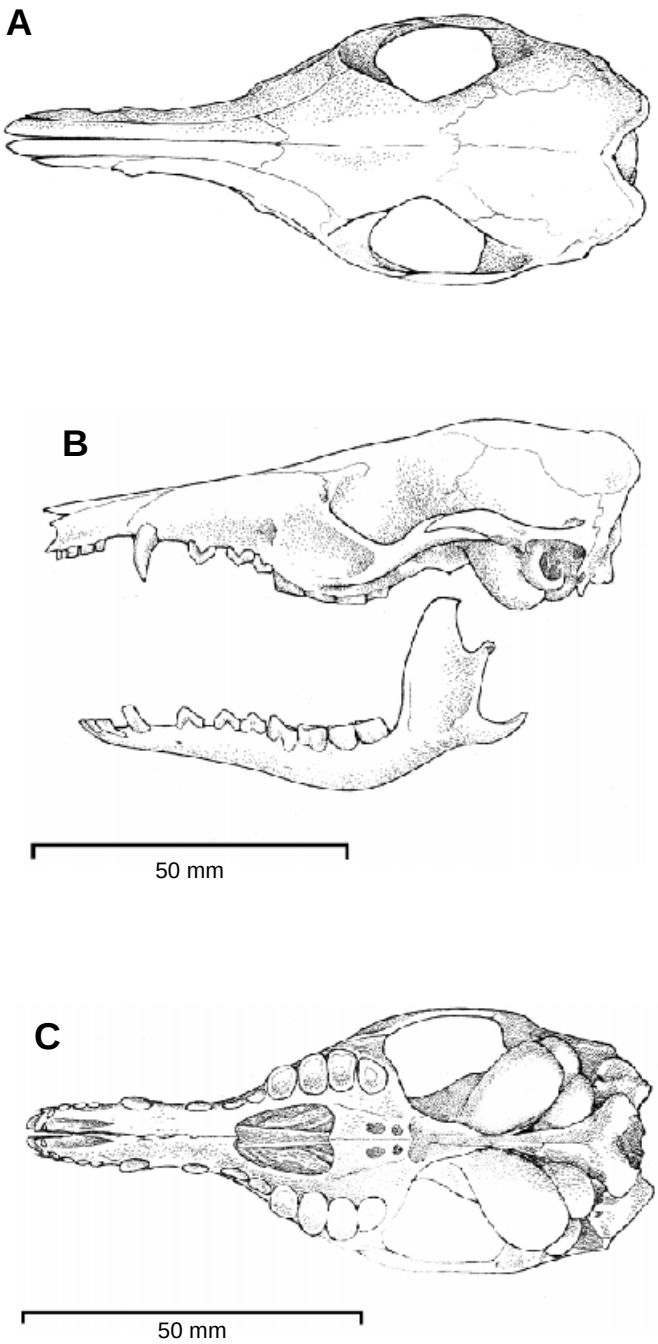

Figure 25.3 The skull of a male Bilby: **A**, dorsal view; **B**, lateral view with mandible; **C**, ventral view. Note especially the small incisors, but large canines. (© ABRS) [F. Knight]

appears awkward, but they are able to show bursts of surprising speed. Animals occasionally stand upright on their hind legs to gain elevation while sniffing the air.

When digging, the front claws are used to rapidly scratch soil backwards under the body where it is pushed from the burrow using the hind legs operating in unison.

Feeding and Digestive System

The Bilby has a simple gut anatomy (Fig. 25.4), consistent with an omnivorous lifestyle. The stomach does not show the complex sacculated structure associated with herbivory and the caecum is relatively small. Jones (1924: 165) found that captive animals readily took small vertebrates, but Johnson & Johnson (1983) observed that their study animals were uninterested in the free living House Mouse (*Mus musculus*) population with which they shared their enclosure. The diet of wild animals comprises appreciable quantities of grass seed, bulbs and insects. The characteristically squared-off molars are ideally adapted for crushing those items. The molars are poorly adapted for macerating muscle, bone and skin tissues.

