

Relicts, reproduction and reintroductions—a century of marsupial research in Western Australia

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Marsupials, the quintessential Australian animals, have attracted considerable interest from the scientific community, both at home and abroad. Nowhere is this more evident than in Western Australia. The following review provides an overview of the history of marsupial research in Western Australia, outlining major contributors and findings along the way. Most research can be grouped within one or more of three major study streams; taxonomy and natural history ('relicts'); reproductive biology and physiology ('reproduction') and conservation ecology ('reintroductions'). Four Australidelphian marsupial orders are represented among the Western Australian fauna: Dasyuromorphia, Peramelemorphia, Diprotodontia and Notoryctemorphia. Many of these species are endemic to Western Australia, some of which represent isolated relicts of ancient phylogenetic lines. Contemporary threatening processes, including habitat change or loss, changes in fire regime and introduced predators, have led to 'modern' relicts, many of which exist in very small, disjointed remnants of their former geographical range. The experimental study of Australian marsupials was pioneered by H 'Harry' Waring, who saw the potential for the application of classical physiological techniques to the unstudied marsupial fauna. The establishment of the field research station at Rottneest Island led to an array of studies of the ecology and physiology of the quokka (*Setonix brachyurus*) from the 1950s to the early 1970s. These became a platform for our understanding of marsupial reproductive biology. More recently, research on the ecophysiology, genetics and immunology of Western Australian marsupials has been strongly tied to conservation. A major management tool has been to use these studies to guide threatened species translocations and similar conservation attempts.

KEYWORDS: conservation, diversity, Marsupialia, reproductive biology, Western Australia.

INTRODUCTION

Marsupials are recognised throughout the world as the quintessential Australian animals (along with dangerous spiders and venomous snakes). The term marsupial is derived from the Latin 'marsupium', meaning pouch, and is used to encompass a group of mammals (the subclass Marsupialia; formerly Metatheria) that was seen, historically, to have a reproductive system and strategy that was 'intermediate' between the egg-laying Prototheria (monotremes) and the placenta-bearing Eutheria (eutherian or 'placental' mammals). The Gondwanan distribution of extant marsupials was also believed to be reflective of this group having been out-competed on the other continents by eutherian mammals. Thus, since their earliest encounters with Europeans, marsupials were regarded as the 'poor cousins' of the evolutionarily 'superior' eutherian mammals. Research in Western Australia during the last century has, however, helped to dramatically change this view. Marsupialia is now recognised as the evolutionary sister group to the Eutheria. That research has also provided some fascinating insight into the ecology and evolution of the 'pouched mammals'.

RELICTS

While the 'flying' kangaroo and koala 'bears' are easily recognised, the diversity of marsupial fauna is less

widely known. Among the marsupials of Australia and New Guinea (the Australidelphian radiation of marsupials) there are four recognised groups: carnivorous marsupials (Order: Dasyuromorphia); omnivorous bandicoots and bilbies (Peramelemorphia); principally herbivorous possums, wombats, koalas, kangaroos and their kin (Diprotodontia); and fossorial marsupial moles (Notoryctemorphia). All four Australidelphian marsupial orders are represented among the Western Australian fauna (Appendix 1). In his presidential address of 1948 to the Royal Society of Western Australia, Glauert (1950) presented a historical account of the early descriptions and development of knowledge of the marsupials of Western Australia. There are numerous species endemic to Western Australia, some of which represent isolated relicts of ancient phylogenetic lines as a consequence of divergent evolution (e.g. bilbies *Macrotis lagotis* and numbats *Myrmecobius fasciatus*: Archer & Kirsch 1977) and others following past extinction events (i.e. megafaunal extinctions in which 90% of Australia's large mammals went extinct during the Pleistocene: Merrilees 1968; Prideaux *et al.* 2007b).

The last century has also seen a massive decline in the number, diversity and distribution of marsupials in Australia, nowhere more so than in the west. These contemporary threatening processes have led to 'modern' relicts, many of which exist in very small, disjointed remnants of their former geographical range. Numerous studies have highlighted the key threatening processes in this decline, including diversion/reduction in

resources, vegetation changes in response to exotic herbivores and dieback disease, changes in fire regime, and introduced predators (e.g. foxes and cats) (Archer 1974; Jenkins 1974; Calver & Dell 1999; Fletcher & Morris 2003; Friend & Wayne 2003; de Tores *et al.* 2007). Burbidge & McKenzie (1989) coined the term ‘critical weight range’ (CWR) to define the marsupial species most susceptible to these threats: medium-sized (35–5500 g), terrestrial animals of the semiarid and arid zones (Johnson & Isaac 2009). Yet, at a time when the extinction of more marsupial species is a real possibility, we are still discovering the true diversity and evolutionary history of Western Australian marsupials.

Dasyuromorphia comprises three families: Dasyuridae (dasyurids), the monotypic Myrmecobiidae (numbat), and Thylacinidae (thylacine). Western Australia is home to a large diversity of small to very small, arid adapted dasyurids, especially dunnarts (*Sminthopsis* spp.; Figure 1a) which typically range in body mass between 10 and 40 g, but also *Pseudantechinus* spp. (15–50 g), the kaluta (*Dasykaluta rosamondae*; 25–40 g), *Ningauai* spp. (6.5–10.5 g; Figure 1b) and *Planigale* spp. (4–10 g). In contrast, mesic genera such as *Antechinus* and the larger bodied *Dasyurus* are represented by only a few species in Western Australia (e.g. the mardo, *Antechinus flavipes*; and northern and western quolls, *Dasyurus hallucatus* and *D.*



Figure 1 Representative marsupials of Western Australia. (a) White-tailed dunnart, *Sminthopsis granulipes*. (b) Wongai ningauai, *Ningauai ridei*. (c) Honey possum, *Tarsipes rostratus*. (d) Spectacled hare-wallaby, *Lagorchestes conspicillatus*. (e) Golden bandicoot, *Isoodon auratus barrowensis*. (f) Northern marsupial mole, *Notoryctes caurinus*. (a–e) courtesy of W Bancroft; (f) courtesy of I Harris.

geoffroi). Endemic CWR species in the mid-west and southwest such as the dibbler (*Parantechinus apicalis*), red-tailed phascogale (*Phascogale calura*) and the numbat have suffered enormously from habitat fragmentation and predation by introduced foxes and cats; and are now restricted to tiny pockets of their original distribution (Woolley 1977, 1980; Morcombe 1967; Burbidge & McKenzie 1989). The numbat is unusual among marsupials in being diurnal and feeding exclusively on termites. It has long been recognised as distinct from other dasyurids on the basis of dental morphology, and basicranial skull structure suggested that Myrmecobiidae was an early divergence from the dasyuroid line (Archer & Kirsch 1977). The now extinct thylacine, however, represented the youngest form of a previously much more diverse family (Murray & Megirian, 2000), distinct from other marsupial carnivores (Archer 1976).

