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Macropus giganteus.

By W. E. Poole

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Macropus giganteus Shaw, 1790

Eastern Grey Kangaroo

Macropus giganteus Shaw, 1790:pl. 33 and text. Type locality Cooktown, Queensland. Generally regarded as a junior secondary homonym of *Jaculus giganteus* Erxleben, until Shaw's name was validated under the plenary powers of the International Commission on Zoological Nomenclature (Opinion 760, Bull. Zool. Nomencl., 1966, 22:292–295) as the type species, by monotypy, of the genus *Macropus*.
Kanguroo gigas Lacépède, 1799:6. Name used in taxonomic grouping based on numbers of teeth.
Macropus major Shaw, 1800:505. Type locality Sydney, New South Wales, as restricted by Iredale and Troughton (1934).
Dipus tridactylus Perry, 1811:pl. 63 and text. Type locality New South Wales.
Kangurus labiatus Desmarest, 1817:33. Type locality, vicinity of Botany Bay and Port Jackson, County of Cumberland, New South Wales.

A number of variant generic assignments and spellings of *canguru*, a dubious name rejected by Opinion 760, and of *giganteus*, are omitted from the synonymies.

CONTEXT AND CONTENT. Order Diprotodonta, Family Macropodidae, Subfamily Macropodinae. Opinions regarding the generic limits of the genus *Macropus* have been diverse. As indicated by Bartholomai (1975), species referrable to *Macropus* have been relegated by interpretation of individual taxonomists to at least 20 additional genera or subgenera. Current usage accepts some 14 extant species of kangaroos and wallabies within the genus *Macropus* (Calaby, 1971; Kirsch and Calaby, 1977; Poole, 1979; Ride, 1970). Among these is the western grey kangaroo *Macropus fuliginosus* (Desmarest), a species closely related to *Macropus giganteus* Shaw (see Kirsch and Poole, 1972). With additional research, three subspecies may be recognized (Kirsch and Poole, 1972), as follows:

M. g. giganteus Shaw, 1790:pl. 33 and text, see above (*gigas* Lacépède a synonym). Neotype, Queensland Museum specimen J10749, collected at King's Plains 32 km south of Cooktown, Queensland; designated by Calaby et al. (1962) and restated by Calaby and Ride (1964).
M. g. major Shaw, 1800:505, see above (*tridactylus* Perry and *labiatus* Desmarest are synonyms). Name validated under the plenary powers of the International Commission on Zoological Nomenclature, Opinion 760.
M. g. tasmaniensis Le Souef, 1923:145. Type locality Tasmania.

DIAGNOSIS. Along with the red kangaroo, *Macropus rufus*, and the hill kangaroos, *Macropus robustus*, grey kangaroos are among the largest living marsupials. For almost two centuries after their discovery, disagreement over their taxonomic status was provoked by the morphological variation recorded throughout their considerable geographic range. Early accounts frequently confused the localities of origin of grey kangaroos and subsequent writings incorporated composite descriptions of the varied morphs (e.g. Thomas, 1888; Troughton, 1967; Wood Jones, 1924).

Distinctive features of all grey kangroos are the hairy muzzle with fine hairs appearing between the nostrils, down nearly to the upper lip, leaving only the margins of the nostrils ringed with naked black skin (Frith and Calaby, 1969; Thomas, 1888; Wood Jones, 1924), the characteristic shape of the zygoma (Wood Jones, 1924), and the strongly double-grooved third incisor with a width equal to, or greater than, the combined width of the first and second incisors (Frith and Calaby, 1969; Thomas, 1888; Wood Jones, 1924).

Recent studies (Kirsch and Poole, 1972) have supported a primary division of grey kangaroos into two species, the light to dark grey colored *M. giganteus* and the brown *M. fuliginosus*. Populations of eastern grey kangaroos with a single transferrin phenotype A may be distinguished from populations of western grey kangaroos with individuals carrying any one of three transferrin phenotypes A, AB or B. *M. giganteus* and *M. fuliginosus* are immunologically distinct and possess characteristic antigens.

GENERAL CHARACTERS. *Macropus giganteus* is a large kangaroo with soft fur, relatively uniform light to dark grey pelage which is somewhat paler ventrally and has darker vertebral shading; the fore and hind digits and distal third of the tail tend to be dark brown or black (Fig. 1). The pelage varies in length and density with locality and season. Animals from north Queensland have short coats whereas those from the southern highlands and Tasmania have longer, more dense and woolly fur. There is marked sexual dimorphism in size; males attain a larger size than females and with maturity, become more heavily developed in head, chest and forelimbs. Maximum weights recorded reach 90 kg for males and 40 kg for females.

