

## *Myrmecobius fasciatus* (Dasyuromorphia: Myrmecobiidae)

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**Abstract:** *Myrmecobius fasciatus* Waterhouse, 1836, is a small to medium-sized dasyuromorph marsupial known as the numbat. *M. fasciatus* is unusual among marsupials in that it is diurnal and feeds exclusively on termites, and it has a number of characteristic adaptations associated with this specialized niche. *M. fasciatus* has at least 8 postcanine teeth in the lower jaw; the dentition is variable between individuals and even between the 2 sides of the jaw of the same individual. Although widespread throughout southern Australia at the time of European settlement, *M. fasciatus* is currently restricted to 2 naturally occurring populations in the southwestern portion of Western Australia, and some additional populations within its historic range resulting from successful reintroductions. It is currently listed as “Endangered.”

**Key words:** diurnal behavior, endangered species, marsupial, numbat, rusty numbat, termitivore

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### *Myrmecobius* Waterhouse, 1836

*Myrmecobius* Waterhouse, 1836:69. Type species *Myrmecobius fasciatus* Waterhouse, 1836, by monotypy.

CONTEXT AND CONTENT. Order Dasyuromorphia, family Myrmecobiidae. *Myrmecobius* is monotypic.

### *Myrmecobius fasciatus* Waterhouse, 1836 Numbat

*Myrmecobius fasciatus* Waterhouse, 1836:69. Type locality “interior of the Swan River settlement, about 90 miles to the S. E. of the mouth of that river,” near Brookton, Western Australia.

CONTEXT AND CONTENT. Context as for genus. Wood Jones (1923b) formally described South Australian specimens of *Myrmecobius* as *M. rufus*. However this form is generally considered to be a subspecies, *M. fasciatus rufus* (Finlayson 1933; Groves 2005), which is presumed now to be extinct. The last anecdotal report of a sighting of *M. f. rufus* was during the 1960s, with the most recent specimen collected near Warburton, Western Australia, around 1950 (Friend et al. 1982). Two subspecies are recognized (Groves 2005):

*M. fasciatus fasciatus* Waterhouse, 1836:69. See above.  
*M. fasciatus rufus* Wood Jones, 1923b:123. Type locality “South Australia.”

NOMENCLATURE NOTES. The vernacular name numbat is derived from Australian Aboriginal terms for *M. fasciatus* including noobat, nombat, nyoombot, and nambart. Terms wai-hoo, wai-hao, weeo, weou, wee-u, weeu, wi-u, wiu, walpurti, mutjurarranypa, and parrtjilaranypa also have been used by Aboriginal people to describe this species (Abbott 2001; Friend 2008). Early European vernacular names included banded anteater, marsupial anteater, and white-banded bandicoot; numbat is the currently accepted common name (Friend 2008; Strahan and Conder 2007; Troughton 1967; Wood Jones 1923b). *M. f. rufus* was commonly known as the southeastern or rusty numbat (Friend et al. 1982; Troughton 1967).



Fig. 1.—Adult male *Myrmecobius fasciatus*. Photograph by C. E. Cooper of a specimen at Perth Zoo.

## DIAGNOSIS

*Myrmecobius fasciatus* has a number of unique characteristics that distinguish it from other dasyuromorph marsupials and warrant its classification in a monospecific family, the Myrmecobiidae. The external appearance of *M. fasciatus* is unmistakable, and it is easily identified from any other marsupial by a combination of its long snout, bold white cross banding on the rear one-half of the body (4–11 white transverse stripes running across the hindquarters, becoming less distinct anteriorly), black line through the eye, underlined by white, and “bottlebrush” tail (Fig. 1). *M. f. rufus* could be distinguished from the nominate subspecies by a redder pelage, particularly on the back, crown, and outer surface of the ears. The forequarters and crown were a rich brick red, and lacked black hairs, and the hindquarters a rich brown between the white stripes. The ventral surface was tawny to buff, and the outer surface of the ear was a bright rufus color (Finlayson 1933; Troughton 1967).

Of particular importance are the dental and basocranial (Fig. 2) differences that differentiate *M. fasciatus* from the dasyurids, and in many cases from other marsupials, and suggest an early divergence of *Myrmecobius* from the dasyurid lineage (Archer 1976, 1984; Archer and Kirsch 1977). The unusual number and structure of the teeth has been recognized since Waterhouse’s 1st description of the species (Waterhouse 1836, 1841). The molar teeth lack the typical tribosphenic structure of dasyurids, and are instead simple conical cusps that in some instances barely extend above the gum (Archer 1984; Archer and Kirsch 1977). Remarkably, there is at least 1 additional tooth, either a supernumerary molar or a retained deciduous premolar, which means that *M. fasciatus* has at least 8 postcanine teeth in the lower jaw. The palate is elongated and complete, and the lachrymal bone is greatly enlarged. The tympanic wing of the alisphenoid forms almost the entire floor of the middle ear. There is an incomplete bony bar behind the orbit, consisting of processes from the frontal and jugal bones. The squamosal is reduced; the jugal forms the majority of the zygomatic arch. A massive process of the frontal bone extends over the orbit. The interparietal is large, there is a complete posterolateral palatal foramen, and the infraorbital foramen on the maxilla is located ventrally (Archer 1976, 1984; Archer and Kirsch 1977).

## GENERAL CHARACTERS

*Myrmecobius fasciatus* is a small to medium-sized marsupial, with a head-body length of 270 mm and an adult body mass of 500–700 g. The snout is elongate and pointed, the ears are twice as long as they are wide, and the eyes are positioned high on the head (Fig. 1; Friend 1993). The short, stiff hair is sparse (2,921 hairs/cm<sup>2</sup>) and the pelt is shallow (1.19 mm depth—Cooper et al. 2003a). The dorsal

background color grades from dark brown or black at the posterior to red-brown at the anterior. The ventral surface is whitish. The tail is about 200 mm long, with long, brown hair flecked with white. This long hair can be erected to take on a “bottlebrush” appearance. There are 5 digits on the manus, and 4 on the pes (Friend 1993).