Bandicoots (family Peramelidae) are medium-sized, terrestrial, omnivorous marsupials with a bounding gait and forelimbs adapted for digging for food (Gordon & Hulbert 1989). Approximately 20 species of bandicoots are known from Australia and New Guinea, eight of which have distributions (at least historically) that include Western Australia. While Western Australian populations of tropical northern brown bandicoot (*Isodon macrourus*) and mesic southern brown bandicoots (*Isodon obesulus*) are stable (IUCN 2012), only small remnant populations remain of western barred bandicoots (*Perameles bougainville*, on the islands of Shark Bay) and golden bandicoot (*I. auratus barrowensis*, in the Kimberley and islands off the northwest coast: Figure 1e). Bilbies (*Macrotis lagotis*; Thylacomyidae), arid-adapted allies of the bandicoots, persist in scattered colonies in the Pilbara and Kimberley (Troughton 1932; Jenkins 1974; Friend *et al.* 2008b), while the lesser bilby (*M. leucura*) and pig-footed bandicoot (*Chaeropus ecaudatus*; Chaeropodidae) have become extinct during the twentieth century (Burbidge *et al.* 2008a, c). While bilbies have had significant publicity, most bandicoots are unremarkable in appearance; and though the southern brown bandicoot is often encountered in gardens in the southwest, little recognition is given to how interesting these marsupials are. The bandicoot skeleton has an unusual combination of a plesiomorphic polyprotodont dentition with derived syndactylous hindlimbs, in which the second and third digits of the foot are relatively reduced in size and bound together developmentally. Bandicoots also have an ossified patella, uncommon among marsupials, and lack a clavicle within the pectoral girdle. The syndactylous pes was historically thought to reflect a close evolutionary relationship with diprotodonts; however, craniodental morphology (Archer 1976) and molecular studies (Springer *et al.* 1998) refuted this view, and suggested a much more ancient origin for the bandicoot group. The reproductive strategy of bandicoots has been of great interest. Bandicoots have among the shortest gestation of any mammals, as short as 12.5 days, and may produce a litter every 60 days in favourable conditions. This great efficiency in reproduction is accomplished by the development of a relatively (among marsupials) complex allantoic placenta and production of very rich milk (Tyndale-Biscoe 2005).

Diprotodonts are principally arboreal herbivores and

consequently are less diverse in Western Australia than in the more heavily forested areas of eastern Australia. The handful of Western Australian species include the scaly-tailed possum (*Wyulda squamicaudata*) endemic to rocky outcrops of the Kimberley region (Alexander 1918; Calaby 1957; Runcie 1999); the ubiquitous brush tail possum (*Trichosurus vulpecula*), the western ringtail possum (*Pseudocheirus occidentalis*) found in localised forest patches of the coastal South West (especially peppermint trees threatened by coastal development) (Wright *et al.* 2007; Thompson & Thompson 2009), the tropical rock ringtail possum (*Petroseudes dahli*) and the western pygmy possum (*Cercartetus concinnus*) of southern Australia. The most intensively studied is the honey possum, *Tarsipes rostratus* (monotypic Family Tarsipedidae: Figure 1c), which feeds exclusively on nectar and pollen (Glauert 1929; Vose 1973; Wiens *et al.* 1980) and displays a suite of adaptations to this unusual diet (Parker 1890; Richardson *et al.* 1986; Slaven & Richardson 1988; Bradshaw & Bradshaw 2012). The honey possum was used to demonstrate the potential for trichromatic vision in marsupials and has adaptations of the visual system for the detection of mature *Banksia attenuata* flowers, their favoured food source (Arrese *et al.* 2002; Sumner *et al.* 2005; Cowing *et al.* 2008). This tiny marsupial (males 7–9 g; females 10–12 g) also has the distinction of having both the largest testes relative to body mass (4.2%) and the longest sperm among mammals (up to 360 μm) (Wooller *et al.* 1981; Renfree *et al.* 1984).

Kangaroos and related taxa (superfamily Macropodoidea) represent the largest terrestrial radiation of the Diprotodontia. Macropodoids of medium to large body size (>10 kg) especially those of the genus *Macropus* are relatively common and often have broad distributions (IUCN 2012): western grey kangaroo (*M. fuliginosus*) and western brush wallaby (*M. irma*) in the south; red kangaroo (*M. rufus*) and euro (*M. robustus*) through the semiarid and arid country; and the agile wallaby (*M. agilis*), antilopine wallaroo (*M. antilopinus*) and northern nailtail wallaby (*Onychogalea unguifera*) in the tropical north. A divergent array of rock-wallaby species is also found in Western Australia including the monjon (*Petrogale burbidgei*), the smallest of the rock-wallabies (Kitchener & Sanson 1978), and the narbarlek (*P. concinna*), which, uniquely among marsupials, has the potential to develop unlimited numbers of supernumerary molar teeth (Sanson *et al.* 1985). W D L Ride, Director of the Western Australian Museum (1957–1975) contributed significantly to our understanding of the evolution of macropodoids (Ride 1957, 1959, 1961, 1962, 1971a, b, 1979; Ride & Serventy 1963).

Small- to medium-sized macropodoids have suffered heavily through loss of habitat and predation or competition by ferals and domestics. Those that have managed to persist are found in small remnants of their former distribution. The burrowing bettong (*Bettongia lesueur*) and rufous hare-wallaby (*Lagorchestes hirsutus*) are now restricted to populations on Barrow Island and the islands of Shark Bay, and the spectacled hare-wallaby (*L. conspicillatus*: Figure 1d) is reduced in range, while Gilbert's potoroo (*Potorous gilbertii*) on the south coast is among the most critically endangered of all mammals (Sinclair *et al.* 2002). The tammar wallaby (*M. eugenii*)

and quokka remain in isolated mainland and island populations in the south west (Main 1961; Eldridge *et al.* 2004; de Tores *et al.* 2007) and explanations as to recent crashes of the formerly recovered populations of the woylie (*Bettongia penicillata*) have proven elusive (Groom 2010; Pacioni *et al.* 2011; Rong *et al.* 2012). The banded hare-wallaby (*Lagostrophus fasciatus*), extinct on the mainland and found only on Bernier and Dorre Islands in Shark Bay, provides an interesting case study on the evolution of macropodoid marsupials. It has many unusual features of craniodental (Flannery 1983; Prideaux 2004), musculoskeletal (Warburton 2009) and reproductive anatomy (Tyndale-Biscoe 1965) which have made it difficult to place within the kangaroo family tree (Flannery 1983; Westerman *et al.* 2002; Nilsson 2006). Previously hypothesised as the sole survivor of the otherwise extinct group of giant, short-faced sthenurine kangaroos, it has most recently been proposed to be the living relic of a more ancient phylogenetic line, subfamily Lagostrophinae (Prideaux & Warburton 2010).

Marsupial moles are highly specialised burrowing marsupials adapted to life underground. These small marsupials (30–70 g) lack eyes and external ears and possess short, stout limbs that are highly modified for digging. Two species are recognised: the central marsupial mole (*Notoryctes typhlops*) and the northern marsupial mole (*N. caurinus*; Figure 1f), the latter endemic to the Pilbara region of Western Australia (Thomas 1920; Corbett 1975; Benshemesh & Johnson 2003). Relatively little is known about these cryptic marsupials, and apart from morphological (Warburton 2006) and physiological (Withers *et al.* 2000) work based on opportunistic specimen finds, few recent studies have been undertaken.

In addition to the extant species, there is a rich, albeit relatively recent, fossil history of marsupials in Western Australia that has attracted the interest of a number of researchers including Royal Society Western Australia past presidents L Glauert (1933–1934, 1947–1949), W D L Ride (1962–1963) and D Merrilees (1966–1967). Principally late Pleistocene in age (126–12 ka) the caves of the Margaret River region (Mammoth Cave, Devil's Lair, Kudjal Yolgah Cave and Tight Entrance Cave) have yielded fossils of a number of extinct marsupials including the marsupial 'lion' (*Thylacoleo carnifex*), wombats, the large diprotodontid *Zygomaturus*, and giant sthenurine (short-faced) kangaroos (Glauert 1910, 1912, 1914, 1921, 1926, 1948; Merrilees 1965, 1967, 1970a, b; Archer & Baynes 1972). Additionally these caves have yielded evidence of the interaction of Aboriginal people with some of these animals (Archer *et al.* 1980). Caves in the Nullarbor region range from early Pleistocene (2.6 Ma–781 ka) to Holocene (<12 ka) and have provided unprecedented opportunities to study the diversity and ecology of extinct species due to the exquisite preservation of semi-articulated specimens (Lundelius 1963; Lowry & Lowry 1967; Lowry & Merrilees 1969; Lundelius & Turnbull 1973, 1981; Prideaux *et al.* 2007a). Among these deposits are a large diversity of marsupials, including many species of kangaroos including tree-kangaroos (Prideaux *et al.* 2007a; Prideaux & Warburton 2008, 2009). The fossil deposits in Western Australia have been key to current understanding of the timing of Pleistocene extinctions of the Australian megafauna and

the factors (interactions of climate/hunting/fire) leading to the drastic changes in biodiversity during this period (Merrilees 1968; Roberts *et al.* 2001; Prideaux *et al.* 2007b; Prideaux *et al.* 2009).