Young kangaroos grow rapidly for about 2 years, then growth slows considerably (Poole, pers. observ.). The range of external measurements (mm) taken at regular intervals from anaesthetised captive-bred males aged 2 to 7 years and females aged 2 to 8.5 years are as follows: total length, males 1,500 to 2,000, females 1,500 to 1,800; length of head, 170 to 220 and 165 to 190; length of ear, 115 to 130 for both sexes; length of forearm (outside dimension, elbow to wrist with the bones forming the joints placed at right angles), 180 to 300 and 170 to 230; length of tibia (outside dimension, knee to sole of hindfoot with the bones forming the joints placed at right angles), 450 to 580 and 440 to 530; length of hindfoot, 310 to 347 and 300 to 320; length of tail (ventral surface from butt to tip), 750 to 1,000 and 700 to 840; weight 25

FIGURE 1. External view of *Macropus giganteus* in forest habitat, south coast New South Wales. Photograph by E. C. Slater.

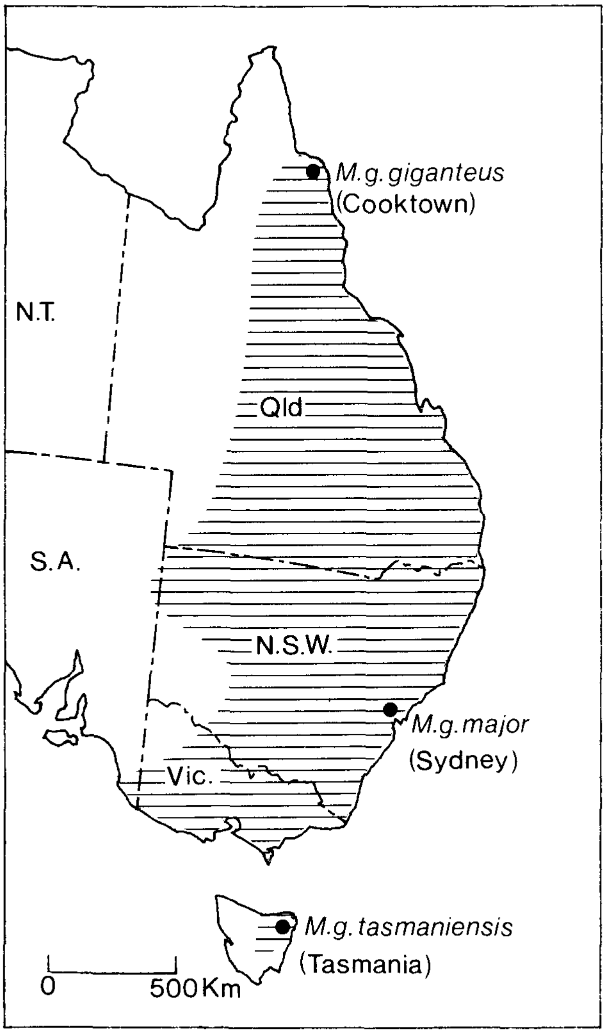

FIGURE 2. The geographic range and type locality of *Macropus giganteus*, together with the type localities of its recognized subspecies.

to 50 kg and 20 to 37 kg. Means and standard deviations (in parentheses) of age-adjusted cranial measurements (mm) from 25 male and 25 female skulls respectively, which give the best discrimination between *M. giganteus* and *M. fuliginosus* on canonical variate analysis (Poole et al., 1980) are as follows: basilar length, 153.3 (8.9), 139.3 (6.6); occipitonasal length, 163.0 (8.8), 149.2 (5.6); nasal length, 72.0 (5.2), 65.9 (2.5); nasal width, 25.6 (1.8), 22.7 (1.4); zygomatic width, 87.4 (4.3), 83.3 (2.8); width of crest (the distance at right angles to the midline of the skull, between the superior ridges of the parietals, at the most posterior points of the frontals), 10.1 (2.0), 12.9 (2.9); mandible width (taken immediately anterior to the ascending ramus), 13.8 (1.1), 12.9 (1.0); mandible depth, 20.0 (1.6), 18.1 (1.6); height of ascending ramus, 69.3 (4.0), 64.8 (3.0); M1: anterior width, 8.2 (0.3), 7.8 (0.3), posterior width, 8.4 (0.3), 8.0 (0.3), length 9.3 (0.3), 8.9 (0.4); M2: anterior width, 9.0 (0.4), 8.7 (0.3), posterior width, 9.1 (0.3), 8.7 (0.4), length, 10.7 (0.5), 10.3 (0.5). Summaries of measurements, with an evaluation of size variation, for all upper and lower cheek teeth from *M. giganteus* were given by Bartholomai (1971).

DISTRIBUTION. Eastern grey kangaroos have a wide and continuous distribution throughout the eastern states of Australia and in addition encroach on South Australia (Fig. 2). Populations also persist in the northeastern corner and central midlands of Tasmania. On the mainland, these kangaroos generally occur in zones of higher annual rainfall (>250 mm) between the inland plains and the coast. Distribution was recorded and figured for Queensland by Kirkpatrick (1967), Kirkpatrick and McDougall (1971); for New South Wales by Caughley (1975), Denny (1975), and Poole (1975*a*); for eastern Australia by Kirsch and Poole (1972) and Poole (1979); for southeast Australia by Poole (1977) and for Tasmania by Wapstra (1976). Live trapping and relocation of eastern grey kangaroos have been undertaken in Tasmania with 45 animals introduced to Maria Island in 1969–70 and 1,500 released at 18 sites in the southern half of their historic range since 1971 (Pearse, pers. comm.; Wapstra, 1976).