## DISTRIBUTION

*Myrmecobius fasciatus* historically inhabited southern and central Australia. Prior to European settlement, its range extended from the southwest of Western Australia east to Laverton, northeast to the Everard Range in northern South Australia, and into western New South Wales (Fig. 3; Connell and Friend 1985). However, its distribution was dramatically reduced with European settlement of Australia, and today there are only 2 naturally occurring disjunct populations in the southwest of Western Australia. One population is at Dryandra Woodland, a 28,000-ha vegetation remnant in the major cereal-growing district of Western Australia, situated 170 km east of Perth. The other population occurs in the 52,000-ha Perup Nature Reserve, near Manjimup, 280 km southeast of Perth. Since the rapid decline in distribution and abundance in the 1970s, a captive breeding and translocation program has reestablished populations of *M. fasciatus* at a number of sites throughout the southwestern portion of Western Australia, with 2 additional populations in fenced reserves in South Australia and western New South Wales (Friend and Thomas 1995, 1998, 2003).

## FOSSIL RECORD

The fossil record is deficient for the Myrmecobiidae. There are 3 published records of fossil or subfossil remains of *Myrmecobius fasciatus* (Friend 1993) but no records of any other species from this family (Archer 1984). Two of the records are from the late Pleistocene, 1 from Lake Menindee in New South Wales and 1 from Madura Cave on the Nullarbor Plain, Western Australia. The 3rd record is a fossil from the lower Murray River, South Australia, dated as Holocene. The Lake Menindee and Murray River records are within the known modern range of *M. fasciatus*, but the Nullarbor Plain record is outside of its known pre-European distribution (Friend 1993).

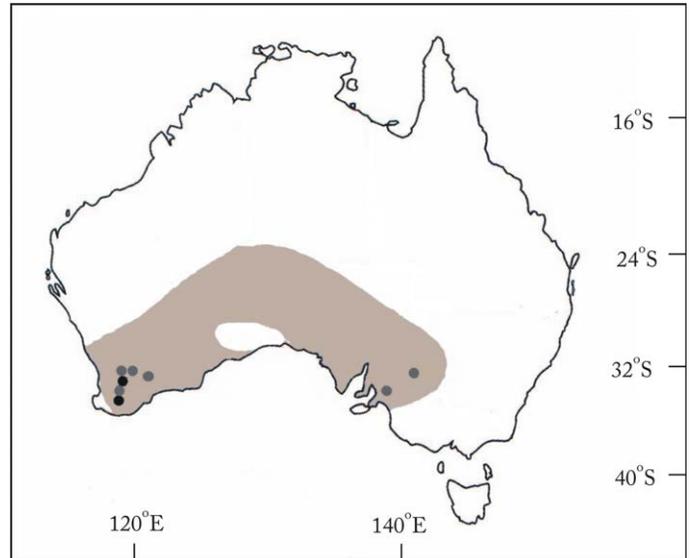
## FORM AND FUNCTION

**Form.**—The morphology of *Myrmecobius fasciatus*, particularly that of the feeding and digestive systems, shares many convergent adaptations with placental and monotreme myrmecophages. The snout is elongated, a consequence of a large, prolonged, completely fused palate and lachrymals



**Fig. 2.**—Dorsal, ventral, and lateral views of skull and lateral view of mandible of a female *Myrmecobius fasciatus* (M5291) from Pingelly, Western Australia (32°32'00"S 117°05'00"E). Greatest length of skull is 60.6 mm. Specimen courtesy of the Western Australian Museum; photographs by C. E. Cooper.

extending well outside the orbit (Fig. 2). The paroccipital processes are completely fused behind the mastoids and the palatal branches of the premaxilla remain separate at the front of the palate (Tate 1951). The teeth are numerous, greatly reduced in size, and modified in form. The dentition is variable between individuals of *M. fasciatus*, and even between the 2 sides of the jaw for the same individual, but can be generalized with the following dental formula:  $i\ 4/3$ ,  $c\ 1/1$ ,  $p\ 3/3$ ,  $dpm\ 1/1$ ,  $m\ 4/4$ , total 50 (Friend 1993). There are always more than 7 postcanine teeth in the lower jaw; this is



**Fig. 3.**—Distribution of *Myrmecobius fasciatus* at the time of European settlement (gray shading), extant natural populations (black dots), and reintroduced populations (gray dots). Modified from Friend (2008).

a unique feature among terrestrial mammals (Friend 1993). It is unclear if the extra teeth result from retention of a normally deciduous premolar (Tate 1951) or from addition of extra molars, made possible by the elongation of the palate (Bensley 1903). The simplicity of the teeth, variation in number and form, and lack of appreciable tooth wear in adult animals suggests that the teeth are used little for feeding (Calaby 1960; Friend 1993). I have observed *M. fasciatus* partially chewing food and documentation of this exists in the literature (Fleay 1942); it is presumed that the relatively soft bodies of termites require little to rupture the chitinous exoskeleton. Examination of stomach contents and scats indicates little maceration of the termite exoskeleton (Cooper and Withers 2004b; Troughton 1967).

The tongue, as for many myrmecophagous mammals, is long and vermiform, and can be extended a considerable distance past the end of the snout (Griffiths 1968). The submaxillary salivary glands are greatly enlarged, and divided into an anterior mucus section and a larger posterior serous section (Ford 1934). Copious sticky saliva from these enlarged glands coats the tongue to facilitate collection of termite prey. The soft palate has 13 or 14 transverse ridges that scrape termites from the tongue when it is withdrawn into the oral cavity (Griffiths 1968). The digestive tract is simple, with a glandular stomach lacking the thick muscular wall, cornified stratified epithelium, or keratinized “teeth” that are adaptations of other myrmecophages for grinding food and managing large quantities of ingested dirt (Griffiths 1968; Hume 1982). This lack of specialization is presumably because termites have less protective chitin than ants and therefore it is not necessary to have a stomach

specialized to break open the indigestible exoskeleton (Friend 1982). Despite the simplicity of the digestive tract, the food of *M. fasciatus* has a slow passage time (50% by 12 h, 100% by 20–30 h) compared to other marsupials feeding on termites, and there is evidence of sorting of digesta (Calaby 1960; Cooper and Withers 2004b) that presumably reflects selective retention of nonchitinous components of the diet to enhance its digestibility.