ECOLOGY, PHYSIOLOGY AND REPRODUCTION

Ecology and general physiology

The experimental study of Australian marsupials was pioneered by H 'Harry' Waring, Professor of Zoology at the University of Western Australia 1948–1975, who saw the potential for the application of classical physiological techniques to the unstudied marsupial fauna (Waring 1959). Waring sought and achieved the establishment of a field research station on Rottnest Island (off the Perth coast) and, together with graduate students and colleagues, produced significant early advances in marsupial physiology using the quokka as a model. These studies fell into two main areas, physiological ecology and reproductive physiology, and paved the way for the current understanding of marsupial biology and reproduction.

Ecological studies examined aspects of breeding and growth of pouch young (Shield & Woolley 1963; Shield 1964, 1968), population studies (Dunnet 1962, 1963; Shield & Woolley 1963), and habitat use (Storr 1964; Nicholls 1971; Kitchener 1972, 1973). An experimental approach was taken up to investigate aspects of marsupial physiology, including digestive physiology (Moir *et al.* 1954; Waring *et al.* 1966), thermoregulation (Bartholomew 1956; Kinnear & Shield 1975), and osmoregulation (Bentley 1955; Barker & Barker 1959; Bentley & Shield 1962; Bakker & Main 1980). These studies on the quokka became a platform for our understanding of marsupial physiology. Conscious of a single-species approach, however, Main (1983) examined the extent to which studies on the quokka could be extrapolated to marsupials more generally. His review drew together the quokka research with studies of other macropods, to assimilate aspects of ecophysiology of macropods, as well as to broader theoretical principles. Many of the results and interpretations from the study of the quokka were shown to be more widely testable and applicable for macropod marsupials. Studies of marsupial ecophysiology, or how an animal 'works' in its environment, have become an important tool in the conservation and management of threatened species.

The highly specialised diet and/or behaviour of some marsupials in relation to their diet have been of particular interest for physiological studies, and Western Australia has provided numerous oddities in this regard. For example, tammars on the Abrolhos Islands are able to drink seawater and maintain body weight while eating poor-quality dry graze (Kinnear *et al.* 1968). Tammars survive this extreme water and nutrient deficit by a combination of marsupial characteristics and physiological adaptations. All marsupials have a relatively low basal metabolic rate (BMR) and a depressed nitrogen metabolism in comparison to eutherian mammals, resulting in a relatively lower requirement for these nutrients generally (Fraser & Kinnear 1969). But tammars are also able to recycle urea

nitrogen throughout the dry season, by cyclic exchange of nitrogen between their body tissues and the microbial community within the pregastric (forestomach) portion of the digestive system, further reducing their nitrogen requirements (Kinnear & Main 1975). In order to cope with the salt loading resulting from drinking saltwater, tamar kidneys have been shown to concentrate urinary electrolytes to a greater degree than highly specialised eutherian mammals (Kinnear *et al.* 1968).

The physiological variables most commonly used to make inferences about the relationship of an animal to its environment are body temperature and metabolic rate (a measure of the total energy used by an animal per unit time). This has been a dominant theme of Western Australian research over many decades (Kinnear & Shield 1975; Withers *et al.* 2000, 2006). As a general rule, marsupials have a lower body temperature and metabolic rate than eutherian mammals of equivalent size (Hume 1999) which, as with the marsupial reproductive strategy, has been hypothesised to be a result of the relatively low productivity of the Australian environment (Tyndale-Biscoe 2001). One particular physiological characteristic of a number of marsupials is an ability to enter shallow, daily torpor to reduce energy use when food resources are scarce or during adverse environmental conditions. Torpor is indicated physiologically by a significant drop in BMR and body temperature. A number of Western Australian marsupials enter torpor in order to conserve energy, including the honey possum (Withers *et al.* 1990), numbats (Cooper & Withers 2004) and many dasyurids (Geiser 1994). Cooper & Geiser (2008) reviewed the relationship between body mass, BMR and thermoregulation and demonstrated that shallow, short-term (daily) torpor is an adaptive physiological mechanism, rather than an inability to maintain body temperature. Investigations of neural control of the heart in the fat-tailed dunnart (Zosky & O'Shea 2003) and western pygmy possum (Zosky & Larcombe 2003) found that torpor is regulated by a physiological decrease in heart rate, under the control of the autonomic nervous system. This mechanism is homogeneous with that found in deep ('true') hibernators, such as bats, suggesting a greater overall similarity between shallow torpor and deep hibernation than was previously recognised.

Two other fields of marsupial physiology have seen significant advancement in Western Australia: immunology (the physiological functioning of the immune system) and endocrinology (the study of hormones, their functions and the glands or tissues that secrete them). Again, the quokka was the subject for much of the early work (Bradshaw 1983a; Stanley 1983). The development of the immune system was of considerable interest, given the altricial nature of marsupials at birth. Two immunological mechanisms were found to help protect marsupial neonates in their relatively underdeveloped state. Initially there is a passive transfer of maternal antibodies to the pouch young through the milk (Yadav 1971). However, the digestive tract is only able to absorb antibodies during pouch life and only a proportion of antibodies are able to be transferred in this way. Secondly, there is a relatively rapid maturation of immune competence, as evidenced in particular by the early presence of immune cells such as lymphocytes, and a rapid development and

functionality of the thymus gland (Stanley *et al.* 1972; Yadav *et al.* 1972; Ashman *et al.* 1975).

Reproduction

Marsupials are distinguished from eutherian ('placental') mammals primarily on the basis of reproductive biology. Marsupial neonates (newborns) are highly altricial at birth; that is they are born in an undeveloped state and, thus, require extensive parental care. Most of the development of the young takes place in the pouch, where the joey is provided with milk by the mother for an extended period of time. All marsupials have fully functioning placentae; they are merely short-lived when compared to those of eutherians (Hill 1900; Flynn 1923; McCrady 1938; Enders & Enders 1969). Eutherian mammals, in comparison, tend to give birth to well-developed (precocial) young, though the range in development is significant if one compares a newborn mouse with a newborn calf, which can walk within hours. Reproductive anatomy also differs between marsupials and eutherian mammals. The female reproductive tract of marsupials has two lateral vaginae which each pass to a separate oviduct (uterine tube), rather than two oviducts converging to one uterus, as in most eutherians. The lateral vaginae function as passages for sperm, while an additional median- or pseudo-vagina forms for the passage of young; in most groups the median vagina must be re-formed each breeding season, though in macropods it remains open post-partum (Tyndale-Biscoe 2005). In male marsupials, the testes and scrotum lie anterior to (in front of) the penis, rather than posterior (behind) as in eutherian mammals. The development of other sexual characteristics, such as mammary tissue, nipples and pouch in marsupials has a different genetic signal to that of eutherian mammals, attributed to a different configuration of the sex chromosomes in marsupials; male marsupials do not possess nipples or a pouch (Tyndale-Biscoe 2005). Other differences in anatomy and physiology are apparent throughout the body of marsupials, although those of the reproductive system are perhaps the most obvious.