FOSSIL RECORD. *M. giganteus* has been recorded from Pleistocene deposits in southeast Queensland at Gore (Bartholomai, 1977), Texas (Archer, 1978), and from southwestern New South Wales, in the region of Lake Victoria (Marshall, 1973). Because *M. giganteus* has affinities with a larger, older fossil form (*Macropus titan* Owen, 1838), it was regarded as a successional species of the latter by Bartholomai (1975). He anticipated that with an improved fossil record it would be difficult to separate the two taxa. Marshall (1973) suggested that species such as *M. titan*, present in the late Pleistocene sediments, represented a 30% larger ancestral form of *M. giganteus*, which may have been subject to 'post-pleistocene dwarfing'. Because the two forms occur in the same deposits in southeast Queensland, Archer (1978) doubted this interpretation. There is debate about contemporaneity of the two forms due to the complex stratigraphic history of the Queensland deposits. Additionally, it is possible that some of the specimens regarded as *M. giganteus* may represent small individuals of *M. titan*, or they may represent the morphologically similar *M. fuliginosus*, not yet formally recorded in Queensland but present in western New South Wales (Archer, 1978).

FORM. The general color of the pelage varies in intensity from light silver grey to dark grey and may exhibit brownish overtones on back and flanks. The pelage along the mid-dorsal line is often dark, frequently giving the impression of a dorsal stripe. The fur is short or long depending on climate. It is soft and dense and in mountainous and southern regions may be thick and wooly. Below the lower thorax the hair on the mid-dorsal line lies with the tips pointing posteriorly. Anterior to the lower thorax the hair points forward, reversing direction again from level with the eyes to the tip of the nose. The hair on the nose is short and fine, there being bare skin only around the edge of the nostrils. The iris is dark brown and the eyelashes long and dark brown to black in color. Vibrissae are well developed, brown to black in color, and include mystacial, supraorbital, genal, submental, interramal, and medial antebrachial. The skin of the ears is darkly pigmented; the hair on the dorsal surface is of similar color or perhaps darker than that on the dorsal surface of the body, whereas that on the ventral surface is sparse and white. Many hairs on the head, body, and tail bear distinct pale bands; those on the face, throat, arms, belly, legs, and tail are generally pale, but those on the fingers, toes, and tail darken towards the tip.

Identification of hair from *M. giganteus* based on the characteristic appearance of cross sections and cuticular scale patterns of primary guard hairs was suggested by Lyne and McMahon (1950) and subsequently was used to discriminate species of mammals, including grey kangaroos, by Brunner and Coman (1974).

The skin lacks a reticular layer (Mykytowycz and Nay, 1964). The two species of grey kangaroos differed in histological structure of the skin, thickness of hair fibre in inverse relation to density of hair cover, density and grouping of hair follicles, and type and distribution of sweat glands. Interspecific differences in follicular patterns were also obvious on the surface of kangaroo leather (Kirsch and Poole, 1972).

Females of *M. giganteus* have four discrete mammary glands with individual teats situated on the dorsal wall of an integumentary abdominal pouch (Morgan, 1833*a*, 1833*b*). In juveniles, the anlage of each of the four teats is located in an invagination of the skin and each teat everts with the onset of sexual maturity at 14 to 18 months of age (Poole and Catling, 1974).

Marsupial milk examined to date, in contrast to eutherian milk, is characterised by high protein, fat, ash, iron, and copper content, low lactose levels, but similar quantities of vitamins (Stephens, 1975). Composition of milk from each suckled gland changed throughout the period of lactation (Thompson, pers. comm.). As a young advanced in age, fats attained a concentration of about 17%, lactose declined to about 4%, while protein remained relatively constant at 7 to 8%. Carbohydrate fractions of milk from *M. giganteus* have been separated and identified by Messer and Mossup (1977).

The osteology of representative Macropodidae, including *M. giganteus*, was described in detail and extensively illustrated by Owen (1877). Post-cranial skeletal elements of modern kangaroos are poorly represented in collections, and this has severely hindered accurate comparisons of fossil and living forms (Bartholo-

FIGURE 3. Photographs of the skull and mandible of a *Macropus giganteus* male, age 6 years. Specimen number CM 11188 in the Australian National Wildlife Collection. Photographs by E. C. Slater.