The kidney of *M. fasciatus* has the typical gross morphology of a dasyurid marsupial's kidney (Cooper and Withers 2010). The cortex and inner and outer medulla can be easily identified, with a relative medullary area of 1.34. The calculated maximal urinary concentration is 3,617 mOsm/kg H<sub>2</sub>O, which is average for a dasyurid marsupial, despite the historically semiarid to arid distribution of *M. fasciatus*. A diet of termites presumably provides sufficient water to limit selection for a high urinary concentrating capacity (Cooper and Withers 2010).

The male urinary system is fairly typical for a marsupial (Fordham 1928). The urethra exits the bladder from the dorsal side, where the sphincter vesicae separate the lumen of the bladder from a small chamber, the collum vesicae. The paired ureters pass into the collum vesicae via a small canal that opens through the wall of the prostatic tract. The ureters have a total length of about 9.25 cm and can be divided into 3 distinct regions; the anterior glandular prostatic tract, a middle membranous region, and the 3rd bulbous region (Fordham 1928). The female urinary system has not been described.

There is little information concerning the endocrine and exocrine glands of *M. fasciatus*. The adrenal glands are not closely associated with the kidneys (Fordham 1928). Like many marsupials, a sternal scent gland is presumably used for territorial marking (Cooper et al. 2005; Russell 1985). This round area of almost hairless, pigmented skin contains sebaceous glands, sweat glands, and sudoriparous follicles, and is often raised above the skin surface and stained an orange-brown color (Beddard 1887; Calaby 1960; Ford 1934; Friend 1993). The enlarged salivary glands were originally mistaken as part of the sternal gland, which they underlie (Beddard 1887; Ford 1934). Females possess anal glands, but these appear to be absent in males (Fordham 1928; Hill 1900).

**Function.**—*Myrmecobius fasciatus* uses scent to detect its termite prey in subsurface soil galleries, but relies primarily on visual detection of predators (Friend 1993). The visual system is a combination of both ancestral marsupial characteristics and adaptations to its current diurnal niche (Arrese et al. 2000). The retinal ganglion topography is characterized by a concentric pattern, which is a primitive marsupial feature. However, there is a pronounced area centralis that suggests accurate vision in the frontal field, and no visual streak. Cones dominate the retina, and there is an absence of pupillary mobility, both features associated with diurnal activity. *M. fasciatus* has the highest visual

acuity yet determined for any marsupial, resulting from a high ganglion cell density, dominance of cones, and posterior nodal distance. This is presumably associated with a diurnal visual organization. The visual field is 240° of visual angle, with 80° overlap of binocular vision in the horizontal plane, presumably a compromise between frontal binocular and peripheral vision; the ventral field of view is poor (Arrese et al. 2000).

An exclusively termitivorous diet is associated in mammals with a low-energy physiology (Abensperg-Traun 1988; Cooper and Withers 2004b; Lubin and Montgomery 1981; Naples 1999; Redford 1987; Redford and Dorea 1984). Termites are patchily distributed in both space and time, they have physical and chemical defense mechanisms that necessitate short feeding bouts and extended foraging, their digestion requires a long passage time, which reduces food throughput, and they have a low energy density due to the high proportion of indigestible chitin and the large amounts of debris ingested during feeding (Cooper and Withers 2004b). Despite these dietary limitations and its obvious morphological adaptations to termitivory, *M. fasciatus* has very few physiological specializations reflecting a low-energy diet. This is unexpected, because a termitivorous diet, along with a semifossorial habit, has been associated with low body temperature and energy expenditure for placental mammals (McNab 1966, 1984). However, the phylogenetic affiliation and geographic distribution of *M. fasciatus* as a semiarid–arid habitat dasyuromorph marsupial presumably preadapts it to a low-energy physiology, typical of placental termitivores (Cooper 2004; Cooper and Withers 2002). The major dietary effects on the physiology of *M. fasciatus* appear to be more a consequence of enforced diurnal activity than energy restriction.

Body temperature of *M. fasciatus* has a strong nycthemeral rhythm, but unlike other marsupials it is higher during the day than at night, reflecting its diurnal activity. Normothermic resting body temperature is 34.1°C, typical of other similar-sized marsupials (Cooper and Withers 2002). *M. fasciatus*, like most other dasyuromorph marsupials, enters shallow daily torpor (Cooper and Withers 2004a; Fleay 1942; Serventy and Raymond 1973). Torpor is spontaneous, occurring even when food is available, and may last for more than 15 h during which body temperature may drop as low as 19.1°C. Torpor is more frequent, deeper, and longer in winter than other seasons, and results in energy savings of 13–42% over 12.5 h (Cooper and Withers 2004a).

The energy requirements of *M. fasciatus* are slightly lower than, but not significantly different from, those of other marsupials; basal metabolic rate (3.89 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) is 87% of predicted for a marsupial of equivalent body mass but is not considered to be unusually low (Cooper and Withers 2002; McNab 1984). *M. fasciatus* has a typical endothermic response to decreasing ambient temperature,

with a proportional increase in metabolic heat production for regulation of body temperature. It responds to high ambient temperatures with a combination of hyperthermia and increased evaporative water loss and thermal conductance (Cooper and Withers 2002). Respiratory ventilation reflects the demand for gas exchange (based on body mass and metabolism—Cooper and Withers 2004d). Basal respiratory frequency is 30.6 breaths/min and tidal volume 6 ml/breath. Respiratory accommodation of increasing oxygen consumption (and carbon dioxide production) at low ambient temperature is achieved by increasing respiratory minute volume rather than oxygen extraction, which is already high at 27.7%. An increase in minute volume is accomplished mostly by an increase in respiratory frequency rather than tidal volume (Cooper and Withers 2004d).