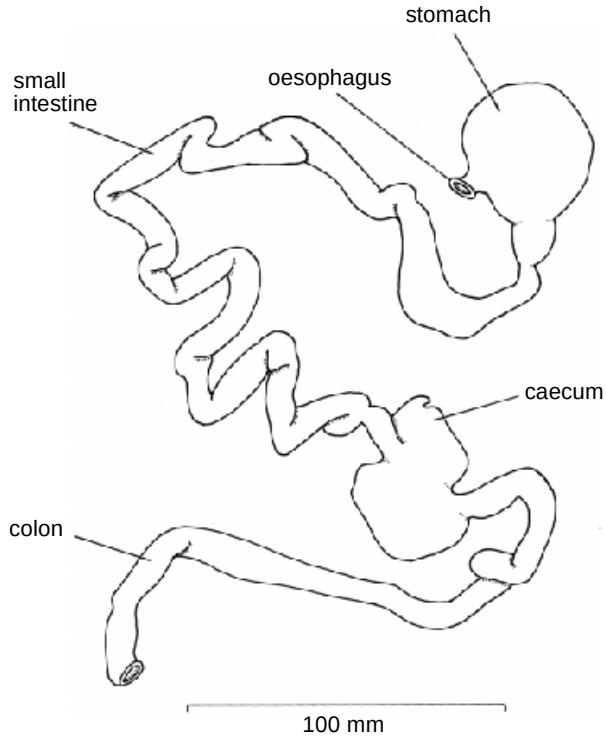

Figure 25.4 The alimentary tract of the Bilby. (© ABRS) [B. Scott]

The Bilby will take small food items, such as seeds from the soil surface, by a rapid flicking of the tongue. Underground food items such as bulbs and insect larvae are sorted with a probing action of the snout in conjunction with scratching with the forelimbs. Large food items are firmly grasped in the mouth and the forelimbs are only used for crude manipulation. Holes dug when foraging vary in depth from a few mm to 500 mm. Soil is generally scattered in all directions from the hole and faecal pellets often are deposited under or on top of the piles of discarded material.

Food appears to be located principally by smell although the extremely acute hearing is important for detecting mobile items such as insects. Sight is of minor importance and, in fact, animals are quite inept at capturing large quick-moving prey items.

Temperature Regulation

Morrison (1962) studied thermoregulation of captive Bilbies and reported the very precise maintenance of body temperature to 37.1°C (S.D. = 0.13) during night-time activity over 9 hours. In contrast, the temperature maintained during 12 hours of daytime activity showed great variability and a S.D. of 0.43°C. Furthermore, daytime temperatures were a little over 36°C at the beginning of the study and had fallen to 34°C two months later with no apparent ill-effects for

the animal. If the resting animal was forced into activity, its temperature could be elevated by about 2°C to 36 to 36.5°C. Night temperatures remained constant throughout the study and were not affected by induced activity.

Excretion

Typical of many animals inhabiting arid regions, the Bilby produces faeces that are firm and low in water content. Faeces also contain appreciable quantities of soil or sand ingested coincidently with food.

Endocrine and Exocrine Systems

The Bilby has interauricular skin glands which form a pyriform structure measuring approximately 25x18 mm in adults (Stoddard 1980). The related skin is furred like adjacent non-glandular skin, but the pock-marked glandular area can be palpated with the fingers. The function of these glands is unknown and, although Johnson & Johnson (1983) did not record scent marking with the use of these glands, males sniff this area when examining females.

Reproduction

The karyotype of the Bilby is 2n=19 (male), 18 (female) (Martin & Hayman 1967) and differs from that of other bandicoots, which is 2n=14. The differing diploid number in male and female Greater Bilbies is due to the XX/XY_1Y_2 sex determining mechanism.

The Bilby shows the normal marsupial pattern of testes anterior to the penis and the presence of lateral vaginae, vaginal caeca and median vaginal culs-de-sac (McCracken 1983). The pouch opens backwards and contains two crescentic rows of four teats each. One or two young normally constitute the litter, but triplets occur infrequently.

Males investigating females sniff them about the face and shoulders (the location of the female's interauricular glands), flank and under the tail. The urogenital opening is sniffed and licked if the female remains still long enough. Females respond by remaining still, moving away or active rebuffing. Attempted copulations have been observed in animals above ground, but it appears that successful engagements occur mainly in burrows (Johnson & Johnson 1983).

Births occur throughout the year among captive specimens held at Alice Springs. McCracken (1983) examined specimens held in the State Museums of New South Wales, Victoria and South Australia and concluded that there was no seasonality in the production of young among wild caught animals collected in New South Wales, South Australia and the Northern Territory. Studies of captive females indicate an oestrus cycle of 20.6 ± 7.3 days (S.E.) with a range of 12–37 days and a gestation period of 14.0 ± 1.4 days with a range of 13–16 days (McCracken 1986). Six females studied by McCracken (1986) were acyclic during the major part of lactation. Four animals recommenced cycling towards the end of lactation while the remaining two females were still lactating at the end of the study period. Further evidence for recommencement of cyclic activity before cessation of suckling was gathered from analysis of breeding records of the captive colony studied. In 13 cases the conception of one litter occurred within one week of evacuation of the pouch by the previous litter and in 11 of these cases conception occurred in the week prior to pouch evacuation.