While gestation in marsupials is short, the lactation period is long in comparison to eutherian mammals of equivalent size (Tyndale-Biscoe 2001). This has been interpreted as a strategy to cope with the relatively low productivity or unpredictable availability of resources within the Australian environment, where the total resource requirements for growth are spread over the extended period of lactation (Tyndale-Biscoe 2001). Other aspects of marsupial reproductive biology have similarly been linked to resource availability. Some marsupials demonstrate embryonic diapause, first described by Sharman (1955b) in the quokka, in which the implantation and development of the embryo is suspended until such time as the mother is capable of supporting the developing embryo. While not unique to marsupials, this adaptive strategy is found in a number of Western Australian species including the honey possum and many macropods (Sadleir & Tyndale-Biscoe 1977; Renfree 1980; Tyndale-Biscoe & Hinds 1981). A more extreme strategy linked to resource availability is male die-off (semelparity; breeding only once in a lifetime), whereby adult males die after breeding; this strategy has the potential to increase juvenile

survivorship by reducing competition for food. Male die-off has been observed in many Western Australian dasyurids, the largest being the northern quoll (Woolley 1991, 2008e; Crowther 2008; Oakwood 2008; Soderquist & Rhind 2008). In many species this die-off is obligate (i.e. all breeding males die, regardless of resource availability) as a physiological-stress-related response to breeding (Woolley 2008c), while in dibblers and northern quolls it appears to be facultative, and dependent on resource supply (Mills & Bencini 2000; Bradley 2003).

Endocrinology became a key tool for the developing understanding of marsupial biology, particularly with regard to the reproductive cycle of marsupials and the hormonal control of pregnancy (Tyndale-Biscoe *et al.* 1974; Tyndale-Biscoe 1978; Cake *et al.* 1980; Tyndale-Biscoe & Hinds 1981). The early studies of the reproductive biology of quokkas (Sharman 1955a, b; Waring *et al.* 1955) led to Western Australia becoming a centre for the study of reproductive endocrinology. The drive to measure hormonal changes during reproduction in marsupials came from Sharman's (1970) claim that marsupials, unlike eutherians, did not show 'maternal recognition of pregnancy', in other words, that the presence of the embryo in the uterus did not bring about any changes in the physiology of the mother. Because gestation is always contained within a single oestrous cycle in marsupials, and thus pregnancy does not inhibit ovulation, the assumption was made that the hormonal changes throughout an oestrous cycle were all that were needed to sustain a pregnancy. This catalysed the development of a specific radioimmunoassay for the hormone progesterone, one of key hormones responsible for the regulation of the female reproductive cycle and pregnancy, to monitor changes throughout both pregnant and non-pregnant cycles. The publication in 1980 of a paper showing the presence of a small but significant spike in progesterone early in the pregnant cycle of the quokka (Cake *et al.* 1980) unleashed a torrent of criticism from others in the field and led to the initiation of a series of studies in the tammar wallaby (Hinds & Tyndale-Biscoe 1982), and other species of macropods, all of which showed the presence of a similar spike in the pregnant cycle. Hugh Tyndale-Biscoe later described this as one of the most important discoveries in marsupial reproductive physiology of the last few decades (Tyndale-Biscoe 1997).

During the reproductive cycle, progesterone is produced in the ovaries (by the corpus luteum; the remains of the follicle after ovulation) and has a number of roles including preparing the endometrium (the lining of the uterus), and helping to support the implantation of the foetus. The role of the foetus in the process of birth had earlier been indicated by cross-breeding experiments with grey-kangaroos (Poole 1973) and from the shortening of the life-span of the corpus luteum by the foetus in the tammar (Merchant 1979). With the demonstration in both the quokka and the tammar that the placenta is an endocrine organ and capable of secreting progesterone (Heller 1973; Bradshaw *et al.* 1978; Heap *et al.* 1980), the marsupial foeto-placental unit was suspected of being more than just a passive occupant of the oestrous cycle. It required the advent of improvement in hormone assays to elaborate the nature of the foeto-placental effect on the mother and the development of

receptor assays for progesterone in uterine tissue (Owen *et al.* 1982). Importantly, the marsupial foetal adrenal gland was shown to secrete cortisol just prior to birth (Sorokin 1981), and to initiate parturition in the marsupial (Shaw *et al.* 1996) as is the case in eutherian mammals, in which cortisol is the trigger for the cascade of hormonal events leading to birth. Progesterone profiles throughout pregnancy in the quokka and the tammar also revealed that the foeto-placental unit shortened the life span of the corpus luteum. This was indeed a startling discovery; it is in direct contrast to gestation in most eutheria, in which the foeto-placental unit significantly prolongs the life-span of the corpus luteum (Bradshaw & Bradshaw 2011).

During pregnancy, the placenta also produces progesterone, and the amount of progesterone within the system has an effect of the rate of embryonic development, and the initiation of parturition (birth) and lactation (Bradshaw & Bradshaw 2011). Bradshaw & Bradshaw (2011) reviewed the role of progesterone in marsupials, in comparison with eutherian mammals. In contrast to historical views, these authors highlighted the fact that all of the basic physiological mechanisms of progesterone observed in the extended gestation of eutherian mammals are also measurable in the relatively short gestation of marsupials. Further, measurable effects of progesterone (prior to formation of the corpus luteum) on the induction of sexual behaviour, female receptivity and ovulation in marsupials were noted.

Endocrinology has also provided insight into the control mechanisms of other aspects of marsupial reproductive biology including embryonic diapause. Diapause in macropods is associated with low levels of circulating progesterone and an undeveloped corpus luteum (Tyndale-Biscoe & Hinds 1981). While seasonal photoperiod provides the ultimate control for obligate diapause (embryos fertilised in late autumn remain in a state of diapause until after the summer solstice (Renfree & Shaw 2000)), facultative diapause is more flexible. In many species, females mate soon after giving birth and the resulting newly fertilised embryo will remain in a state of diapause while there is a young in the pouch. If the pouch young does not survive, for whatever reason, the absence of suckling triggers activation of the corpus luteum and reactivation of the embryo (Tyndale-Biscoe 1978). Embryonic diapause in honey possums, similarly, has hormonal controls that respond to lactational cues and photoperiod, as well as exhibiting their own entrained rhythm (Oates *et al.* 2007). To study hormone levels in such tiny, and fragile animals, new methods for examining the hormones present in faeces have been established (Bradshaw *et al.* 2004; Oates *et al.* 2004). Such studies have provided significant advances detailing the reproductive physiology of the honey possum (Oates *et al.* 2007) as well as providing important data for conservation programs including captive breeding programs (Stead-Richardson *et al.* 2010) and translocation attempts (Mills *et al.* 2012).

REINTRODUCTION

By the middle of the twentieth century it was recognised that iconic Western Australian species such as the numbat were threatened and that conservation efforts

were needed (Fleay 1952; Calaby 1960; Serventy 1962). As noted in preceding sections, the threatening processes are many and varied, and include habitat loss, feral cats, foxes, cane toads, agriculture, fire regimes, logging and climate change. Attempts to conserve species may involve the mitigation or minimisation threats, but where populations are extremely vulnerable this may not be enough. A major management tool has been translocation (movement by humans) of individuals of threatened species to areas from where they were once known but no longer occur (reintroduction) or to areas outside this range but that are considered suitable and secure habitats, for example offshore islands (introduction). It is important to note that, for many species, reliable estimates of population size are not available, and a recently published study on the decline in woylie numbers, by Wayne *et al.* (2013), highlights the conservation and management implications of 'getting the numbers right'.

