



Survival Strategies of the Echidna *Tachyglossus aculeatus* Shaw 1792 (Monotremata: Tachyglossidae)

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ABSTRACT

*The area occupied by the Western Australian wheatbelt has experienced extensive land clearing for agriculture between 1900 and 1970. In many areas >90% of the original vegetation has been cleared, and exotic predators (fox and cat) are common. Of the 56 mammal species recorded for the region since agricultural settlement, 25% have become extinct and a further 21% have declined in range. Yet not all species have been equally affected. The echidna *Tachyglossus aculeatus* acanthion, a termite- and ant-eating specialist, remains ubiquitous and its populations are stable. It is successful because (a) it is not restricted by habitat; (b) it specializes on an abundant and reliable food source for which there is no apparent competition; (c) it is metabolically capable of tolerating low energy conditions, such as drought- or fire-induced food shortages; (d) its shelter requirements are independent of vegetation; (e) predation on adult animals is minimal; and (f) it can survive outside nature reserves, and is capable of dispersing to distant remnants.*

*Morphological and physiological adaptations to myrmecophagy (termite- and ant-eating) now enable *Tachyglossus* to cope with exotic predators and the loss and fragmentation of habitat. These adaptations are likely to benefit other mammalian myrmecophages living in similar environments. The native numbat *Myrmecobius fasciatus* is an exception. It has declined to <10% of its former range because it lacks an effective defence against exotic predators.*

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and is today restricted to habitats where log shelters provide a measure of protection from fox and feral cat.

INTRODUCTION

As a result of the European colonization of Australia, which commenced 200 years ago, a large proportion of the continent has been subjected to detrimental influences affecting all components of the environment, from individual plant and animal species to habitats and ecosystems (Saunders *et al.*, 1990). The decline and extinction of species among plants (Patrick, 1985), mammals (Kitchener *et al.*, 1980a) and birds (Saunders & Curry, 1990) have been attributed to a combination of factors such as land clearing for agriculture (Saunders *et al.*, 1985; Hobbs, 1987), exotic predators (Kinnear *et al.*, 1988; Friend, 1990), a change in fire regimes (Burbidge, 1985; Smith, 1985), and competition for food and habitat modification by introduced herbivores (Dawson & Ellis, 1984; Morton, 1990). Reptiles have been more resistant to European colonization (Kitchener *et al.*, 1980b). The long-term effects of land clearing on invertebrates are poorly understood, although termites and ants re-establish themselves rapidly in areas formerly cleared (Bunn, 1983; Majer *et al.*, 1984).

Of the Western Australian geographical regions surveyed, Burbidge and McKenzie (1989) found highest rates of mammalian decline and extinction in the wheatbelt (Fig. 1), with medium-sized mammals (34–4200 g) the most severely affected. Twenty-five percent of the 56 species of mammal recorded from the wheatbelt since European settlement are now extinct and a further 21% have declined in range (Kitchener *et al.*, 1980a; Burbidge & McKenzie, 1989), but there are exceptions to this pattern. The echidna *Tachyglossus aculeatus acanthion*, a mammalian myrmecophage (termite- and ant-eating specialist), is an outstanding example. It is one of the few medium-sized native mammals to have survived loss and fragmentation of habitat, as well as exotic predators, apparently unscathed. There is no evidence for range contraction, or significant population declines in areas of native vegetation remnants (Burbidge & McKenzie, 1989). It remains ubiquitous and sightings are reported regularly, even in areas such as the wheatbelt that have experienced severe loss and fragmentation of habitat (Kitchener *et al.*, 1980a; Arnold *et al.*, 1987).

Until recently the ecology of *Tachyglossus* was poorly known, and the first comprehensive ecological investigation was conducted in the Western Australian wheatbelt by Abensperg-Traun (1990). That study provides the background to this paper, which aims to examine the evidence for the success of *Tachyglossus* in coping with the combined effect of habitat loss and exotic predation.