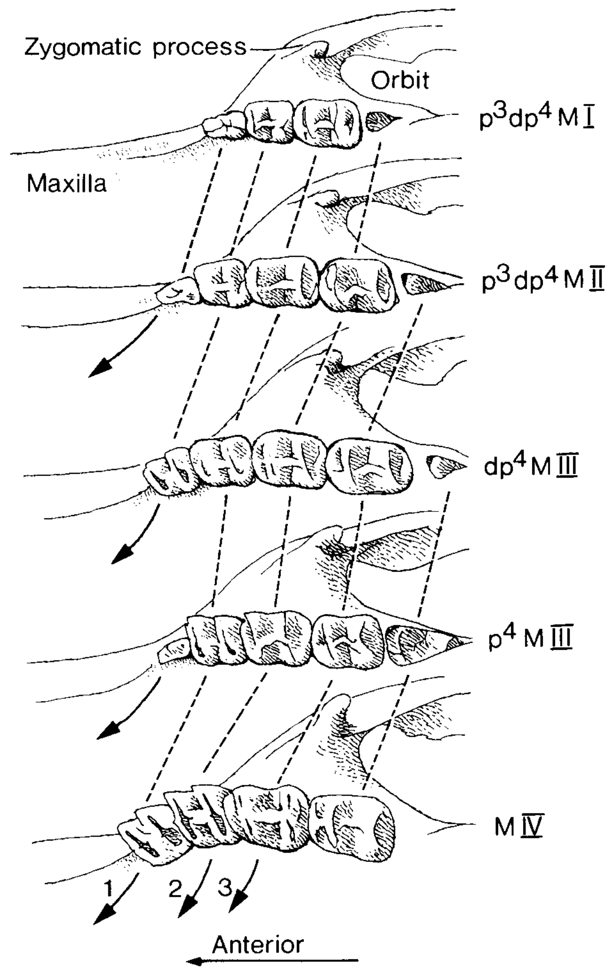

FIGURE 4. Palatal view of the left upper molar toothrow of *Macropus giganteus* indicating the sequence of eruption, progression, and shedding of the teeth with advancing age (from top to bottom).

mai, 1978). The skeleton of *M. giganteus* exhibits a number of special features in common with most other marsupials, including an incomplete inferior arch of the atlas; nineteen vertebrae in the trunk; thoracic vertebrae with well-developed transverse processes which form secondary articular surfaces for the ribs; metapophyses and anopophyses that are prominent and largest in the lumbar region; one sacral vertebra; chevron bones associated with the caudal vertebrae; a foramen in the medial epicondyle of the humerus; and a pair of epipubic bones articulating with the pubis. In neonates, there is a transient coracoid articulation with the sternum. The tympanum is covered by a backward extension of the alisphenoid, which in kangaroos forms the elongated paroccipital process. The lacrymal foramen is on the anterior margin of the orbit and the lacrymal bone extends beyond the orbit onto the face in its junction with the maxilla. The jugal extends backward beneath the squamosal roots of the zygoma, and with it forms the glenoid fossa, thereby being associated in articulation of the mandible (Fig. 3). The mandibular symphysis is cartilaginous, permitting some independent movement of the mandibles. The masseteric canal passes through the mandible behind the tooth row and is associated with a downward projection of the masseteric fossa on the outer side of the ascending ramus. The inner side of the angle of the mandible formed at the junction of the dentary and ascending ramus bears a robust angular process providing a medial inflection of the mandible. In common with other macropodids, the dentition of grey kangaroos was derived from the phalangerid pattern with a reduction in the number of front teeth, followed by a marked diastema, then robust check teeth. The dental formula is i 3/1, c o/o, p 2/2, m 4/4, total 32. The two procumbent lower incisors move laterally against the six incisors in the upper jaw (Ride, 1959). The first two cheekteeth, the sectorial P3 and the molariform dP4, are gradually replaced after about 18 months by a single sectorial premolar, P4. Four hypsodont molars follow and erupt sequentially, moving forward in the jawline with advancing age (Fig. 4). The position of the molars relative to a reference line drawn at right angles to the median line of the palate and tangentially to the anterior rims of the orbits was used to determine age in grey kangaroos by Kirkpatrick (1964, 1965*a*). The molars bear characteristic anterior and posterior ridges joining the prominent cones, and these ridges are bridged in turn by a conspicuous mid-link. Morphology of the cheekteeth was described by Bartholomai (1971) and their ontogeny was described by Kirkpatrick (1969).

The manus bears five long flexible digits each with a long, curved and pointed dark nail utilized in grooming or scratching and in defense. The manus may be used to grasp or pull shrubs within reach to facilitate browsing, or to hold items of food first picked up by the mouth. The pes is considerably modified, and its structure is common to all the Macropodidae, other than the primitive *Hypsiprymnodon*. There is no hallux, and the sydactylous second and third digits are reduced in size but retain small claws used in grooming the fur. The major toe (digit 4) bears a long, straight, sharply-pointed three-sided claw extending clear of the hairs. A similar though smaller outer toe is digit 5.