The success of a number of translocation attempts of endangered macropodoids was reviewed by Short *et al.* (1992), including quokka and tammar wallaby to Jandakot between 1971 and 1988, banded hare-wallaby to Dirk Hartog Island in 1974 and woylie to Perup (1977), Collie and Nannup (1982–1983). The majority of these reintroductions was unsuccessful. Mainland populations were under most threat from foxes and cats, though habitat degradation and infection may also have been contributing factors (Short *et al.* 1992). Reintroductions on islands were significantly more successful than attempts on the mainland. Banded hare-wallabies, however, did not manage to establish a viable population on Dirk Hartog Island. Though Dirk Hartog Island was fox free, it was a pastoral station carrying sheep, with degraded habitat, and large numbers of feral goats and cats (Short *et al.* 1992). Other documented reintroductions have included burrowing bettong, rufous hare-wallaby, banded hare wallaby and western barred bandicoot as part of the 'Return to Dryandra Project' (Anon. 2012), rufous hare-wallaby and banded hare wallaby to Peron Peninsula (2001) (Hardman & Moro 2006) and numbats into the Arid Recovery Reserve, Roxby Downs, South Australia in 2005 (Bester & Rusten 2009). Often, however, the results of these reintroductions are difficult to monitor, and detailed studies of survivorship over the long-term are not always possible due to lack of funding.

A high profile case study of a successful translocation attempt is that of the critically endangered Gilbert's potoroo, the most endangered mammal in Australia. Gilbert's potoroo was rediscovered in 1994 at Two Peoples Bay reserve near Albany, having been considered extinct for over one hundred years. Fewer than 50 individuals remained and a management programme was established in order to conserve the population by habitat preservation, predator control and captive breeding (Courtenay & Friend 2004). Genetic studies of the population indicated a substantial genetic bottleneck consistent with significant population decline (Sinclair *et al.* 2002). Captive-breeding attempts have been unsuccessful and faecal hormonal measurements demonstrated a lack of reproductive hormonal activity in captive females (Stead-Richardson *et al.* 2010). In order to protect the extant population from stochastic events such as fire, and with no sites within the species' former

mainland range deemed suitable, 10 animals from the wild population were introduced to Bald Island, a predator-free island off Cheynes Beach, in 2005–2007 (Anon. 2010). The introduction has been successful and a breeding population has established on the island. Following the success at Bald Island, Gilbert's potoroos have been subsequently reintroduced to a mainland site at Waychinicup National Park near Mt Manypeaks (Anon. 2011).

Where translocation is not practicable, the *in situ* management of persisting populations of threatened species (and the threats) can also be an effective conservation strategy. Almost invariably, predation by introduced foxes and cats is one of the most significant pressures threatening the survival of native species (Kinnear *et al.* 1988; Hayward *et al.* 2003; Clarke *et al.* 2008; Wayne *et al.* 2011). In some cases, the removal of introduced predators has led to the successful management of threatened native species. At the time of European settlement, quokkas were widespread throughout the South West, and their subsequent and critical decline on the mainland was strongly correlated with the arrival of the red fox (*Vulpes vulpes*) (White 1952; Hayward *et al.* 2003). In 2003 Hayward *et al.* found that three of seven previously recorded mainland populations had become extinct, and that those remaining were under serious threat of extinction. In addition to ongoing pressure from predation and habitat changes, the large separation of these populations as a result of habitat fragmentation was a contributing factor to local extinctions. On the basis of metapopulation theory, however, they predicted that appropriate management of local populations through fox control and the restoration of habitat may result in increased population size (Hayward *et al.* 2003). Seasonal trapping during 2010–2011 demonstrated substantial increases in population size correlated with fox baiting. Viable quokka populations were found at six mainland sites, including two previously pronounced locally extinct (Dundas *et al.* 2012). Fox baiting has been successful in the management of a number of threatened marsupial species, including the numbat and rock wallabies (Kinnear *et al.* 1988; de Tores *et al.* 2007; Wayne *et al.* 2011). Cats, however, are notoriously difficult to control in open systems (Risbey *et al.* 1997; Short & Turner 2005).

Obviously, translocations also require *in situ* management, and a combination of the above approaches can improve success. In practice this requires clear objectives to be set and a commitment to long-term management (Short *et al.* 1992). An example of the successful outcome of well-thought out and well-managed reintroduction programs is that of the dibbler. The dibbler had been considered extinct for almost a century before being rediscovered near the south coast in 1967 (Morcombe 1967). It is currently regarded as endangered (Friend *et al.* 2008a). A very successful captive breeding program was established at Perth Zoo in 1997 from a colony of wild caught individuals from Whitlock and Boullanger Islands near Jurien Bay. These animals provided study specimens for intensive research into the reproductive biology and behaviour of the dibbler (Lambert & Mills 2006). Subsequently, more than 80 captive bred individuals were released on Escape Island (Jurien Bay) from 1998 to 2000. Radiotelemetry

and intensive trapping were used to monitor the Escape Island population. Breeding and dispersal of young were recorded within the first year and by 2001 a third generation of wild-born dighters had been recruited into the population (Moro 2003). The success of this project reflects the combination of detailed reproductive and ecophysiological research, a clear set of objectives and careful monitoring of reintroduced population.

The success of reintroductions is improved with greater knowledge of species and their ecology to guide conservation attempts. While this is a very broad area of research, many such studies in Western Australia appear to fall into three discrete fields: ecophysiology, genetics and immunology.

That ecophysiological principles could be applied to conservation and management strategies was advocated by Bert Main (Main 1961, 1968; Main & Yadav 1971). Through his series of papers, intensive ecological studies were made of eight macropodoid species on Western Australian offshore islands in order to determine the characteristics of both animals (habitat cover, nutritional and water requirements) and the islands (size, floral diversity including trees) which accounted for the observed diversity of fauna. Following this, he considered the likely implications for the management and conservation of those systems. Main & Yadav (1971) highlighted the importance of Barrow Island as a refuge for many species as a result not only of its large size, but more importantly by the fact that Barrow Island retains the topographic diversity (including stable rocky outcrops) and floral assemblages of the adjacent mainland. In a few instances habitat disturbance has had the opposite effect, for example significant population growth of spectacled hare-wallabies on Barrow Island and quokka on Rottnest Island. In such cases, careful management is required in order to minimise the possible detrimental effects of large population size, especially on islands (Bradshaw 1983b; Bakker & Bradshaw 1989).

More recently, the application of genetic methods and techniques to conservation problems has become an important area of research. Population genetics, as a field, measures genetic variation within and between populations in order to understand patterns of gene flow and evolution of species. It is understood that decreased genetic variation within a population leads to reduced fitness in an evolutionary sense. Conservation genetics, then, seeks to understand genetic variation within populations in order to conserve genetic diversity. Further, it is important to establish baseline data of genetic variation within and between donor and recipient population prior to mixing populations (Alacs *et al.* 2011). For example, in order to better understand the effects of range reduction on gene flow and genetic variation in the numbat, Fumagalli *et al.* (1999) analysed mitochondrial DNA (mtDNA) sequences of free-ranging individuals and museum specimens. Though reduced genetic diversity following population decline was evident, relatively recent connectivity between remnant populations was indicated. For management purposes, then, remnant populations could be treated as a single historical lineage and translocation might be a successful strategy for the maintenance of genetic diversity (Fumagalli *et al.* 1999). Historical patterns of interconnectedness have also been elucidated between

populations of woylie, though genetic variation between populations was evident (Pacioni *et al.* 2011). In contrast, the genetic diversity of the quokka (measured by microsatellites and other molecular techniques) indicated significant genetic differences between island and mainland populations (Alacs *et al.* 2011), highlighting the need for caution when considering the translocation of possibly maladapted island individuals to supplement mainland populations of this species; while the Barrow Island population of black-footed rock wallabies has been shown to have the lowest level of genetic variation found in any mammal (Eldridge *et al.* 1999).