The field metabolic rate of *M. fasciatus* (269 kJ/day) is equivalent to that of other arid-habitat marsupials (Cooper et al. 2003b). Termites consumed by *M. fasciatus* weigh about 0.935 mg<sub>dry mass</sub>, contain approximately 22.9 kJ/g<sub>dry mass</sub>, and *M. fasciatus* can digest 64–81% of this available energy; these values are similar to those calculated for other animals feeding on ants and termites (Cooper and Withers 2004b). Consequently, *M. fasciatus* consumes about 20,000 termites/day (Cooper and Withers 2004b; Friend 1987a, 1993).

The hygric physiology of *M. fasciatus* is typical of other marsupials, despite their historically semiarid and arid zone distribution. Although *M. fasciatus* has a relatively low evaporative water loss (<50% of the allometrically predicted value for a marsupial—Cooper and Withers 2002), its field water turnover rate of 84.1 ml H<sub>2</sub>O/day conforms to that of other marsupials (101% of the allometric prediction—Cooper et al. 2003b). The combination of low energy content, low digestibility, and high water content (77%) means that the termitivorous diet of *M. fasciatus* provides a high water economy index (0.2–0.29 mg H<sub>2</sub>O/ml O<sub>2</sub>) compared to other animal-based diets. Therefore, *M. fasciatus* is presumably more energy than water limited, and does not require drinking water even during summer (Cooper and Withers 2004b). Kidney structure also suggests little selection for water conservation, with the calculated maximal urine concentration of 3,617 mOsm/kg H<sub>2</sub>O being typical of that of other dasyurid marsupials (Cooper and Withers 2010).

The diurnal activity of *M. fasciatus* allows exploitation of solar radiation to reduce the energetic costs of thermoregulation, and there is a close association of activity with light intensity (Cooper and Withers 2004c). The sparse and shallow pelt has a low thermal resistance, low reflectivity, and high absorptivity, facilitating a high solar heat load at the skin surface, of 60–63% of incident solar radiation (Cooper et al. 2003a). Interestingly, *M. fasciatus* has a solar heat gain equivalent to the highest measured for any mammal, but without as great a

reduction in thermal resistance. Solar heat gain can contribute 0.5–3.6 times resting metabolic heat production, and therefore is important for energy conservation (Cooper et al. 2003a).

## ONTOGENY AND REPRODUCTION

**Ontogeny.**—The gestation period of *Myrmecobius fasciatus* is 14 days (Friend and Whitford 1986, 1988, 1993) after which a litter of 4 young is produced. Newborn young are about 20 mm long and attach to the nipples and entwine their forelimbs in the specialized crimped hair of the mammary area, in the absence of a pouch. The young have a remarkably compressed snout, presumably to facilitate oral attachment to the nipple (Wood Jones 1923a). They remain attached to the female for up to 6 months (Calaby 1960). Milk of *M. fasciatus* is characterized by 29% solids, 14% protein, 12% fat, and 2% hexose (Griffiths et al. 1988). Lipids are almost all triglycerides, with a very high concentration of oleic acid and some arachidonic acid. *M. fasciatus* milk is remarkably similar to that of the myrmecophagous short-beaked echidna (*Tachyglossus aculeatus*); the very high oleic acid concentration presumably reflects the high oleic acid concentration in ants and termites (Griffiths et al. 1988).

Young *M. fasciatus* develop a light downy coat by the time they are 30 mm in length, but their distinctive striped markings do not become apparent until about 55 mm in length (Calaby 1960). In late July or early August, at about 75 mm in length, they are deposited in a nest in a burrow or hollow log (Friend 1987b; Friend and Burrows 1983). At this stage females may carry their young between nests on their back. The young begin foraging for themselves in late September and they are independent by November (Friend 1987b). Females may breed in their 1st year, but males are not sexually mature until their 2nd year (Friend 1990).

**Reproduction.**—Female *Myrmecobius fasciatus* entirely lack a pouch, and in this way differ from many other marsupials. On the abdominal region there are 4 nipples, which are covered in crimped, golden hair that differs markedly from the rest of the longer white hair of the ventral surface (Friend 1993). Following estrus, swelling of the lower abdomen and inner thighs provides a protective depression of the mammary area (Friend 1997). The ovaries are situated ventral to the anterior ends of the uteri. The fallopian tubes are thin and convoluted, and somewhat continuous with the uteri. The uteri are composed of body and neck regions, and lie transverse to the long axis of the animal. At the posterior end the somewhat bulbous body narrows into the neck region, which opens into 2 median vaginae that in turn end in cul-de-sacs close to the anterior tip of the urogenital sinus. Two long, coiled lateral vaginae branch off from the uterine necks, and together with the urethra empty into the unusually long urogenital sinus.

There is a distinct cloaca into which both the urogenital sinus and the anus empty (Hill 1900).

The male reproductive system is typical of a marsupial. The testes are contained in a prepenile scrotal sac suspended by a peduncle. The distal portion of the penis is cleft for about 5 mm and the tips are covered in smooth skin, contrasting with the spiny keratinized shaft. The prostate of *M. fasciatus* is remarkably enlarged compared to that of other marsupials, extending from the kidneys to the pelvis. The testes are ellipsoid, with the efferent ducts passing to the epididymis from the median anterior region. The vas deferentia enter the urethra near the bladder on a longitudinal ridge, the verumontanum. The accessory glands consist of 3 sets of Cowper's glands, 1 of which is greatly enlarged (Fordham 1928).