Pouch life (±S.E.) is 80 ± 2 days and by about age 90 days the young take solid food (McCracken 1986). The termination of pouch life occurs over a period of less than 5 days (Hulbert 1972; McCracken 1983). Johnson & Johnson (1983) recorded a young being cached down the maternal burrow for 14 days during

which time the mother returned frequently, for short periods, presumably to suckle it. This juvenile was fully independent of its mother when it emerged from the burrow after the 14th day. It did not consort with her and did not share her burrow during the day. The suckling of young outside the pouch and down a burrow was later observed in other animals housed outdoors and provided with a deep, glass fronted false burrow. In females and young confined in small concrete floored pens, McCracken (1986) observed extended lactation periods of 21–88 days.

Milk composition varies considerably during lactation and McCracken (1983) reported a four fold increase in total milk solids from day 37–102. This increase is caused mainly by changes in the lipid and protein fractions while carbohydrate components decrease.

Sexual maturity occurs at about age 175–220 days and a weight of 450–650 g in females and about 270–420 days and at 850–1500 g in males. Young are born soon after the incumbent young leave the pouch and McCracken (1983) obtained evidence of a post-partum oestrus. The lighter weight females, however, do not appear to successfully raise young to independence (R. Southgate personal communication). One captive female produced the following during 12 months: twins, a single, twins and another single (six young altogether) at intervals of 77, 99 and 135 days, respectively. For the Lesser Bilby, Spencer (1896c) recorded one set of twins and one set of triplets while Finlayson (1935a) noted one set of twins and one single young, but regarded twins to be the normal situation. McCracken (1983) observed no seasonality in breeding among nine female specimens held in various museums.

Embryology and Development

Young are born with the classical marsupial morphology of well-developed forelimbs for making passage from the urogenital opening to the pouch and very poorly developed hind limbs. New born young attach to teats not suckled by the previous young and remain fixed for about 60 days. The initially naked young become fully furred by about day 68 at which time the eyes become fully open. Young weigh approximately 180 g at the time they first leave the pouch. Females reach their normal adult weight of about 1000 g by about age 280 days, but males continue to grow for a considerable period before stabilising at a maximum of about 2500 g.

NATURAL HISTORY

Life History

How long bilbies normally live in the wild is not known, but captive animals have survived longer than 5 years. Only 22 specimens of the Greater Bilby have been taken and not all of these remain in museums. There have been no field studies of the species and the only records available on the living animal are notes by Spencer (1896c) and Finlayson (1935a).

There is some disagreement as to the number of mammae in the Lesser Bilby. Spencer (1896c) noted eight mammae as in the Bilby, but commented that the posterior mamma on the right side was missing. Finlayson (1935a) reported six mammae, but examination of a spirit specimen in the South Australian Museum indicated eight mammae, the anterior pair of which are very small (Johnson unpublished data).

Ecology

Little is known of the diet of bilbies. The Bilby occupied approximately 70% of continental Australia until early this century and, although centred on arid lands, much of this former range included more temperate environments such as the regions south of Adelaide. In the desert areas where they still persist, bilbies eat mainly insect and plant material and ingest, coincidently, large quantities of soil. Analysis of faecal pellets of bilbies in the Northern Territory has revealed underground fruiting bodies of the fungus *Endogone*, the tap root centres of *Solanum* species and *Boerhavia diffusa* (Watts, 1969). Fruits of *Solanum* species and *Scaevola parvifolia*, small amounts of leaf material and large quantities of the bulb *Cyperus bulbosus* have been found in the faeces of bilbies in the Tanami Desert, Northern Territory, where seed, principally that of grasses such as *Yikirra australiense*, is a regularly and heavily used food material. Smyth & Philpott (1968) found the termites *Hamitermes rubriceps* (Froggat) and *Eutermes tumuli* (Froggat) to be the main food items of bilbies near Warburton in Western Australia.

Insects including ants, termites, beetles, grasshoppers and a variety of lepidopteran and coleopteran larvae inhabiting the underground roots and stems of shrubs and forbs form an important component of the diet. Much of the seed appears to be dug from the underground granaries of harvester ants and these appear as incidentally ingested components of the diet. No vertebrate material has been found among faecal pellets analysed from widely separated groups of Bilbies in the Northern Territory (Johnson unpublished data) although captive Bilbies have been reported to eat birds and mice (Jones 1924: 165). Bilbies kept in outdoor yards in Alice Springs, Northern Territory, were observed nibbling leaves from lucerne, *Medicago sativa* and enthusiastically plucking unripe fruits of caltrope, *Tribulis terrestris*, runners. In the field they have a remarkable ability to detect and extract insect larvae from underground stems. Some larvae such as those of cossid moths, the colloquial witchetty grub, are large food items measuring as much as 80 mm in length and 14 mm in diameter and undoubtedly form a moisture- and energy-rich food item. Cossid moth larvae live in the woody roots of acacias from where it must be a difficult task for Bilbies to extract the food, let alone detect it from above ground. Biennial sub-shrubs such as *Cassia notabalis* sometimes suffer waves of insect larva infestations and, in the Tanami Desert, the Bilby has been observed to return to patches of these plants to harvest such infestations. (K.A. Johnson unpublished data).