An opportunity to investigate a population response in the face of a threatening process, from a conservation genetics perspective, has been taken up in the case of the northern quoll. Using a variety of genetic markers, How *et al.* (2009) have investigated the population structure of the northern quoll, which is threatened by the spread of the introduced cane toad (*Chaunus marinus*). Varied patterns of gene-flow between island and mainland populations, and genetic divergence between populations in the Pilbara, Kimberley and offshore islands has implications for conservation of genetic diversity in this keystone marsupial predator (How *et al.* 2009).

The last two decades have seen a rapid increase in the immunological study of marsupials. Immunological threats to marsupial populations, and particularly captive-bred populations, have led to extensive characterisation of viruses, microbes and parasites in marsupials. Haematological studies may be performed for assessments of animal health as an element of management strategies (Bennett *et al.* 2007). Such a study in the quokka found differences in the blood characteristics of wild versus captive populations, potentially reflecting nutritional deficiency in the wild. The same study also identified a number of haemoparasites in wild populations of quokka, highlighting the need for more work in order to understand the risk such parasites might pose to sympatric species, for example the endangered Gilbert's potoroo which overlaps the range of the quokka in the far South West (Clark & Spencer 2006). The ongoing identification and characterisation of parasites has been an important focus and a recent review has demonstrated the importance of understanding the conservation implications of parasite diversity, both within species and more broadly at the level of ecosystems (Thompson *et al.* 2010).

Captive breeding of individuals for reintroduction requires a high level of care to ensure that disease is not introduced to wild populations. For example, *Cryptosporidium muris* infection detected in captive-bred bilbies was most likely acquired from mice by faecal contamination of food and water (Warren *et al.* 2003). Viral infections, too, have been identified and may be hampering conservation attempts. A bandicoot papillomatosis carcinomatosis virus that causes lesions and may have a severe impact on locomotion, sight or feeding, has been described in some wild and captive-bred populations of the endangered western barred bandicoot (Bennett *et al.* 2008; Woolford *et al.* 2009). Often, the impact of parasites and viruses is difficult to determine and it is often unknown to what extent the microbes and parasites found may be correlated with

population health. Polymicrobial infection in a high percentage of all three populations of Gilbert's potoroos directly affects the reproductive system, and while not systemic, is likely to have an impact of the fecundity of infected individuals (Vaughan-Higgins *et al.* 2011). The woylie population crashes since 2000 have led to extensive investigation through a range of disciplines including parasitology. While various parasites have been discovered no clear causal agent for the recent population crashes has been identified (Smith *et al.* 2008; Paparini *et al.* 2012).

CONCLUSIONS

The understanding of marsupial biology has risen exponentially over the last century and the Western Australian contribution has been substantial. The application of the knowledge derived from studies such as those highlighted in this review will drive future conservation attempts, as the pressure on our natural environment continues to rise. In addition to preserving our unique biota, the conservation of our marsupials also has the potential to help in the restoration of threatened ecosystems, as highlighted by a recent review of the role of digging mammals in ecosystem processes (Fleming *et al.* 2014). The success of conservation strategies also relies on the interest, engagement and support of the wider community. Hopefully the publication of reviews such as presented here will spark the collective imagination.

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Appendix 1 Marsupials of Western Australia.

| Taxa | Common names | Body mass | Habitat | Status | Reference |
|---|--|---|---|----------|-----------------------------|
| Dasyuridae | | | | | |
| <i>Antechinus flavipes</i> (<i>A. fleucogaster</i> ^{End}) | Yellow-footed antechinus, mardo | 26-79 g males 21-52 g females | Varied habitats from forests to swamps and dry mulga country. | | Crowther 2008 |
| <i>Dasyercus blythi</i> | Brush-tailed mulgara | 75-110 g males 60-90 g females | Constructs burrows in sandy swales in spinifex grassland; medium to dense cover. | P4 | Woolley 2008a |
| <i>Dasyercus cristicauda</i> | Crest-tailed mulgara, ampurta | 110-185 g males 65-120 g females | Constructs burrows in desert sand dunes with sparse cover. | V, S1[v] | Masters 2008 |
| <i>Dasykaluta rosamondae</i> ^{End} | Kaluta | 25-40 g males 20-30 g females | Hummock grasslands of the Pilbara. | | Woolley 2008e |
| <i>Dasyurus geoffroii</i> | Western quoll, chuditch | mean 1310 g males mean 890 g females | Sclerophyll forest, dry woodland or shrubland of the south-west WA. | V, S1[v] | Serena & Soderquist 2008 |
| <i>Dasyurus hallucatus</i> | Northern quoll | 340-1120 g males 240-690 g females | Most commonly rocky escarpments; also woodlands. | E, S1[e] | Oakwood 2008 |
| <i>Ningai ridei</i> | Wongai ningai | 6.5-10.5 g | Inland red sandplains supporting spinifex hummock grassland. | | McKenzie & Dickman 2008 |
| <i>Ningai timealeyi</i> ^{End} | Pilbara ningai | 3.6-9.5 g males 3.5-7.5 g females | Along drainage lines in spinifex grasslands of the Pilbara. | | Dunlop <i>et al.</i> 2008 |
| <i>Ningai yoonnae</i> | Southern ningai, mallee ningai | 6-14 g | Spinifex grasslands Great Victoria Desert. | | Carthew & Bos 2008 |
| <i>Parantechinus apicalis</i> ^{End} | Dibbler | 60-125 g males 40-73 g females | Coastal and subcoastal areas. | E, S1[e] | Woolley 2008c |
| <i>Phascogale calura</i> | Red-tailed phascogale, red-tailed wambenger | 39-68 g males 38-48 g females | Isolated patches of forest in the south-west. | E, S1[e] | Bradley <i>et al.</i> 2008 |
| <i>Phascogale tapoatafa</i> | Brush-tailed phascogale, common wambenger | 175-311 g males 106-212 g females | Arboreal specialist; open forest with sparse groundcover. | S1[v] | Soderquist & Rhind 2008 |
| <i>Antechinomys laniger</i> | Kultarr, jerboa marsupial mouse | mean 30 g males mean 20 g females | Desert plains, grasslands and acacia woodland. | | Valente 2008 |
| <i>Planigale ingrami</i> | Long-tailed planigale | 2.8-6.6 g males 2.6-5.8 g females | Blacksoil plains of the tropical north. | | Fisher 2008 |
| <i>Planigale maculata</i> | Common planigale | 4-16.3 g males 3.5-17.2 g females | Coastal and subcoastal areas of north-west. | | Burnett 2008 |
| <i>Pseudantechinus macdonnellensis</i> | Fat-tailed pseudantechinus | 25-45 g males 20-40 g females | Rocky hills, breakaways, red sandplains of northern deserts. | | Woolley 2008d |
| <i>Pseudantechinus ningbing</i> | Ningbing false antechinus | 20-25 g males 15-20 g females | Limestone and sandstone outcrops of the Kimberley. | | Woolley 2008f |
| <i>Pseudantechinus roryi</i> ^{End} | Rory's pseudantechinus | 19-32 g males 17-26 g females | Open woodland, spinifex sandplain, granite rockpiles of the Pilbara. | | Cooper 2008 |
| <i>Pseudantechinus woolleyae</i> ^{End} | Woolley's pseudantechinus | 35-50 g males 30-45 g females | Rocky habitats through Pilbara and western deserts. | | Woolley 2008h |