*Myrmecobius fasciatus* has a seasonal reproductive cycle, with females producing 1 litter per year during summer, although some young may be produced as late as April (Calaby 1960; Friend and Burrows 1983; Friend and Whitford 1988, 1993). Examination of data from captive *M. fasciatus* suggests that it is facultatively polyestrous with a restricted breeding season, because females that have failed to conceive after mating or have lost pouch young may conceive with subsequent mating (Power et al. 2009; Power and Monaghan 2003). Males also have a distinct fertility cycle, with sperm beginning to appear in the urine in early December, declining in early February, and absent by March (Power et al. 2009).

## ECOLOGY

The historical distribution of *Myrmecobius fasciatus* encompassed a variety of terrestrial biomes, from the mesic forests of the southwest of Western Australia to the arid grasslands of the central deserts. In desert regions, *M. fasciatus* appears to have inhabited mulga (*Acacia aneura*) woodland, spinifex (*Triodia*) grassland, and sand-dune country (Bester and Rusten 2009; Finlayson 1933; Friend 1993; Friend et al. 1982). In the more westerly parts of its distribution, *M. fasciatus* inhabited woodland dominated by *Eucalyptus* species, with an open shrubby understory (Calaby 1960). In the semiarid eastern wheat belt of Western Australia, it was found in salmon gum (*Eucalyptus salmonophloia*) woodlands, and in wandoo (*E. wandoo*) woodlands in the western wheat belt (Calaby 1960; Friend 1993). In forested areas, *M. fasciatus* preferred jarrah (*Eucalyptus marginata*) and marri (*E. calophylla*) with a sparse shrubby understory (Connell and Friend 1985). Fallen logs were an important habitat component in forested areas, although *M. fasciatus* used burrows for shelter in arid regions (Bester and Rusten 2009; Friend 1993). The 2 remaining natural populations of *M. fasciatus* are found in eucalypt forest (Fig. 4). Dryandra Woodland is a remnant of open shrub and



**Fig. 4.**—*Myrmecobius fasciatus* habitat: Top, Wandoo (*Eucalyptus wandoo*) woodland at Dryandra Woodland and bottom, Jarrah (*Eucalyptus marginata*) forest at Perup Nature Reserve, Western Australia.

savannah eucalypt woodland, dominated by wandoo with a shrub understory consisting of the sandplain poison pea (*Gastrolobium microcarpum*) in the valleys and lower slopes, and powderbark (*E. accedens*) with a sandplain poison pea and *Dryandra* understory on the upper slopes and hilltops (Calaby 1960). Fallen logs are abundant on the ground, and the majority of these are hollow due to the activities of termites *Coptotermes acinaciformis*. Perup Nature Reserve is dominated by jarrah and marri, with some patches of wandoo. The valley understory consists of *Gastrolobium bilobum* and *Melaleuca viminea*, whereas the uplands are characterized by *Bossiaea*, *Leucophogon*, and *Hakea*. Fallen timber is abundant on the forest floor (Christensen et al. 1984). *M. fasciatus* is predominately found in areas dominated by jarrah at Perup Nature Reserve (Friend 2005), despite Calaby's (1960) observation

that jarrah forest was unsuitable habitat for *M. fasciatus*. It is possible that human modification of the jarrah forest structure by logging, such as reduced timber density and increased abundance of fallen timber, has improved the suitability of these jarrah forest areas for *M. fasciatus* (Christensen et al. 1984).

*Myrmecobius fasciatus* is exclusively termitivorous, feeding on a variety of subterranean termite species in proportion to their abundance in the feeding area. *C. acinaciformis* and *Amitermes obeuntis* are generally the most common species in the current distribution of *M. fasciatus*, and are eaten most frequently (Calaby 1960; Christensen et al. 1984). Ants appear to be very uncommon in the diet, and are presumably only incidentally consumed as those found in scats of *M. fasciatus* are small predatory species that probably feed on the exposed termites. While feeding, *M. fasciatus* invariably ingests a variety of debris that adheres to the tongue along with the termites (Calaby 1960); it consumes at least 0.33 g of dirt for every gram of organic matter (Cooper and Withers 2004b).

Radiotracking studies and direct observations have confirmed predation of *M. fasciatus* by domestic cats (*Felis catus*), red foxes (*Vulpes vulpes*), and carpet pythons (*Morelia spilota*), as well as a variety of birds of prey including the brown goshawk (*Accipiter fasciatus*), collared sparrowhawk (*Accipiter cirrocephalus*), little eagle (*Hieraaetus morphnoides*), wedge-tailed eagle (*Aquila audax*), and brown falcon (*Falco berigora*—Bester and Rusten 2009; Friend 2008; Friend and Thomas 1995, 2003). Other presumed predators include the western quoll (chuditch [*Dasyurus geoffroii*]) and the dingo (*Canis lupus dingo*).

*Myrmecobius fasciatus* has a variety of ecto- and endoparasites. Ectoparasites include ticks (*Ixodes vestitus*, *I. myrmecobii*, and *Amblyomma triguttatum*—Calaby 1960; Roberts 1962), fleas (*Echidnophaga myrmecobii* and *E. perilis*—Hopkins and Rothschild 1953), and a mite (*Mesolaelaps australiensis*—Domrow 1958). Three nematodes, *Beveridgeiella calabyi*, *B. inglisi*, and an undescribed *Echinonema* species, have been identified from the alimentary tract (Humphrey-Smith 1980; Smales 1997). A new species of acanthocephalan, *Mulusentis myrmecobius*, which appears to be related to other Oligacanthorhynchidae genera that infect insectivores and edentates, was identified from the small intestine of *M. fasciatus* at Dryandra Woodland, and was associated with mortality of some individuals (Friend and Thomas 2003; Smales 1997). Because acanthocephalans typically use arthropods as intermediate hosts, termites probably play a role in the life cycle of this species, and the termitivorous diet of *M. fasciatus* leads to infection (Smales 1997). Mycobacterial infections (*Mycobacterium intracellulare* and *M. chelonae abscessus*) have been identified in captive individuals (Gaynor et al. 1990).