The general anatomy of the grey kangaroo was covered in an early comprehensive review of marsupial anatomy (Owen, 1841). Recent descriptions and illustrations of the pectoral and pelvic musculature have been reported by Hopwood (1974) and Hopwood and Butterfield (1976), and details of carcass composition were provided by Hopwood (1976), Hopwood et al. (1976), and Tribe and Peel (1963). The histological structure of salivary glands was described by Forbes and Tribe (1969). A high correlation was found between gland weight and total body weight minus weight of the contents of the digestive tract. The pattern of flow through the digestive system and the topographic anatomy and histology of the stomach were described by Langer et al. (1980). The structure of the female reproductive system is similar to that of other marsupials. Details of early investigations of the female urogenital system, its structure and changes occurring during the estrous cycle and pregnancy, were given by Clark and Poole (1967). Gross appearance of the external cloacal eminence of females was described and illustrated by Poole and Catling (1974). In common with other marsupials examined, oocyte and follicular diameters were larger than the corresponding structures in eutherians (Lintern-Moore et al., 1976). Blood supply to the female reproductive tract involves four major sets of paired vessels, which form substantial anastomoses on each side and across the midline (Lee and O'Shea, 1977). Equivalent testicular vessels occur in males of two species of kangaroos examined by Setchell and Waites (1969). The structure of spermatozoa from *M. giganteus* is similar to that of other members of the Macropodidae (Hughes, 1965). Pineal weights and indole content in both adult *M. rufus* and *M. giganteus* show no obvious evolutionary or functional distinction from some other vertebrate groups (Quay and Baker, 1965).

FUNCTION. Studies of blood include comparative examination of amino acid sequences in haemoglobin (Thompson and Air, 1971; Thompson et al., 1969) an evaluation of thyroxine-binding proteins in serum (Davis et al., 1969), age-related changes in the proportion of nucleated red-cell and haemoglobin types in pouch young (Richardson and Russell, 1969); biochemical properties of glucose-6-phosphate dehydrogenase of red blood cells (Richardson and Czuppon, 1970), and the distribution of isoenzyme patterns of lactic acid dehydrogenase from red blood cells, which has also been used to assist in discrimination between both species of grey kangaroos and other members of the Macropodidae (Clark, 1972; Clark and Poole, 1973; Clark and Richardson, 1968). Of 19 species of macropodids tested, all exhibited electrophoretically identical forms of supernatant malate dehydrogenase activity except the two species of grey kangaroos, confirming that the latter are phylogenetically more closely related to each other than to other macropodid species (Holmes et al., 1974).

Of detected corticosteroids in adrenal venous blood of eastern grey and red kangaroos, the major component (72 to 92%) was cortisol, the remainder being 11-deoxy and 21-deoxy cortisol, corticosterone, aldosterone, and 11β-OH and 17α-OH progesterone. Cortisol was the major corticosteroid (2.0 to 8.1 μg/100 ml) in peripheral blood plasma. The unusual secretion of 21-deoxy cortisol suggests there may be some aspects of adrenocortical biosynthesis which differ from those of eutherians (Weiss and McDonald, 1967). The levels of aldosterone in peripheral blood of kangaroos from areas high in dietary sodium are comparable to those of man and sheep, but increased levels of aldosterone, lower plasma and urinary sodium concentrations, associated with larger *zona glomerulosa* were found in most animals from areas deficient in dietary sodium. Mean levels of cortisol and corticosterone exhibited no dramatic differences between the same two areas (Coghlan and Scoggins, 1967). An examination of the effects of cortisone on nitrogen balance and glucose metabolism in diabetic and normal kangaroos was undertaken by Griffiths et al. (1969). Injection of 10 mg alloxan induced a severe hypoglycemic phase in grey kangaroos which culminated in death. Red kangaroos survived similar treatment, and ate sufficient food to achieve a positive N balance.

The physiological, morphological and behavioral adaptation of grey kangaroos to sodium deficient environments was investigated by Blair-West et al. (1968). Ribonuclease concentrations in the pancreas of the eastern grey kangaroos (530 μg/gm) and other macropodids was shown to be closest to that found in true ruminants (>1,000 μg/gm; Barnard, 1969). Total body water content of eastern grey kangaroos during non-stress conditions averaged 17.17 ± 1.07 l (78.0 ± 2.50% of body weight) with a daily water turnover value of 78.5 ± 5.75 ml/kg$^{0.8}$ (Denny and Dawson, 1975). Specific whey proteins appear in the milk of grey kangaroos during the latter half of lactation. Synthesis probably begins after a particular period of lactation and is unrelated to the occurrence of estrus, ovulation, or mating (Lemon and Poole, 1969).

Grey kangaroos have an intrinsic metabolic capacity to operate on a low protein intake as long as there is sufficient energy available from soluble carbohydrates in their food (Griffiths and Barker, 1966; Griffiths et al., 1974). When fed dry roughage ad libitum, *M. giganteus* and *M. rufus* ate slightly less per unit metabolic body weight (g/kgW$^{0.75}$) than sheep. Kangaroos digested a percentage of lucerne (alfalfa) hay similar to sheep, but digested much less of oat straw because of a poor ability to digest crude fibre. Because nitrogen intake was low on the straw diet, kangaroos retained nitrogen less well than sheep although the digestibility of crude protein was similar in each case. Kangaroos appeared to have lower energy and nitrogen requirements than sheep, but similar weight losses, on the oat straw diet, despite their much lower intake of digestible dry matter (Forbes and Tribe, 1970). Captive animals held in metabolism cages had lower intakes of dry matter, lower apparent digestibility coefficients, and lower methane production from sites of apparent high microbial growth in the gut than sheep (Kempton et al., 1976).