Finlayson (1935a) notes that the Bilby is strictly nocturnal. The stomachs of those dug from their burrows in the morning contained large quantities of skin and fur of rodents (but no bone fragments), seeds of what appeared to be *Solanum* species and some sand. No insect fragments were apparent.

The Greater Bilby occupies a variety of habitats with differing soil and vegetation cover components. The population in south-west Queensland inhabits undulating downs country of clayey and stony soils and sparse, short grass and forb cover (R. Southgate personal communication). In the Tanami, Great Sandy and Gibson Deserts, the Bilby occurs mainly along the desert fossil drainage systems of saline clayey sands with hummock grass (*Triodia* species and *Plectrachne* species) and *Acacia* species shrubland. Deep sands of similar vegetation and massive red earths with mainly mulga (*Acacia aneura*) shrubland and grass understorey are also occupied, although few animals now occur in the latter habitat type (R. Southgate unpublished data).

Densely vegetated areas are avoided where it seems that movement and ability to forage are impeded. In the hummock grasslands, fire is instrumental in maintaining areas with sparse vegetation (Fig. 25.5) while coincidentally

promoting short lived plants important as a primary or secondary food source. The Bilby is not sedentary and moves in response to apparently changing food and vegetation cover conditions.

Figure 25.5 Excavation made by a Bilby when foraging in open spinifex country. [Photo by K.A. Johnston ©]

The Bilby occurs in scattered pockets of up to about three individuals consisting usually of a male, female and independent young. Studies of captive animals have shown that while they exhibit little intraspecific aggression (in contrast to other perameloids), males are intolerant of other males occupying their burrows. Individuals simply tend to avoid company and this is probably responsible for the occurrence of scattered small groups in the wild (Johnson & Johnson 1983).

Groups in the sandy deserts occupy small areas, which, in the Tanami Desert, Northern Territory, measure approximately 250 m in radius and contain upwards of 25 individual burrows. Smyth & Philpott (1968) recorded 58 burrows in an ovoid (approx. 3.7 km by 2.0 km) area of mixed mulga, spinifex and tussock grassland from which two females were captured. On each of 8 consecutive nights only 2%–27% of burrows were used. Of 35 representative burrows, 14 were not used on any night and none were used on more than 4 nights. Watts (1969) reports three colonies at Yuendumu in the Northern Territory which covered areas of 11.3, 15.4 and 16.2 ha, respectively and together with additional colonies averaged 17 burrows each. In the Tanami Desert, burrows normally occur singly and some tens of metres from their nearest neighbour. Some appear to be used regularly, while others appear to be occupied infrequently or only transiently during the night. For reasons best known to bilbies, but probably related to changing food availability, colony areas may be suddenly vacated in favour of some new home range. These contain many burrows, requiring the considerable energy of the owner to construct. This behaviour is an advantage to desert dwelling animals faced with food resources that change rapidly in space and availability.

Further towards the rocky ranges at Yuendumu, Northern Territory (22°15'S–136°53'E) Watts (1969) reports burrow complexes containing several entrances and a series of interconnecting tunnels spread over an area of a little over 9 m^2. Southgate (personal communication) and Watts & Aslin (1974) recorded similar warren type complexes in south-western Queensland.

Examination of faecal pellets (G. Wilson personal communication) indicates low gastro-intestinal parasitism in wild Bilbies. Of 271 faecal samples collected from captive animals under conditions of husbandry, where parasite transfer

should be facilitated relative to that occurring in free ranging animals, only 15 examined by the flotation method were positive for nematode eggs or larvae. No eggs, larvae, coccidial oocysts or other protozoa were seen in approximately 200 wet preparation examinations. No nematode eggs were found in six faecal samples collected from different locations in the field. A nematode, *Cyathospirura* species, was isolated from captive animals. Jones (1924: 166) reported hair loss in Bilbies and attributes this to moulting, but hair loss among captive specimens held at Alice Springs, Northern Territory, is usually associated with stress conditions such as overcrowding or the late stages of lactation in females carrying twins. The condition does not appear to cause the animals any discomfort and pelage is quickly regrown. R. Southgate (personal communication) has recorded similar hair loss in animals captured in the Tanami Desert.

Finlayson (1935a) observed no external parasites on Greater Bilbies. Johnston & Mawson (1940) reported the nematode *Physaloptera peragale* from '*Peragale minor*' (*Macrotis leucura*) and apparently took the specimen from the stomach.

Behaviour

Captive Bilbies form a linear hierarchy, strongest among males, which is maintained with little actual fighting. Threat displays consist of a gape which exposes the canines and two curious yellowish pea-shaped bodies at each corner of the mouth. A nasal hiss is made, but biting is rare. Frightened or harassed animals often make a short spitting sound and pouched young sometimes make soft squeaks if disturbed (Johnson & Johnson 1983). Wild animals tame readily in captivity where they are easily handled and rarely, if ever, bite.