## HUSBANDRY

*Myrmecobius fasciatus* may be maintained and bred successfully in captivity, but its specialized termite diet makes husbandry difficult (Power and Monaghan 2003). *M. fasciatus* has been successfully housed in enclosures measuring at least 2 by 4 m, which need to be completely enclosed to prevent escape; *M. fasciatus* is an agile climber. Enclosure walls must be sunk at least 0.6 m below the ground surface to prevent digging out. Health issues such as dermatitis may result from damp conditions, so good drainage is recommended (Power and Monaghan 2003). A natural substrate that allows for foraging and burrowing behavior is desirable, and the root systems of live plants in the enclosure provide soil stability and reduce the chance of burrows collapsing. Hollow logs or nest boxes also should be provided, along with nesting material such as couch grass and dried seagrass (Power and Monaghan 2003). Solitary housing is recommended for most of the year. Individuals can be paired for breeding; a male is generally introduced to a female's enclosure where he remains until pouch young are produced. At this time the male should be removed to prevent interference with the pouch young. Young *M. fasciatus* should be gradually separated from the mother at 10–11 months of age in readiness for the next breeding season (Friend and Whitford 1988; Power and Monaghan 2003).

Female *M. fasciatus* require a pure termite diet during the breeding season for successful reproduction. Termites can be harvested using metal drums filled with wood placed on termite mounds or galleries and once separated from the wood can be stored frozen for several months without any apparent loss of nutrition or palatability. An artificial diet consisting of lactose-free milk powder and eggs can be used to supplement the termite diet of males and nonbreeding females (Friend and Whitford 1988; Power and Monaghan 2003).

No unfurred *M. fasciatus* pouch young has been successfully hand-reared, but young that are 6 months or older have been reared to independence (Power and Monaghan 2003). Two low-lactose formulas have been successfully used for hand-rearing; 150% concentrated Wombaroo kangaroo milk (Wombaroo Food Products, Adelaide, South Australia) and 100% concentrate Digestelact mix (Sharpe Laboratories, Ermington, New South Wales, Australia). Syringes, tube feeding, and possum-sized artificial teats have been used to administer artificial milk formulas, until the young are able to lap the milk themselves. Young have been successfully fostered onto other lactating females with recently weaned young (Power and Monaghan 2003).

*Myrmecobius fasciatus* is best handled in a cloth bag to reduce stress, but it does not bite, rarely scratches, and makes little attempt to escape while being held (Fleay 1942). Individuals can be restrained by gripping firmly around the

shoulders with one hand, with the other hand supporting the lower part of the body and hind feet (Calaby 1960; Power and Monaghan 2003). Observations of *M. fasciatus* in the wild are best conducted from a vehicle, because it is less disturbed by observers in a vehicle than on foot (Calaby 1960). *M. fasciatus* cannot be trapped using conventional cage trapping techniques, and therefore surveys are best conducted by slowly driving along prescribed transects and recording the number of individuals spotted, or searching for diggings, scats, or hair (Connell and Friend 1985).

## BEHAVIOR

*Myrmecobius fasciatus* is unusual among marsupials in particular, and Australian mammals in general, in that it is exclusively diurnal. There are anecdotal reports from Aboriginal people of nocturnal activity (Friend et al. 1982) and early studies described the species as crepuscular or arrhythmic (Le Souef and Burrell 1926; Wood Jones 1923b). However, monitoring of captive individuals (Cooper and Withers 2004c) and radiotracking of wild *M. fasciatus* (Christensen et al. 1984; Friend 1986; Maisey and Bradbury 1983) has confirmed that it is only active during the day. The diurnal activity of *M. fasciatus* is a consequence of its specialized termitivorous diet, and is closely associated with the increased abundance of termites in subterranean soil galleries during the day (Evans and Gleeson 2001; Friend 1986). *M. fasciatus* is not powerful enough to break into termite mounds to extract prey, unlike many other mammalian myrmecophages, and therefore must feed on termites when they are active in shallow subsurface soil galleries.

There are strong seasonal patterns in activity of *M. fasciatus*, which are related to photoperiod, prey abundance, and reproductive condition. During spring and summer, which also coincides with the breeding season, *M. fasciatus* is active for longer periods than during autumn and winter (Cooper and Withers 2004c). In summer, wild *M. fasciatus* has a distinctly bimodal pattern of activity, being active in the mornings and late afternoons and sheltering in hollow logs or burrows during the middle of the day (Christensen et al. 1984; Friend and Burrows 1983; Maisey and Bradbury 1983). During winter, *M. fasciatus* is active mostly during the middle of the day (Christensen et al. 1984; Maisey and Bradbury 1983). These activity patterns not only reflect seasonal changes in the timing of prey availability, but also minimize thermoregulatory costs.

Weather also influences activity of *M. fasciatus*, because it avoids periods of low light intensity and high relative humidity (Cooper and Withers 2004c). Solar heat gain presumably plays an important role in thermoregulation and energy balance for *M. fasciatus* (Cooper et al. 2003a), which minimizes its activity when light levels are low. High relative humidity is associated with rain, which *M. fasciatus* avoids (Calaby 1960), and may also compromise evaporative cooling at high ambient temper-

atures. Ambient temperature and wind speed appear to have little direct effect on activity of *M. fasciatus* (Cooper and Withers 2004c; Maisey and Bradbury 1983).

*Myrmecobius fasciatus* shelters at night in hollow logs, tree hollows, and burrows, and also uses these refuges to escape from predators during the day. It uses a large number of refuges within its home range during the day, although frequents a few night refuges in which a nest of bark, grass, or leaves is constructed (Friend 1993). *M. fasciatus* preferentially selects single-entrance hollows of approximately 8 cm in diameter (Christensen et al. 1984; Maisey and Bradbury 1983) and digs burrows consisting of a straight, shallow shaft about 1 m long, with a terminal chamber 15–23 cm in diameter and 10–60 cm below ground level (Christensen et al. 1984; Friend 1993). Refuge logs and burrows used by *M. fasciatus* buffer environmental conditions, such as temperature, but there are only minor differences between refuge and ambient gas composition or relative humidity. Occupied night refuges are on average 5°C warmer than ambient temperature, which, together with the increased insulation provided by a nest, results in considerable energy savings by reducing thermoregulatory costs (Cooper and Withers 2005).