ONTOGENY AND REPRODUCTION. Grey kangaroos are capable of breeding throughout the year, but most breeding occurs in summer, with the young leaving the pouch the following spring, the most favorable time of the year (Kirkpatrick, 1965*b*; Poole, 1973; Poole and Pilton, 1964). Males show interest in females approaching estrus, and remain near them for some days prior to mating. Males usually sniff the female's urogenital opening and entrance to the pouch, make clucking sounds, paw the head and clutch at the tail, and attempt to mount before successful copulation occurs. Copulation frequently lasts as long as 50 minutes, incorporating a series of ejaculations during a single intromission. The large volume of semen grossly distends the female's lateral vaginal canals. Semen congealed with blood produces a characteristic urogenital sinus plug which drops out within a few minutes to several days after mating (Poole and Pilton, 1964). Gestation lasts 36.4 ± 1.6 days (Poole, 1975*b*), and prior to birth or estrous the teats become tumescent and clear fluid may be readily expressed. The female actively licks the pouch clean. At parturition, the female adopts a crouching position, with the tail behind and legs thrust forward with toes in the air and weight on the heels, bringing the urogenital opening closer to the opening of the pouch. The neonate climbs unaided over the fur and reaches the pouch within a few minutes. Shortly afterwards it attaches to a non-lactating teat (Poole, 1975*b*; Poole and Pilton, 1964). Twin young have been recorded, but usually only one young, weighing just over 800 mg, is produced (Poole, 1975*b*). Caughley and Kean (1964) found a highly significant discrepancy in favor of male pouch young, but others have not found sex ratios significantly different from parity (Kirkpatrick, 1965*b*; Poole, 1973, 1975*b*).

Neonates are naked and blind, the pinnae are pointed forward and attached to the head by a thin membrane, the forelimbs are well developed and digits bear claws; hindlimbs are small and rudimentary.

Neonates initially attach firmly to one teat from which they subsequently continue to suckle throughout pouch life and as young-at-foot until weaned (Poole, 1975*b*). If removed from the teat when older than 50 days, young reattached unaided; if dropped from the pouch, young with a minimum mean age of 233.7 ± 16.9 (SD) days were capable of standing and could gain entry to the pouch provided the mother remained stationary (Poole, 1975*b*). Young voluntarily left the pouch for the first time at a mean age of 283.9 ± 24.7 days, when they remained out of the pouch for short periods, but by the mean age of 319.2 ± 18.4 days they no longer returned to the pouch.

When females continued to suckle a young-at-foot, the mean interval from the birth of that young to the birth of the next was 373.7 ± 58.7 (SD) days (Poole, 1975*b*). Mean length of estrous cycle is 45.6 ± 9.8 days (Poole and Catling, 1974). An estrous cycle considerably longer than the length of gestation, with an associated lactation-induced absence of immediate post-partum estrous, is a reproductive pattern characteristic of grey kangaroos (Sharman et al., 1966). Loss or removal of pouch young results in a return to estrous after a mean delay of 10.9 ± 4.8 days. Under certain conditions, possibly associated with a sudden improvement in nutrition following heavy rains, females carrying pouch young have been found with a quiescent blastocyst in their uterus. An estrous and mating some 112 days after the birth of the incumbent pouch young could account for this (Clark and Poole, 1967; Kirkpatrick, 1965*b*; Poole, 1973; Poole and Catling, 1974; Poole and Pilton, 1964). Length of estrous cycles may be determined as the interval between a non-fertile mating and the next mating or may be determined as the interval between one estrous and the next as indicated by characteristic post-estrous changes in the cellular content of smears taken from the distal end of urogenital sinus (Poole and Catling, 1974; Poole and Pilton, 1964). Estrous occurs in all months of the year but least often in winter when, depending on the severity of seasonal conditions, up to 65% of females may be without pouch young and in anestrous (Poole, 1973). Those with pouch young usually exhibit a lactation-induced, anestrous condition (Poole, 1973; Poole and Catling, 1974).

Sexual maturity in males and females was attained beginning at 20 and 17 months, respectively, in southern Queensland (Kirkpatrick, 1965*b*) and by both sexes in 20 months in central New South Wales (Poole, 1973). In captive males, testis biopsies revealed changes in the tubules by month 15, the presence of some spermatozoa by 20 months, and active spermatogenesis with sperm free in the lumen by 48 months. In captive females, sexual maturation was indicated by eversion of the teats at about 18 months, with first matings beginning at 19 months (Poole and Catling, 1974).