Finlayson (1935a) found that individuals of the Lesser Bilby: '... belied their delicate appearance by proving themselves fierce and intractable, and repulsed the most tactful attempts to handle them by repeated savage snapping bites and harsh hissing sounds, and one member of the party, who was persistent in his intentions, received a gash in the hand three quarters of an inch long from the canines of a male.'

Little grooming was seen among Bilbies kept in large yards where they constructed deep burrow systems (Johnson & Johnson 1983), although animals kept in confined quarters without burrows undertook prolonged grooming sessions using the syndactylous hind claws to comb the long silky fur, by nibbling and licking and by wiping either side of the snout with the forepaws (Aslin 1982b). Bilbies observed by Johnson & Johnson (1983) via false burrows undertook extensive grooming. Under natural conditions most grooming probably is carried out in the security of the burrow. The Bilby occasionally and briefly lies on its side above ground at night during periods of hot weather. By day it sleeps in a curious squatting position, with the snout tucked under the body between the front legs and the ears laid back and then folded forward with the tips covering the eyes. The animal thus forms a silky round ball with its tail usually protruding straight out behind. Individuals sleeping in nest boxes in small pens or observed in false burrows use this posture. If disturbed, the animals move about for a short time with the ears flopping forward in an impotent manner before attaining their normal erect position. Although the ears are kinked forward for extensive periods during the day, no animals show any evidence of a permanent or temporary crease or fold line at the point of flexure.

Deep burrows of up to two metres are dug, usually entering the ground at a steep angle and making a spiral descent with few offshoots (Fig. 25.6). No nest material is used. Burrows are 100–150 mm in diameter and usually trend towards horizontal at the extremity which shows no special chamber. The

entrance is usually against a bush or surface irregularity, although many are dug in flat, featureless locations. In the Tanami Desert, burrows are commonly encountered in the base of giant *Nasutitermes triodae* termitaria.

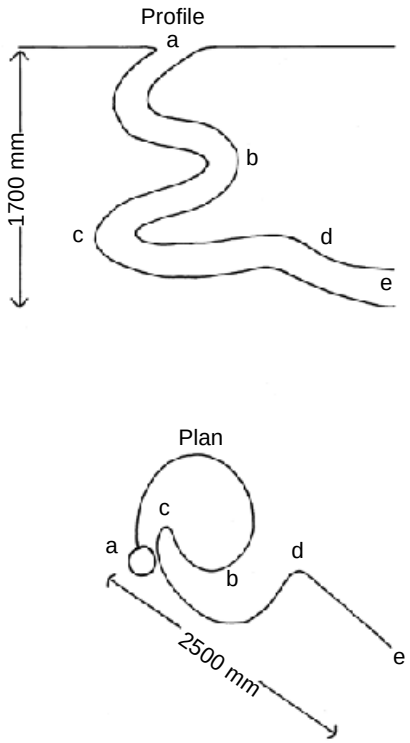

Figure 25.6 Plan and profile of a typical burrow system of the Bilby. The hole is about 100 mm in diameter, otherwise the diagram is to scale. Corresponding points in burrow system indicated by a, b, c, d and e.

Finlayson (1935a) collected 12 Greater Bilbies in sand dune country with swales containing clay pans and loams of varying degrees of stoniness. The burrows of the Lesser Bilby were found only in the sand dunes and never in the flats, whereas the reverse was true for the Greater Bilby. The burrow of the Lesser Bilby is blocked with loose sand when the animal is within and during windy periods. The position of the burrow is indicated by no more than a shallow dimple in the sloping surface of the dunes. Finlayson (1935a) employed the services of an Aborigine to collect for him and remarked on the considerable skills he had in locating the inconspicuous burrows. ‘He seldom returned without two or three after a mornings work and I suspect many found their way to the cooking fires... as well’ (Finlayson 1935a).

Finlayson (1935a) observed and recorded the securing of two specimens which were dug from their burrows. The burrows descended steeply for about 600 mm from the entrance whereupon they turned sharply, sometimes in a vertical and sometimes in a horizontal plane. From the entrance to the end was 2.5–3.0 m in a straight line. Though there were several turns in both planes, the resultant course was not a complete spiral.

Spencer (1896c) reported that in winter the animal lies within 300 mm or so of the entrance and that Aborigines exploited this by jumping on the surface behind the animal to cut off its retreat, thus securing it without extensive digging. The two specimens Finlayson (1935a) observed being taken in summer were at the end of their burrows and evidently extending them by frantic digging when seized. He did not observe any pop holes or ventilation shafts nor any nest or dwelling chamber.