*Myrmecobius fasciatus* is generally solitary, except for mothers with their young, although males and females may share a nest during the reproductive season (Calaby 1960; Christensen et al. 1984). Play behavior, such as running and chasing, has been observed among young litter mates until they reach about 10 months of age (Byers 1999). Once independent, young disperse from their natal area (in 1 study, between 0.6 and 10 km, mean 3.6 km) and establish a territory that they maintain for life (Friend 1987a, 1987b; Friend and Burrows 1983). Adult *M. fasciatus* maintain individual home ranges of about 50 ha, from which members of the same sex are excluded, although males and females may have overlapping territories (Friend 1987b, 1997).

*Myrmecobius fasciatus* is unable to feed directly from termite mounds, but extracts termites from shallow subsurface soil galleries and rotting vegetation (Calaby 1960). While searching for food, *M. fasciatus* walks slowly, sniffing the ground. When termites are located, *M. fasciatus* sits on its hind feet and digs at the soil with the sharp claws of the forefeet, turning over the top 2 or 3 cm of soil to expose the subterranean termite galleries. This digging forms distinctive conical holes, not unlike ant-lion (Myrmeleontidae) traps. The exposed termites are then rapidly licked up with the long tongue coated in sticky saliva. *M. fasciatus* also turns over small pieces of wood and other vegetation with its paws or snout to locate termites, and scratches bark and decaying wood from logs. Favored foraging locations include the bases of large trees, around fallen logs, close to termite mounds, and alongside partly exposed tree roots (Calaby 1960; Christensen et al. 1984). *M. fasciatus* feeds for only a few minutes at a particular location before moving some distance to a new location.

Locomotion is generally a walk or trot, and movements tend to be jerky. *M. fasciatus* periodically ceases feeding, and appears to scan its surroundings, presumably looking for predators; it often sits vertically on its hind feet, or raises a forepaw in a manner characteristic of alert dasyurids. The tail is carried horizontally, with a slight upward curve. If *M. fasciatus* is excited or stressed, the tail is arched over the back and the fur erected to give a characteristic bottlebrush appearance (Fleay 1942). If disturbed or threatened, *M. fasciatus* runs with a bounding gait typical of similar-sized mammals; one *M. fasciatus* was timed running at 32 km/h (Calaby 1960; Fleay 1942). When disturbed it will flee rapidly to a hollow log, although not necessarily the nearest, sometimes pausing briefly before entering to look around (Calaby 1960). Once inside a hollow, *M. fasciatus* presses its body firmly against, and uses its claws to grasp the walls of, the hollow, to brace itself against any attempt at extraction. The dorsoventrally flattened hindquarters allow *M. fasciatus* to turn in very confined spaces, and it always emerges from hollows or burrows headfirst (Christensen et al. 1984; Friend 1982). A variety of vocalizations have been recorded, usually when *M. fasciatus* is handled or otherwise disturbed. These include a low growl produced with the mouth closed, a repetitive “tut tut tut,” and the hissing noises typical of many marsupials (Calaby 1960; Fleay 1942).

## GENETICS

*Myrmecobius fasciatus* has a diploid number (2n) of 14 chromosomes, as is typical for many marsupials, and the chromosome form is also similar to that of other marsupials (Archer and Kirsch 1977). Mitochondrial DNA sequences of *M. fasciatus* from Dryandra Woodland and Perup Nature Reserve indicate that there was recent connectivity between these remnant populations, and that they can be managed as a single genetic lineage (Fumagalli et al. 1999). However, there is evidence that the Perup population has reduced genetic diversity, presumably due to a recent population bottleneck. Translocation of *M. fasciatus* to Perup Nature Reserve from Dryandra Woodland may be an appropriate management strategy to improve the genetic diversity of the Perup population if disease issues can be addressed appropriately (Fumagalli et al. 1999). Molecular evidence supports morphological phylogenies placing *M. fasciatus* at the base of the Australian dasyurid radiation, with a divergence date from the dasyurids of 32.8–42.2 million years ago (Bininda-Emonds et al. 2007; Kirsch et al. 1997).

## CONSERVATION

*Myrmecobius fasciatus* is currently listed by the International Union for Conservation of Nature and Natural Resources as “Endangered,” with a population of fewer

than 2,500 individuals and an estimated continuing decline of at least 20% within 5 years, together with a continuing decline in numbers of mature individuals and a population structure with fewer than 250 individuals in any subpopulation (International Union for Conservation of Nature and Natural Resources 2009). It is listed by the Australian Department of Environment, Water, Heritage and the Arts as “Vulnerable” (Department of Environment, Water, Heritage and the Arts 1999), and under the Western Australian Wildlife Conservation Act as a Schedule 1 species (i.e., rare or likely to become extinct—Department of Environment and Conservation 2008).

The distribution of *M. fasciatus* has contracted dramatically since European settlement in Australia (Friend 1990). Once widespread across southern Australia, the range of *M. fasciatus* began to retract almost immediately postsettlement. The last specimen from western New South Wales was collected in 1857. *M. fasciatus* was present in Adelaide at the time of settlement, but was extinct there by the early 1920s, although there is anecdotal evidence of survival further inland in the rangelands of South Australia until the 1930s or 1940s (Friend et al. 1982). In the central deserts, *M. fasciatus* appears to have persisted until the 1950s or 1960s (Friend et al. 1982) and it persisted in parts of the Western Australian wheat belt into the 1970s. During the late 1970s there was a dramatic decline in the distribution and abundance of *M. fasciatus* throughout its remaining range. It became extinct in the northern jarrah forest, on the Swan Coastal Plain, and in jarrah forest west of Collie during the 1980s, and by the mid-1980s only 2 small, disjunct populations survived, at Dryandra Woodland and Perup Nature Reserve (Abbott 2008; Friend 1987a, 1990, 2010).