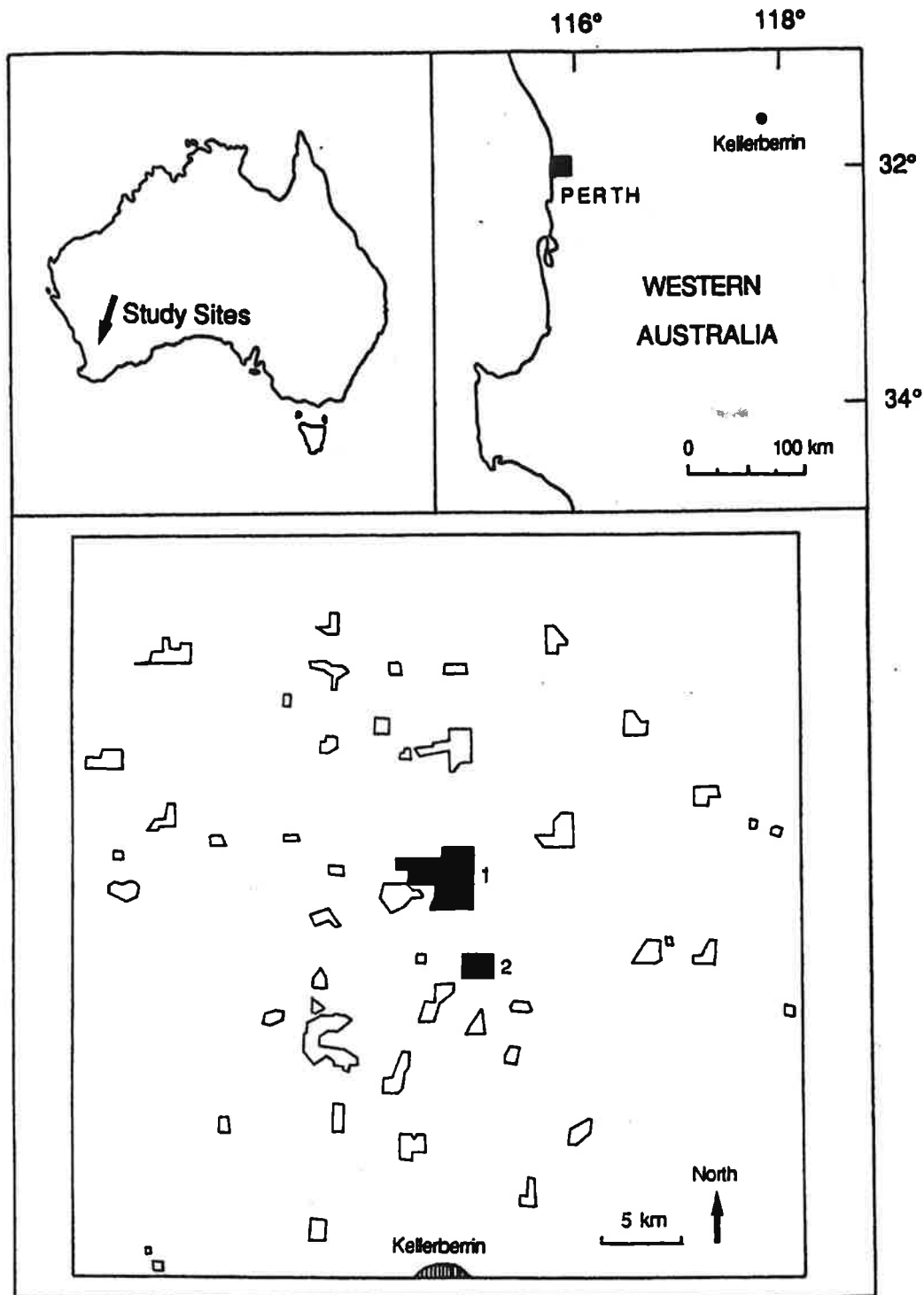


Fig. 1. Location map for Durokoppin (1) and Kodj Kodjin (2) nature reserves within the Kellerberrin district of Western Australia, showing the size and distribution of other vegetation remnants within the Kellerberrin district (□). (Reproduced by courtesy of the Western Australian Museum.)

STUDY AREA

The Western Australian wheatbelt is a wheat- and sheep-farming district that encompasses an area of approximately 140 000 km². Most of the original vegetation was cleared between 1900 and 1970, and the region now contains in excess of 600 nature reserves, varying in size from 0.4–309 000 ha, with a median size of 114 ha. The great majority of reserves are thus very small. Nature reserves occupy approximately 7% of the total area of the wheatbelt, but road verges and private land also carry significant areas of native vegetation (Beard & Sprenger, 1984; Wallace & Moore, 1987). All such patches of native vegetation will be referred to as remnants.