Longevity in the field is almost certainly modified by the particular seasonal conditions pertaining through an animal's lifetime. Approximately 50% of young failed to live to independence in southern Queensland (Kirkpatrick, 1965*b*). A mortality rate of 1.82% per 28 days was estimated for sets of pouch young through the age range of 113 to 280 days in central New South Wales (Poole, 1973), and 17% mortality of young was recorded in a captive colony. Most of these losses occurred within the first few days after birth, although deaths also resulted from accidental injury and coccidiosis in the first month after leaving the pouch (Poole, 1975*b*). The greatest age of kangaroos taken in the field has been estimated as 19.9 ± 3 years (Kirkpatrick, 1965*a*). Animals kept in captivity may reach slightly older ages, as indicated by specimen number CM3283 housed in the Australian National Wildlife collection. This animal had been obtained as a pouch young and kept as a pet until its death 25 years later.

ECOLOGY. Eastern grey kangaroos are widely and continuously distributed throughout zones of higher rainfall between the inland plains and the east coast of Australia, inhabiting the semi-arid mallee scrubs, shrub woodlands, and forests. These habitats were described by Frith (1973); study sites in central New South Wales and southeastern South Australia were described by Poole (1973, 1977). Kirkpatrick (1965*c*) demonstrated that grazing in southern Queensland was confined to pasture and was essentially non-selective in the plant species consumed. In mulga-box habitat in southwestern Queensland, however, *M. giganteus* and sheep ate different plants despite depletion of the number of available species of plants during drought. Kangaroos preferred monocotyledons, which had a lower protein content than the forage selected by sheep (Griffiths and Barker, 1966). In coastal lowland in southeastern Queensland, kangaroos actively moved and grazed only in habitats with open undergrowth where the density of their fecal pellets correlated with the abundance of available food (Taylor, 1980).

Apart from humans, the effects of predators on kangaroo populations are limited. Aboriginal men with primitive weapons took kangaroos for food and hides but could not be considered significant predators. Some adults may be taken by dingoes; pouch young dropped by mothers in flight and young-at-foot are vulnerable to dingoes, foxes, and perhaps wedge-tailed eagles, *Aquila audax* (Frith and Calaby, 1969).

Because *M. giganteus* dwells in relatively stable environments of eastern forests, it is probably *K*-selected, whereas the red kangaroo, which occupies unpredictable low-rainfall areas of inland Australia, is likely r-selected (Richardson, 1975).

Although possibly capable of travelling considerable distances, long-distance movements of *M. giganteus* have not been confirmed; most frequently movements appear to be local in nature, between shelter, feeding areas, and water. Unless disturbed, animals tend to remain in the same general area, which may be considered as home range. Actual defense of a particular area appears to be limited to individual protection of favored shelter and basking sites or competition between males for estrus females.

Incidences of disease in wild and captive marsupials, including macropodids, was summarized by Arundel et al. (1977) and Barker et al. (1963). Twenty-eight species of strongyloid nematodes, two oxyuroid species, two filaroid species, and six species of anoplocephalid cestodes were subsequently reported from grey kangaroos (Beveridge and Arundel, 1979). Lumpy jaw, the most commonly reported disease of captive kangaroos, results from an infection due to *Fusobacterium necrophorum* (Samuel, 1978). The most comprehensive account of disease, health, and management of grey kangaroos is found in Hungerford (1978).

The history of the kangaroo industry, the management of harvesting, and government controls have been reviewed by Poole (1978). Immediately subsequent to European settlement in Australia, kangaroos were valued as a source of fresh meat and hides. Later they were regarded as agricultural pests, and local reductions in numbers were achieved by organized drives, shooting, and occasionally by poisoning. Initially, bounties were paid on scalps; then skins were sold for leather manufacture. Subsequently, as a means of controlling numbers of kangaroos, both hides and meat were marketed by a small industry licensed by fauna authorities for local and export trades.

Population sizes and distributions were ascertained in some states from aerial surveys (Caughley et al., 1976). A combined population of *M. giganteus* and *M. fuliginosus* (indistinguishable from the air) of 1,578,000 ± 84,000 (SE) was estimated on the plains of New South Wales between January 1975 and June 1976, a period when the legal harvest represented 3.8% of the population (Caughley et al., 1977; Sinclair, 1977). Subsequent aerial counts made in 1977 showed that grey kangaroos had increased by 13% in each of the additional 2 years, while the yearly rate of harvest had remained constant at around 3.8% of the population (Caughley et al., 1979). Others assessed population changes by monitoring changes in distribution within the species' known range and changes in the proportion of age classes and sexes within populations (Kirkpatrick, 1974; Wilson, 1975). Fecal pellets have been utilized to confirm the presence or absence of grey kangaroos and their distribution in relation to particular habitats (Caughley, 1964*a*; Grant, 1974*a*). Counts of fecal pellets also provide a means of estimating abundance of kangaroos (Hill, 1978).