The rapid disappearance of *M. fasciatus* from the central deserts during the 1940s to 1960s coincided with the extinction in this region of the vast majority of critical weight-range (5–5,000 g) mammals (Burbidge et al. 1988). According to Burbidge et al. (1988), a combination of changing fire regimes as Aboriginal people abandoned traditional land management practices, effects of predation by introduced red foxes and feral cats, and competition with exotic herbivores such as European rabbits (*Oryctolagus cuniculus*) accounts for much of the observed faunal attrition. Reduction in ground cover caused by extensive wildfires and increased herbivory presumably increased the vulnerability of *M. fasciatus* to efficient exotic predators, and its decline closely matches the spread and increase in numbers of the red fox throughout this region (Friend 1990).

Peacock (2006) and Abbott (2006) suggested that epizootic disease, with drought and predation by feral cats as secondary factors, may have been responsible for a significant decline of native mammals, including *M. fasciatus*, in Western Australia from 1880 to 1920, well before the establishment of foxes in the region. Existing populations of *M. fasciatus* in the southwest of Western

Australia also were observed to decline during the 1920s, 1930s, and 1940, with suggested causes including clearing for agriculture, collection of firewood, fumigation of burrows for rabbit control, scientific collection, and bushfires (Abbott 2008). Predation by red foxes is certainly a major factor implicated in the decline of the species in the region. *M. fasciatus* appeared reasonably common in many southwestern locations until the appearance of the red fox (Abbott 2008; Peacock 2006), and the response of populations of *M. fasciatus* to fox control programs adds further evidence that this introduced predator contributed greatly to the decline of *M. fasciatus* (Friend 1990; Friend and Thomas 2003; Kinnear et al. 2002; Peacock 2006).

In the southwest of Western Australia, *M. fasciatus* persisted in regions where there was a high density of hollow logs, abundance of poison peas (*Gastrolobium*), or low density of foxes (Friend 1990). However, even in these strongholds, populations of *M. fasciatus* have now declined to less than 10% of their 1970s abundance. This recent decline has been attributed to an increase in red fox predation associated with the cessation of a rabbit control program (which presumably caused secondary poisoning of foxes), an increase in fire frequency, and several years of reduced rainfall that may have reduced termite abundance (Friend 1987a, 1990). A study during the early 1980s of the effects of red fox baiting on abundance of *M. fasciatus* provided evidence that populations of *M. fasciatus* increased with a reduced density of these introduced predators. Since that time, ongoing fox control programs at Dryandra Woodland have resulted in an increase in abundance of *M. fasciatus*, at times comparable to their high abundance in the 1950s (Friend 1990; Friend and Thomas 2003; Kinnear et al. 2002). By the early 1990s there were an estimated 800 *M. fasciatus* at Dryandra Woodland, and this area was used as a source of animals for translocation and, later, captive-breeding programs (Friend and Thomas 1995, 2003).

The 1st translocation program of *M. fasciatus* was carried out at the 5,000-ha Boyagin Nature Reserve, 40 km north of Dryandra Woodland during 1985–1988 (Friend and Thomas 1995). *M. fasciatus* had been recorded at the reserve until the 1970s but was locally extinct at the time of the introduction. A fox-baiting program was established and a total of 35 *M. fasciatus* were transferred from Dryandra to the eastern part of the reserve. All individuals established a home range within 6 weeks of release, and 90% of the females bred in their 1st breeding season. Subsequent surveys indicated that a self-sustaining population of *M. fasciatus* was established at the reserve, with all available habitat colonized, and that *M. fasciatus* also had colonized the western block of the reserve. This study provided evidence that *M. fasciatus* could be successfully reintroduced into areas within its prior distribution (Friend and Thomas 1995, 2003).

*Myrmecobius fasciatus* has been subsequently reintroduced to a further 7 sites in the southwest of Western

Australia (Batalling State Forest, Dale Conservation Park, Dragon Rocks Nature Reserve, Karakamia Sanctuary, Karroun Hill Nature Reserve, Stirling Range National Park, and Tutanning Nature Reserve), as well as Yookamurra Sanctuary near Sedan, South Australia, and Scotia Sanctuary in western New South Wales (Friend and Thomas 2003). An additional trial release of 5 individuals was conducted at the Arid Recovery Reserve, Roxby Downs, South Australia (Bester and Rusten 2009). Many of these reintroductions have resulted in self-sustaining populations of *M. fasciatus* that are an important addition to the remaining natural populations at Dryandra Woodland and Perup Nature Reserve. The majority of translocated *M. fasciatus* have been sourced from Dryandra, with a total of 325 individuals taken from this site up to 2001. During the late 1980s, up to 33 individuals per year were removed for translocation, but after a population decline during the early 1990s this was reduced to no more than 5 individuals per year. Perth Zoo developed a captive-breeding program to supply *M. fasciatus* for translocation, and 74 captive-bred *M. fasciatus* were contributed by the zoo to the translocation programs between 1993 and 2001 (Friend and Thomas 2003). Translocations appear to have been most successful in discrete remnant patches surrounded by cleared areas, where *M. fasciatus* cannot disperse long distances and is concentrated for breeding (e.g., Boyagin, Tutanning, and Dragon Rocks Nature Reserves). *M. fasciatus* reintroduced to areas with little understory vegetation (Karroun Hill and Stirling Range) suffered considerable predation by raptors, whereas *M. fasciatus* in fenced reserves (Karakamia, Scotia, and Yookamurra sanctuaries) has undergone the most rapid increase in numbers, either due to reduced fox predation or restricted dispersal (Friend and Thomas 2003).

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