| Taxa | Common names | Body mass | Habitat | Status | Reference |
|---|-----------------------------|--|---|----------|----------------------------------|
| <i>Sminthopsis butleri</i> | Butler's dunnart | 15-30 g | Open tropical woodland on blacksoil/sand ; Kulubaru WA and Tiwi Islands NT | V, S1[v] | Woolley 2008b |
| <i>Sminthopsis crassicaudata</i> | Fat-tailed dunnart | 10-20 g | Varied habitats across the southern half of the continent. | | Morton & Dickman 2008a |
| <i>Sminthopsis dolichura</i> | Little long-tailed dunnart | 11-20 g males 10-21 g females | Semi-arid and arid south-western WA and SA. | | Friend & Pearson 2008 |
| <i>Sminthopsis gilberti</i> ^{End} | Gilbert's dunnart | 14-25 g | Woodlands of the Darling Scarp, mallee-heaths in the central and southern wheatbelt. | | Morris & McKenzie 2008 |
| <i>Sminthopsis granulipes</i> ^{End} | White-tailed dunnart | 18-37 g | Proteaceous shrublands of semi-arid regions of south-west WA. | | McKenzie & Kitchener 2008 |
| <i>Sminthopsis griseoventer</i> | Grey-bellied dunnart | 15-24 g males 14-20 g females | Coastal plain and lateritic ranges of south-west WA. | | Dickman 2008 |
| <i>Sminthopsis hirtipes</i> | Hairy-footed dunnart | 13-19.5 g | Open low woodlands or spinifex grasslands of south-central red sandplains | | Pearson & McKenzie 2008 |
| <i>Sminthopsis longicaudata</i> | Long-tailed dunnart | 15-25 g | Arid, rocky country through the Pilbara, Gibson Desert to Alice Springs. | P4 | Burbidge, <i>et al.</i> 2008d |
| <i>Sminthopsis macroura</i> | Stripe-faced dunnart | 15-25 g | Widely through arid and semi-arid Australia, particularly shrubland and tussock grasslands. | | Morton & Dickman 2008b |
| <i>Sminthopsis ooldea</i> | Ooldea dunnart | 9-17 g males 8-15 g females | Primary mulga shrublands and woodlands with tussock understory, through the Pilbara and central continent. | | Foulkes 2008 |
| <i>Sminthopsis psammophila</i> | Sandhill dunnart | 26-55 g males 25-42 g females | Tussock grasslands, low open woodland; isolated populations in the Great Victoria Desert. | E, S1[e] | Pearson & Churchill 2008 |
| <i>Sminthopsis virginiae</i> | Red-cheeked dunnart | 31-58 g males 18-34 g females | Tropical savannah woodlands; isolated populations in the Kimberley. | | Woolley 2008g |
| <i>Sminthopsis youngsoni</i> | Lesser hairy-footed dunnart | 8.5-12.0 g | Open shrublands of hummock grasslands through Pilbara and central Australia. | | McKenzie & Cole 2008 |
| Myrmecobiidae | | | | | |
| <i>Myrmecobius fasciatus</i> | Numbat, banded anteater | 405-752 g males 305-647 g females | Open woodlands with abundant termite activity. | V, S1[v] | Friend 2008b |
| Peramelidae | | | | | |
| <i>Chaeropus ecaudatus</i> | Pig-footed bandicoot | 200 g (estimated) | Sand dunes and sandplains with hummock grassland and tussock grass. | Ex, S2 | Johnson & Burbidge 2008a |
| <i>Isoodon auratus</i> (<i>I. a. auratus</i> ; mainland) (<i>I. a. barrowensis</i> ^{End} ; Barrow Island) | Golden bandicoot | 300-670 g (<i>I. a. auratus</i>) 250-600 g (<i>I. a. barrowensis</i>) | Sandplain or sand-dune spinifex grasslands. | V, S1[v] | McKenzie <i>et al.</i> 2008 |
| <i>Isoodon macrourus</i> | Northern brown bandicoot | 500-3100 g males 500-1700 g females | Varied habitats through tropical north and eastern states. | | Gordon 2008b |

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|--|---|--|--|--|-------------------------------|
| <i>Isoodon obesulus</i> (<i>I. o. fusciventer</i> ^{End} ; Western Australia) | Southern brown bandicoot, quenda | 500-1850 g males 400-1200 g females | Forest, woodland, shrub and heath communities. | P5 | Paull 2008 |
| <i>Perameles bougainville</i> (<i>P. b. bougainville</i> ; Shark Bay) (<i>P. b. myosuroides</i> ; mainland Western Australia) | Western barred bandicoot | 168-280 g males 165-379 g females | Dense scrub, low heath or hummock grasslands. | E, S1[e] (<i>P. b. bougainville</i>) Ex (<i>P. b. myosuroides</i>) | Friend 2008c |
| <i>Perameles eremiana</i> | Desert bandicoot | unknown | Sandplain and sand-ridge desert with spinifex grassland. | Ex, S2 | Gordon 2008a |
| Thylacomyidae | | | | | |
| <i>Macrotis lagotis</i> | Bilby, rabbit-eared bandicoot | 1000-2500 g males 800-1100 g females | Desert sandplains and dunes fields, hummock grasslands and acacia shrubland. | V, S1[v] | Johnson 2008a |
| <i>Macrotis leucura</i> | Lesser bilby | 360-435 g males 311 g female | Gibson desert. | Ex, S2 | Johnson 2008b |
| Notoryctidae | | | | | |
| <i>Notoryctes caurinus</i> ^{End} | Northern marsupial mole, kakarratul | 30-50 g | Sand-dune deserts of north-western Australia. | E, S1[e] | Benshemesh & Aplin 2008 |
| <i>Notoryctes typhlops</i> | Southern marsupial mole, itjaritjari | 40-70 g | Sand-dune deserts of central Australia. | E, S1 [e] | Benshemesh 2008 |
| Vombatidae | | | | | |
| <i>Lasiorchinus latifrons</i> | Southern hairy-nosed wombat | 19-36 kg males 17.5-36 kg females | Semi-arid grasslands of southern Australia. | | Taggart & Templesmith 2008 |
| Burramyidae | | | | | |
| <i>Cercartetus concinnus</i> | Western pygmy possum | 8-21 g | Mallee woodlands, heathlands, shrubland and dry sclerophyll of southern Australia. | | Carthew <i>et al.</i> 2008 |
| Tarsipedidae | | | | | |
| <i>Tarsipes rostratus</i> ^{End} | Honey possum | 7-11 g males 8-16 g females | Coastal sandplain heaths with abundant nectar-producing Proteaceae and Myrtaceae. | | Renfree 2008 |
| Petauridae | | | | | |
| <i>Petaurus breviceps</i> | Sugar glider | 115-160 g males 95-135 g females | Forest containing tree hollows and varied food sources. | | Suckling 2008 |
| Pseudocheiridae | | | | | |
| <i>Petroseudes dahli</i> | Rock ringtail possum | 1280-2000 g | Rocky outcrops of the Kimberley and tropical northern Australia. | P3 | Webb <i>et al.</i> 2008 |
| <i>Pseudocheirus occidentalis</i> ^{End} | Western ringtail possum | 700-1300 g males 750-1200 g females | Jarrah, wandoo, marri and especially coastal peppermint forest and woodland. | V, S1[v] | de Tores 2008b |
| Phalangeridae | | | | | |
| <i>Trichosurus vulpecula</i> | Common brushtail possum | 1300-4500 g males 1200-3500 g females | Varied, though prefers dry eucalypt forests and woodlands. | | Kerle & How 2008 |
| <i>Wyulda squamicaudata</i> ^{End} | Scaly-tailed possum | 900-2000 g | Open woodland and closed forests of the rugged, rocky country of the Kimberley. | P3 | Burbidge & Webb 2008 |