Specimens of grey kangaroos are usually collected by shooting with a high velocity rifle fitted with a telescopic sight. Most are taken at night with the aid of a spotlight. Live capture may be achieved by driving animals along specially prepared fences into holding yards, or by enticing animals into yards fitted with one-way gates and built around a water source, food, or salt bait. The kangaroos are caught and restrained in sacks. Deaths may occur from spinal injury following collisions with fences, exhaustion, shock, and capture myopathy. Demountable weld-mesh panels (1.8 × 2.1 m), formed into square traps and placed against runs through fences to which a netting funnel has been attached, were successful in catching grey kangaroos. Kangaroos readily entered this trap by forcing their way through the netting funnel, which subsequently collapsed during their attempt to find an exit (Wapstra, 1976). The large ears lend themselves to most common means of ear marking and tagging, but are not suitable for tattooing because they are darkly pigmented and have hairy surfaces. A wide variety of collars carrying identifying marks or radio transmitters may be fitted.

BEHAVIOR. The understanding of social organization among grey kangaroos has been confused by the popular misconception that aggregations or mobs of these kangaroos consist largely of females controlled by adult males which fight to retain possession of their harems. Observations have not substantiated the establishment of territories or the accumulation of harems. Mobs are loose aggregations of kangaroos formed on the basis of a strong tendency for kangaroos to avoid being alone, and are maintained in a state of flux by an essentially random process of animals joining and leaving (Caughley, 1964*a*). Large mobs are formed by the coalescence of smaller family units, comprising females and their young of the previous year, and the transient association between males and an estrus female. Adult males and juveniles are irregularly distributed among mobs (Kirkpatrick, 1966).

Social organization and habitat use of nine sympatric species of macropodids, including *M. giganteus*, was investigated by Kaufmann (1974*a*). Because of their large body size they need a large area of open grazing land to support all individuals. Group coordination in detecting and reacting to danger and comparative lack of within-group aggressiveness are adaptations to their required habitat (Kaufmann, 1974*a*). Evolution of particular patterns of social behavior in relation to the ecological needs of each species of macropodid, including *M. giganteus*, was discussed further by Bell (1973), Caughley (1964*b*), and Kaufmann (1974*b*).

Major types of behavior observed in captive and free-living grey kangaroos were described by Grant (1974*b*). Studies of dominance and association revealed that the complex social organization noted for grazing eutherians was not observed in *M. giganteus*. Hierarchial organization, however, was noted among confined animals, and the potential for social organization in the wild was apparent (Grant, 1973). Individual behaviors and interactions between two groups of *M. giganteus* living adjacent to the sea shore were recorded by Herrmann (1971).

Windsor and Dagg (1971) classified the gaits of 19 species of Macropodinae and attempted to correlate these with the habitat of each species. In common with all species, *M. giganteus* exhibited slow progression while grazing, with all limbs and the tail being involved. The bipedal hop, a fast gait, was used at other times. The proportion of time per stride when the foot remained on the ground was greater for *M. giganteus* than with species of large kangaroos whose favored habitat is rocks or dense scrub. The time was less than that of the plains dwelling *M. rufus*, however.

Clucking sounds are used to communicate between mother and young, and between females in estrus and males. A loud cough is used by both sexes when alarmed, and by aggressive males. A loud growl emitted by an aggressive male, was noted by Eisenberg et al. (1975), who claimed that the larger macropedids produced vocal sounds remarkably similar to those of other marsupials.

GENETICS. The diploid chromosome number for *M. giganteus* is 16 (McIntosh and Sharman, 1953; Sharman, 1961). The sex chromosome system in both populations is XX/XY. Inherited electrophoretic variation in the enzyme phosphoglycerate kinase A (PGK-A) from erythrocyte samples was demonstrated in *M. giganteus* and other species of kangaroos. These results suggested that PGK-A is X-linked in grey kangaroos, the paternally derived X chromosome being inactive in the nucleated erythroblast precursors of the erythrocytes of females (Cooper et al., 1971). Pedigree analysis of PGK-A allozymes for *M. giganteus* and *M. fuliginosus* confirmed this hypothesis. The discovery of different allozyme variants in eastern and western grey kangaroos further supports the conclusion that they represent different species (Vandeberg et al., 1977). The predominant PGK in mammalian sperm is a second form of phosphoglycerate kinase, PGK-B. Unlike many mammals, some kangaroos express low PGK-B activity in somatic tissues in addition to having high activity in testes. *M. giganteus* exhibited polymorphism of PGK-B and family data supported the hypothesis of autosomal co-dominant inheritance in kangaroos (Vandeberg et al., 1980).

Reactions of marsupial (including grey kangaroo) and monotrematal proteins with monospecific rabbit antisera to 30 different human plasma proteins indicate that these non-eutherians have less in common with man than any of the other eutherian species examined (Bauer, 1971).

REMARKS. Eastern grey kangaroos are also known as great grey or Forester kangaroos.

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Principal editors of this account were DANIEL F. WILLIAMS and SYDNEY ANDERSON. Managing editor was TIMOTHY E. LAWLOR.

W. E. POOLE, DIVISION OF WILDLIFE RESEARCH, CSIRO, P.O. BOX 84, LYNEHAM 2602, AUSTRALIA.