The Bilby remains deep in the burrows by day emerging after dark and returning before sunrise (Johnson & Johnson 1983). Because they quickly become heat stressed at temperatures above 30°C (Morrison 1962), it is clear that burrows offer an important refuge from heat in the central deserts. Newsome (1962)

commented that bilbies had no sweat glands and did not pant. Bilbies occur in areas where surface water is usually absent, but captive animals readily lap provided water. The large ears are densely vascularised and probably have a role in radiation of excess heat.

Individuals were observed by Johnson & Johnson (1983) to occasionally press and drag their urogenital openings along the ground in a behaviour that appeared to have a scent marking function. Marking usually lasts 2–3 seconds and for a distance of up to 500 mm. The male usually sniffs the place marked before and after the activity. Marking was seen 54 times among three males and once among three adult females. The behaviour was directly correlated with dominance rank. Burrow entrances are the most frequently marked areas (49%). Male-male social interactions (16%), male-female interactions (4%), alarm response (6%) and no associated activity (25%) were the other behaviours in which marking was involved.

Burrows are generally marked before or after use and all males sniff about the entrance before entering. Dominant males mark over a spot recently marked by a subordinate. On the one occasion a female was seen to mark, the spot was overmarked by the alpha and beta males on the same night. The intense interest shown by males in sniffing burrow entrances and other areas recently marked by other males, together with overmarking by the dominant male of recently placed scent marks and the correlation of marking frequency with dominance rank, suggest that scent-marking is used by males to express their presence and dominance. Females rarely mark and they ignore the marks of males.

Economic Significance

Bilbies were generally regarded as benign creatures of some use in the control of insect pests and were sometimes kept as household pets (Jones 1923). Their appeal cannot have been universal, however, because Rolls (1969: 394) notes that drovers in the Hillston region of New South Wales in the 1870s exercised caution lest their stock horses put their forelegs into burrows. Bilbies were briefly entered on the stock and pastures scalp bounty list of Narrandera in southern New South Wales late last century and pelts were marketed in Adelaide in large numbers (Jones 1923).

The white tail-tips, ‘alpita’ to the Arunta Aborigines, were extensively used for decorative purposes by central Australian Aborigines to the extent that Spencer & Gillen (1912), referring to their 1901 expedition, noted that ‘Judging by the supply of ‘alpita’ in every native camp, these bandicoots... must abound; and must also be prolific breeders, otherwise the constant depredations of the natives would have exterminated it.’ By 1923, the white rabbit tail had replaced that of the bilby for decoration (Spencer 1928: 562). Bilbies were an important food for Aborigines and, although the animals are now uncommon, they are still a favoured dietary item. Gould (1863) remarked that its flesh was ‘sweet and delicate’ and recommended that it be imported to Europe as an article of food. Anon. (1925) reported a comment by a man from Brobenah (near Leeton, New South Wales) that ... ‘nearly 40 years ago I visited the house of ... he had curried bilbie [*sic*] and my word it made a fine meal.’

The Bilby, is on the official Australian list of endangered fauna and is among those listed in the I.U.C.N. Red Data Book (Thornback & Jenkins 1982). The species is protected by legislation in all States and Territories where it has been recorded historically.

The Lesser Bilby is probably extinct, although the remoteness of its range, the cryptic nature of its burrows and the disappearance of Aborigines with knowledge of it would greatly reduce the probability of its detection.

The Western Australian, New South Wales, South Australian, Queensland and Northern Territory Government wildlife agencies have conducted recent surveys of varying intensity in an effort to locate bilbies. The World Wildlife Fund has supported a three year project (1983-1986), conducted by Northern Territory and Western Australian wildlife agencies, aimed at determining the current range of the species. The Northern Territory Government has a research and management program in which the Bilby is being bred in captivity and released in a nearby national park, where it is anticipated that it can be re-established.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The Bilby has suffered a dramatic reduction in range since European settlement. Krefft (1866) notes that bilbies had disappeared from the Victorian side of the Murray River at its confluence with the Darling River in response to the recent occupation of the area by cattle. There are no specimen records from Victoria, but Brazenor (1950) noted that the species was '... originally recorded from the north-west area of the State'. The last specimen to be taken in New South Wales was collected at Moree in 1908. The species rapidly vanished from New South Wales during the early part of this century and the last known to survive were killed by shooters near Wagga in 1912 (Troughton 1932). Jones (1923) regarded it as a rapidly diminishing species in South Australia at the time, noting that '... to the north and south of the city (Adelaide) itself rabbit bandicoots lived in abundance but little more than twenty years ago.' Finlayson (1961) thought it had gone from the far north-west of the State by the time of his expeditions in the mid-1950s. The cause of widespread decline of the Greater Bilby has been the subject of speculation by several authors who variously regard the fox, rabbit, feral cat and the effects of grazing livestock as important contributing factors. In the desert sandplain areas, a changing fire regime has also been important. The traditional burning patterns of Aborigines produced a patchwork of habitat types in different stages of regeneration after fire. The present regime of large hot wildfires in late spring and summer results in an homogeneity of habitat which is less favourable for bilbies. This and drought probably combined with the foregoing factors to produce the spectacular decline in distribution of the Bilby.