Most of the information given here originates from a study into the foraging ecology of *Tachyglossus* (Abensperg-Traun, 1990). Study sites were located in Durokoppin (31° 24' S, 117° 45' E; 1040 ha) and Kodj Kodjin (31° 27' S, 117° 47' E; 204 ha) nature reserves between 1987 and 1989 (Fig. 1). Although surrounded by farmland, these reserves are connected by a strip of native vegetation 2.7 km long and 40 m wide. The climate is semi-arid (Gentilli, 1965). Surface water, with the exception of ephemeral pools, is absent. The vegetation consists of patches of woodland, mallee, shrubland and heath, and has been described elsewhere (Beard, 1980; Abensperg-Traun & De Boer, 1990).

SURVIVAL STRATEGIES OF THE ECHIDNA

Examination of literature (e.g. Main & Yadav, 1971; Kitchener *et al.*, 1980a; Burbidge & McKenzie, 1989) indicates that the mechanisms most likely to contribute to *Tachyglossus*' success can be usefully discussed under the headings of (a) food and habitat requirements (e.g. dietary specialization, habitat restriction, shelter requirements); (b) environmental fluctuations and metabolic requirements (e.g. drought, fire); (c) predation (exotic predators); and (d) mobility (e.g. dispersal).

Food and habitat requirements

In the Western Australian wheatbelt *Tachyglossus* feeds almost exclusively on termites and ants (Abensperg-Traun, 1988; Abensperg-Traun *et al.*, in press). Termites are the main food in all seasons (Abensperg-Traun & De Boer, in press). Because termites and ants are abundant and clumped in their distribution they can be readily found and exploited. As a consequence *Tachyglossus*, in common with most other mammalian myrmecophages, has evolved highly specialized morphological and physiological adaptations

such as an elongate snout and tongue, broad spatulate forelimbs and digging claws, and a low metabolic rate, which enable it to exploit this resource (McNab, 1984). Such dietary specialization would appear non-adaptive because the wheatbelt is characterized by significant seasonal fluctuations in rainfall (Fitzpatrick, 1970), and hence termite availability (Abensperg-Traun & De Boer, 1990). However, even when termite abundance is low (summer), *Tachyglossus* remains in positive energy balance (Abensperg-Traun & De Boer, in press), suggesting that food is not in short supply. This might be explained by the fact that termite population levels are kept relatively constant by the buffering effect of the mound or nest against climatic extremes, and because they offer very concentrated, easily exploitable sources of energy. An additional advantage of a diet consisting predominantly of termites is their high moisture content (~74%, as against ~64% in ants; Abensperg-Traun & De Boer, in press), which presumably accounts, in part, for *Tachyglossus*' apparent independence of surface water (Bentley & Schmidt-Nielsen, 1967; McKelvey, 1987). However, by itself this ability is not a key to its survival because other mammal species now absent from the wheatbelt were similarly independent of surface water.

A diet of termites and ants also reduces interspecific competition. In the wheatbelt there are no introduced species that compete with *Tachyglossus* for food, and other indigenous myrmecophages are few—the numbat *Myrmecobius fasciatus*, now almost extinct in the region (Calaby, 1960; Friend, 1990); at least two species of lizard, *Ctenotus schomburgkii* and *C. pantherinus* (G. Smith, pers. comm.); and invertebrates such as ants (Greenslade, 1979) and spiders (Main, 1987). Despite the fact that *C. schomburgkii* and *C. pantherinus* are apparently abundant in the wheatbelt, competition for food with *Tachyglossus* is unlikely to occur because of the abundance of the resource and their different foraging strategies—lizards capture surface-active prey while *Tachyglossus* obtains most of its food by digging in the soil. Intraspecific competition is absent or minimal (Abensperg-Traun, 1990).