| Taxa | Common names | Body mass | Habitat | Status | Reference |
|---|--|--|--|---|------------------------------|
| Potoroidae | | | | | |
| <i>Bettongia lesueur</i> | Burrowing bettong | mean 680 g | Coastal heath with limestone cap-rock, though formerly more widespread. | V, S1[v] | Burbidge & Short 2008 |
| <i>Bettongia penicillata</i> (<i>B. p. olgibyi</i> ; Western Australia) | Woylie | 980-1850 g males 750-1500 g females | Wheatbelt thickets containing <i>Gastrolobium</i> spp.; historically broad arid and semiarid distribution. | E, S1[e] | de Tores & Start 2008 |
| <i>Bettongia pusilla</i> | Nullarbor dwarf bettong | | | Ex, S2 | Burbidge 2008a |
| <i>Potorous gilbertii</i> ^{End} | Gilbert's potoroo | 845-1200 g males 708-1205 g females | Melaleuca heath with dense sedge understory or adjacent closed woodland. | CE, S1[ce] | Friend 2008a |
| <i>Potorous platyops</i> | Broad-faced potoroo | unknown | Unknown. | Ex, S2 | Kitchener & Friend 2000 |
| Macropodidae | | | | | |
| <i>Lagorchestes asomatus</i> | Central hare-wallaby | unknown; similar to burrowing bettong | Arid sandplains and dunes of Gibson Desert and surrounding areas. | Ex, S2 | Burbidge <i>et al.</i> 2008b |
| <i>Lagorchestes conspicillatus</i> (<i>L. c. conspicillatus</i> ; Barrow Island) (<i>L. c. leichardti</i> ; mainland) | Spectacled hare-wallaby | 1600-4750 g | Tropical grasslands and open shrublands. | V, S1[v] (<i>L. c. conspicillatus</i>) P3 (<i>L. c. leichardti</i>) | Burbidge & Johnson 2008 |
| <i>Lagorchestes hirsutus</i> (<i>L. h. bernieri</i> ^{End} ; Bernier and Dorre Islands) (<i>L. h. NTM U2430</i> ; mainland) | Rufous hare-wallaby, mala | mean 1580 g males mean 1740 g females (<i>L. h. bernieri</i>); mean 1220 g males mean 1310 g females (<i>L. h. NTM U2430</i>) | Spinifex hummock, tussock grasslands and shrublands of arid and semi-arid areas. | E, S1[e] (<i>L. h. NTM U2430</i>) V, S1[v] (<i>L. h. bernieri</i>) Ex SW mainland | Johnson & Burbidge 2008b |
| <i>Macropus agilis</i> | Agile wallaby | 16-27 kg males 9-15 kg females | Riparian vegetation in open forest and adjacent grasslands of the tropic north. | | Merchant 2008 |
| <i>Macropus antilopinus</i> | Antilopine kangaroo | 18.6-51 kg males 14-24.5 kg females | Scattered to dense vegetation with grass-dominated understory of monsoonal tropical woodlands. | Ritchie 2008 | |
| <i>Macropus eugenii</i> (<i>M. e. derbianus</i> ^{End} ; Western Australia) | Tammar wallaby | 6-10 kg males 4-6 kg females | Dense low scrub with adjacent grassy areas for feeding. | P5 | Hinds 2008 |
| <i>Macropus fuliginosus</i> | Western grey kangaroo | 18-72 kg males 17-39 kg females | Varied habitats across southern Australia; consumes principally graze but also some browse. | | Coulson 2008 |
| <i>Macropus irma</i> ^{End} | Western brush wallaby, black gloved wallaby | 7-9 kg | Open forest or woodland with low grass and open thickets. | P4 | Morris & Christensen 2008 |
| <i>Macropus robustus</i> (<i>M. r. erubescens</i> ; mainland) (<i>M. r. isabellinus</i> ^{End} ; Barrow Island) (<i>M. r. woodwardi</i> ; mainland Kimberley) | Euro, common wallaroo | 7.25-60 kg males 6.25-28 kg females | Varied habitats across arid, semi-arid and tropical Australia usually containing steep escarpments or rocky hills. | V, S1[v] (<i>M. r. isabellinus</i>) | Clancy & Croft 2008 |

| | | | | | |
|--|--|---|--|--|----------------------------|
| <i>Macropus rufus</i> | Red kangaroo | 22-92 kg males 17-39 kg females | Open plains of arid and semi-arid Australia. | | Croft & Clancy 2008 |
| <i>Onychogalea lunata</i> ^{End} | Crescent nail-tail wallaby | ~3.5 kg | Varied habitats in arid and semi-arid Australia. | Ex, S2 | Burbidge 2008b |
| <i>Onychogalea unguifera</i> | Northern nail-tail wallaby | 6-9 kg males 4.5-7 kg females | Open woodlands with tussock grass or grasslands with scattered trees or shrubs of northern Australia. | | Ingleby & Gordon 2008 |
| <i>Petrogale brachyoti</i> | Short-eared rock-wallaby | 3.2-5.6 kg males 2.2-4.7 kg females | Rocky hills, gorges and escarpments with savannah woodland in the Kimberley and NT. | | Eldridge & Telfer 2008 |
| <i>Petrogale burbidgei</i> ^{End} | Monjon | 960-1430 g | Low open woodland and vine thickets with rocky outcrops. | P4 | Pearson <i>et al.</i> 2008 |
| <i>Petrogale concinna</i> | Nabarlek, little rock wallaby | 1050-1500 g males 1070-1700 g females | Varied vegetation including floodplain, vine thickets, rainforest, and grassland with rocky shelter. | | Sanson & Churchill 2008 |
| <i>Petrogale lateralis</i> (<i>P. l.</i> ANWC CM15314 ^{End} ; MacDonnell Ranges) (<i>P. l. hacketti</i> ; south coast islands) (<i>P. l. lateralis</i> ; mainland) (<i>P. l.</i> WAM M15135 ^E ; West Kimberley) | Black-flanked rock-wallaby, Black-footed rock-wallaby | 4.1-5.3 kg males 3.1-3.8 kg females | Varied and discontinuous rocky habitats. | V, S1[v] | Eldridge & Pearson 2008 |
| <i>Petrogale rothschildi</i> ^{End} | Rothschild's rock-wallaby | 3.7-6.6 kg mainland 2.6-3.9 kg Dampier Archipelago | Rocky environments with surrounding spinifex grasslands and shrublands of the Pilbara and Ashburton regions. | | Pearson & Eldridge 2008 |
| <i>Setonix brachyurus</i> ^{End} | Quokka | 2.7-4.2 kg males 1.6-3.5 kg females | Shrub thickets and sedges on Rottneest Island; riparian vegetation. | V, S1[v] | de Tores 2008a |
| <i>Lagostrophus fasciatus</i> (<i>L. f. albipilis</i> ; mainland) (<i>L. f. fasciatus</i> ^{End} ; Bernier and Dorre Islands) | Banded hare-wallaby, merrine | 1.0-2.3 kg | Dense thickets of <i>Acacia</i> spp. | Ex (<i>L. f. albipilis</i>) V, S1[v] (<i>L. f. fasciatus</i>) | Prince & Richards 2008 |

^{End} indicates taxa endemic to Western Australia.

Environment Protection and Biodiversity Conservation Act 1999 status codes:

Ex, extinct (taxa not definitely located in the wild during the past 50 years)

CE, critically endangered (taxa facing an extremely high risk of extinction in the wild in the immediate future)

E, endangered (taxa facing a very high risk of extinction in the wild in the near future)

V, vulnerable (taxa facing a high risk of extinction in the wild in the medium-term future)

Western Australian Wildlife Conservation Act 1950 status codes:

S1, Schedule 1 (threatened fauna; fauna that is rare or is likely to become extinct) with rankings shown in square parentheses: [ce], critically endangered; [e], endangered; [v], vulnerable.

S2, Schedule 2 (fauna that is presumed to be extinct)

Western Australian Department of Environment and Conservation (DEC) priority species status codes:

P1, Priority 1 (poorly known species on threatened lands)

P2, Priority 2 (poorly known species on conservation lands)

P3, Priority 3 (poorly known species, some on conservation lands)

P4, Priority 4 (rare, near threatened and other species in need of monitoring)

P5, Priority 5 (conservation dependent species)