R. Southgate (personal communication) surveyed potential habitat for the species in Queensland, South Australia, the Northern Territory and Western Australia and gives the current distribution in Fig. 25.7. He has evidence that the range is continuing to decline.

Museum records of the distribution of the Lesser Bilby indicate its confinement to the tall sand dune country to the north of South Australia and the south of the Northern Territory (Figure 25.8). The record of the Lesser Bilby from MacDonald Downs station in the Northern Territory (Johnson & Mawson 1940) is unsubstantiated, but lies within the specimen based distribution of the species. Aborigines of the sand dune country in the Gibson and Great Sandy Deserts of Western Australia know the species and maintain that it survived there until recent times (Burbidge *et al*. 1988).

Affinities with other Groups

The perameloid group containing *Macrotis* shares the characteristics of polyprotodont dentition with the Dasyuroidea and syndactyly with the diprotodonts. Kirsch (1977) considers syndactyly to have evolved convergently, but Marshall (1972) and Hall (1981) conclude that there is no evidence to support convergence. Szalay's (1982) studies of tarsal bone morphology lead

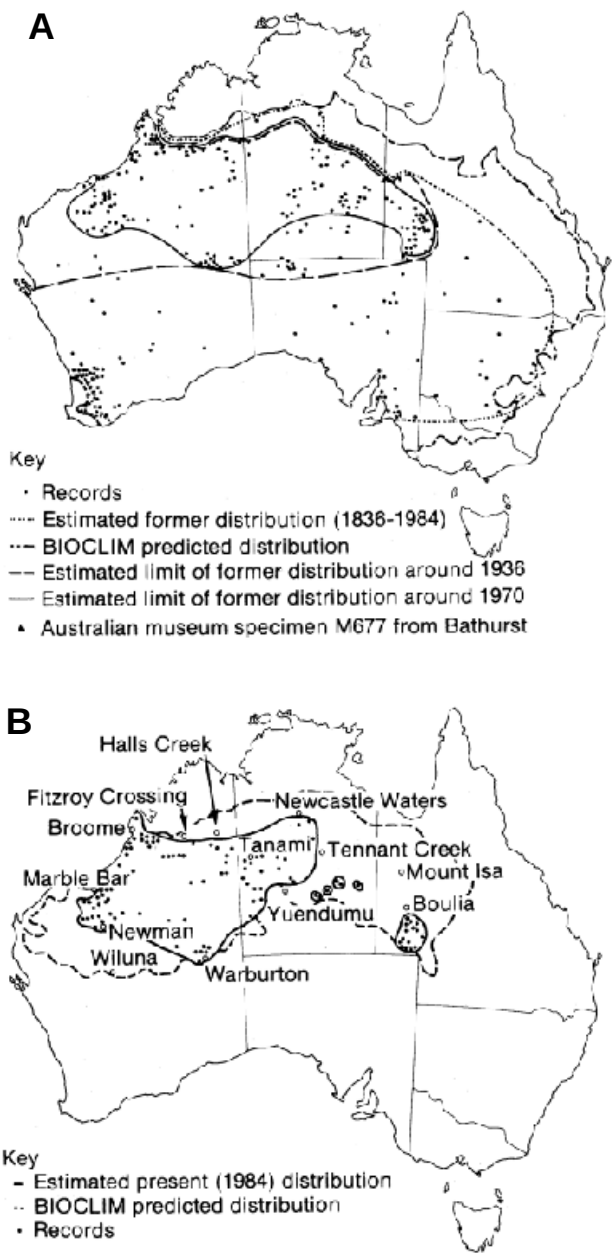

Figure 25.7 A, Distribution of the Bilby at the time of European settlement and the contraction in range over the periods 1936, 1970 and **B**, 1984. Note that the BIOCLIM prediction is also shown in A and B. (After R.I. Southgate, personal communication)

him to conclude that the perameloids and diprotodonts were monophyletic and derived from the same microbiotheriid stock as the dasyuroids. This proposal was supported by Archer (1981b) on the basis of dental patterns.

The perameloids were divided into the Thylacomyidae and the Peramelidae by Archer & Kirsch (1977) on the basis of dental structure, basicranial differences and serological evidence. Archer (1984b) was less certain of this division at the family level, but supported the arrangement in the absence of evidence that the thylacomyids bear closer relationship to any particular group within the Perameloidea.