A factor contributing significantly to *Tachyglossus*' success is that the species is not restricted by habitat because both food and shelter are ubiquitous and apparently unlimited (Abensperg-Traun, 1991; Abensperg-Traun & De Boer, in press). This agrees with evidence from other parts of Australia, where *Tachyglossus* occurs in all major terrestrial environments (Griffiths, 1989).

Fluctuating resources

Although food and shelter are not limited, this may not apply in times of drought, or following extensive fires. Several factors suggest that

Tachyglossus will cope comparatively well with such events. (1) It is well adapted to low energy conditions. When active it spends less metabolic energy than placental and marsupial mammals because of its low metabolic rate (Dawson *et al.*, 1979); it can also adopt torpor (Grigg *et al.*, 1989) and is thus capable of reducing metabolic requirements should energy conditions fall below a critical level. (2) When surface conditions are unfavourable many termite species benefit from stored food, such as grass and plant debris from shrubs, or they utilize subterranean sources of food *in situ*, such as dead roots. Consequently their populations suffer relatively small fluctuations during periods of drought or after fire. (3) Because *Tachyglossus* in the wheatbelt is semi-fossorial (Abensperg-Traun, 1991) destruction of vegetation and hollow logs through fire is unlikely to increase mortality through exposure or increased predation, as has been observed for *Myrmecobius* (Friend, 1990).

Predation

Predation pressure on *Tachyglossus* appears to be low. Prior to European colonization, mammalian predators were probably restricted to Aboriginal man (Leake, 1962), the dingo *Canis familiaris dingo*, the thylacine or Tasmanian tiger *Thylacinus cynocephalus* and the Tasmanian devil *Sarcophilus harrisii*. Today few Aboriginals maintain a traditional way of life, *Thylacinus* is extinct (Archer, 1984), *Sarcophilus* is restricted to the island of Tasmania (Guiler, 1978) and dingos are absent from the southwest of Western Australia (Newsome & Coman, 1989). But European settlers introduced the red fox *Vulpes vulpes* and the cat *Felis catus*. These occur in the wheatbelt (King & Smith, 1985) and are known to ingest *Tachyglossus* flesh (McKenzie & Burbidge, 1973; Triggs *et al.*, 1984). However, given that by six months of age *Tachyglossus* is protected by a coat of long stout spines (Abensperg-Traun, 1989), I believe such faecal material to be evidence of scavenged carcasses (e.g. road kills) rather than predation *per se*, especially of fully grown animals (Griffiths, 1989). Using spines in combination with other strategies, *Tachyglossus* has a range of options to escape being eaten: rolling into a ball, with spines protecting it on all sides; using its powerful claws to dig into the soil until only spines are visible on the surface, simultaneously claspng root structures; or expanding its coat of spines, and using its powerful dorsal musculature to wedge itself into narrow parts of hollow logs and other crevices. Spines thus play a crucial role in minimizing predation, and these may have evolved so as to compensate for its low speed. Lacking hard spines, young animals are known to be occasionally taken by feral cats (Griffiths, 1989), but the extent of such predation is poorly understood. However, one may surmise that fox and cat predation on

juveniles is not excessive because the distribution and abundance of *Tachyglossus* in wheatbelt vegetation remnants has not apparently changed since European settlement (Burbidge & McKenzie, 1989).

Mobility

Given that most remnants in the wheatbelt are small and frequently isolated by farmland, the well-being of *Tachyglossus* populations within such refuges may depend on their ability to disperse to outlying remnants, thus preventing the deleterious effects of inbreeding or chance crashes in population levels (Soulé, 1980). However, *Tachyglossus* is able to exist permanently outside reserves, utilizing road verges and other small vegetation remnants, and is known to cross long distances of farmland (Kitchener *et al.*, 1980a; Arnold *et al.*, 1987; Abensperg-Traun, 1991). In such circumstances the species benefits from the large number of rabbit burrows, which it uses regularly (Abensperg-Traun, 1990).