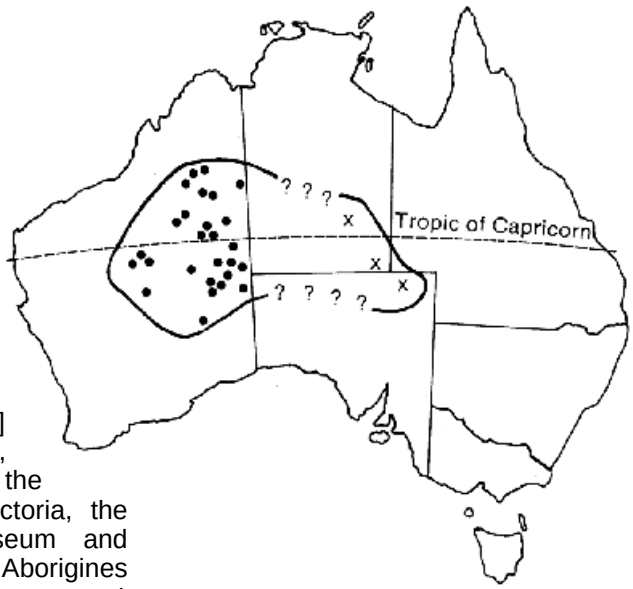

Figure 25.8 Distribution of the Lesser Bilby based on specimen records [+] from Spencer (1896c), Finlayson (1935), the National Museum of Victoria, the Northern Territory Museum and anecdotal records from Aborigines [.] collected by Burbidge *et al.* (1988).

Fossil Record

There is fossil material of the Bilby among the fauna obtained from the Wellington Caves in eastern New South Wales, but the species has not been recorded from this area in historical times. There are various other Pleistocene specimens, but none that are earlier.

Ischnodon australis is the only known Tertiary thylacomyid and was taken from a deposit at Lake Palankarinna in South Australia. On the basis of its better developed paraconids, Archer (1984b) suggested that it might be ancestral to *Macrotis*.

COLLECTION

Most Bilbies have been live caught by digging them from their burrows. Animals are usually taken at the furthest extremity of the tunnel where they are rapidly and frantically extending it. It generally requires a person of great knowledge of burrow systems and great energy to obtain specimens.

Aborigines display a great deal of skill in being able to predict the turns in burrows, thereby making the process of excavating animals a good deal easier. During one exercise in extraction a man was able to determine that the quarry was digging rapidly upwards and managed to secure the animal just before it broke to the surface and escaped (K. Johnson personal observation). When captured in burrows, most specimens are in the process of rapidly and frantically extending them at a rate that exhausts and defeats most people.

Maintenance in Captivity

The Bilby breeds readily in captivity when fed diets as simple as dried dog pellets and bird seed having grains of *Panicum* species size. It is relatively docile and quickly becomes accustomed to being handled. A wild caught animal will accept seed from the hand after just 7 days of confinement in an indoor cage. Water is readily accepted. Unlike many other perameloids, the tail is a convenient appendage to grasp during handling; this does not result in stripping of its skin or breakage.

Animals kept out of doors in earthen floored pens must be contained by a curtain of netting, weldmesh or similar impenetrable material. This material must be buried to a depth of at least 2 metres around the perimeter or to the limit of burrowable substrate. Netting for the above ground fence and the curtain must be of about 25 mm size: young animals can escape through mesh of 50 mm. Young bilbies are able to climb a 12 mm x 12 mm mesh fence to a height of 2 m (J. Byres personal communication).

Specimens can be maintained in concrete-floored pens providing a nest box in a warm environment is available or thick straw or tumbled hay bales are available for nesting in during the day. Animals are susceptible to pneumonia infections if not allowed access to warm rest places.

Several females and males may be kept in large enclosures of 6 x 18 m without serious fighting and with normal reproduction in females. A male and several females live peaceably in small enclosures of 3 x 4 m, but lower reproduction rates are experienced. If daytime sleeping areas are restricted in size, bilbies will rest in a tumbled furry heap in the one place without apparent ill-effects.

Differentiation of *Macrotis lagotis* from *Macrotis leucura*.

The two species of bilby can be differentiated using a number of different characteristics that are shown in Table 25.1.

Table 25.1 Characteristics that differentiate the two *Macrotis* species. (from Spencer 1896c; Jones 1923; Troughton 1932; and unpublished data)

	M. lagotis	*M. leucura*
Body weight (g)	1 000-2 500♂	362-435♂
	660-1 100♀	310-312♀
Tail colour	proximal half black around the full circum-ference	tail uniformly white or with dorsal band of slate coloured hair
Basal length of skull (mm)	66-104	62-66♂
	71-87	61-62♀
Tail length (mm)	200-290♂	127-167♂
	200-278♀	118-152♀
Head and body length (mm)	330-550♂	241-270♂
	290-390♀	200-250♀

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