DISCUSSION

The above evidence suggests that *Tachyglossus aculeatus acanthion* remains ubiquitous and relatively common in the Western Australian wheatbelt because (1) it can utilize all types of habitat; (2) it specializes on an abundant and reliable food source for which there is no apparent competition; (3) it has a metabolic ability to tolerate conditions of low prey availability, which allows it to cope with potential drought- or fire-induced food shortages; (4) it is independent of plants for shelter; (5) adults are rarely preyed upon; and (6) it can survive outside nature reserves, and is able to disperse to distant remnants. These adaptations are absent, or less well developed, in placental and marsupial mammals of the region, many of which have declined in range, or have become extinct, in historical times (Burbidge & McKenzie, 1989). What deserves further emphasis is that some of these adaptations, such as protective spines and a low metabolic rate, have probably evolved as a direct consequence of myrmecophagy (McNab, 1984; Redford, 1987).

Is mammalian myrmecophagy an effective strategy in disturbed and fragmented environments?

Worldwide over 200 species, or some 5%, of living mammals depend to some extent on termites and ants for food, and of these at least 18 species eat little else, i.e. >90% by volume (Redford, 1987). Five percent is surprisingly low considering the abundance and diversity of termites and ants in Australia,

Africa and South America, where most myrmecophages are found. Lubin (1983) explains this phenomenon by suggesting that because termite and ant defence strategies are often effective in reducing mammalian predation to short surprise attacks (Lubin & Montgomery, 1981; Abensperg-Traun *et al.*, in press) myrmecophages need to visit large numbers of prey colonies, and hence have large spatial requirements. Such a foraging strategy, he argues, effectively restricts the number of species (and individuals) that can coexist in a given area. There is evidence from Western Australia to support this explanation: both *Myrmecobius* and *Tachyglossus* exist at low population densities (Calaby, 1960, personal observations) and have large home ranges, up to 100 and 190 ha, respectively (Christensen *et al.*, 1984; Abensperg-Traun, 1991).

Despite this apparent limitation on the diversity of species and the density of populations, mammalian myrmecophages are generally considered successful (Redford, 1987), with no extinctions in historical times (Nowak & Paradiso, 1983). There are some general explanations to account for this apparent success. First, a myrmecophage diet acts as an insurance policy. Once adaptations to a diet based on termites and ants have evolved, ecological replacement, for example by more effective exotic competitors, is difficult because it requires high rates of reproduction and metabolism. Both of these, however, are incompatible with specialized feeding on termites and ants because of the poor quality of such foods (McNab, 1984). Second, their continued survival benefits by a range of factors: the tendency for termite and ant populations to persist despite land clearing or reductions in habitat quality (Bunn, 1983; Majer *et al.*, 1984); wide habitat tolerance, as in echidnas, pangolins *Manis* spp., lesser anteaters *Tamandua* spp. and giant anteaters *Myrmecophaga tridactyla* (Nowak & Paradiso, 1983); and protection against exotic predators by a combination of large size, as in aardvarks *Orycteropus afer* (to 82 kg) and giant armadillos *Priodontes maximus* (to 60 kg); protective scales or spines, as in armadillos *Cobassous* spp., pangolins and echidnas; arboreality, as in lesser anteaters; and the construction, or use, of deep burrows, as in aardvarks, aardwolves *Proteles cristatus*, armadillos, echidnas and some pangolins (Nowak & Paradiso, 1983). However, exotic mammalian predators are possibly less of a threat on other continents because of the presence of large- and intermediate-sized native predators, which, with the exception of the dingo, are absent from Australia today.

From the foregoing it could justifiably be argued that mammalian myrmecophagy is a lucky preadaptation for species under threat from exotic predators, or whose habitat has become fragmented and disturbed. The Australian exception is *Myrmecobius*, which has come close to extinction, possibly because it lacks an effective defence against fox and cat (e.g. spines),

and is today dependent upon hollow logs for safety. In the wheatbelt such shelter is largely restricted to wandoo *Eucalyptus wandoo* woodland, which has suffered a >90% reduction in its former distribution (Beard & Sprenger, 1984). Whereas the future of *Tachyglossus* in the wheatbelt appears to be encouraging, it needs to be kept in mind that it is only a short time since land clearing started and ceased, and that *Tachyglossus* is a very long-lived species, with a recorded maximum of 49 years in captivity (Griffiths, 1989). By implication, any ill effect the species may have suffered from loss and fragmentation of habitat would take longer to manifest itself than were the species short-lived. It would thus be prudent at least to maintain the existing network of wildlife habitat in the region to maximize its ability to survive and successfully reproduce.

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