Burnett, Scott Edward (2001) ***Ecology and conservation status of the northern spot-tailed quoll, Dasyurus maculatus with reference to the future of Australia's marsupial carnivores.*** **PhD thesis, James Cook University.**

Chapter 1.

General Introduction: rationale and scope of this work

Spot-tailed Quolls, *Dasyurus maculatus*, are regarded as Threatened, Endangered or Extinct throughout their range. In this thesis I use data from my field studies on *D. maculatus* and three Eutherian carnivore species and data from a literature review of the fossil record, to assess the short and long term conservation status of the Spot-tailed quoll and other marsupial carnivores. Subsequent Chapters present and discuss these data and my thesis concludes with a conceptual model for the conservation of the Spot-tailed Quoll.

Although this thesis focuses on the ecology and conservation status of the north Queensland population of *D. maculatus* the results are applicable throughout the species' Australian range, and to other species of *Dasyurus*.

Chapter 1. General Introduction: rationale and scope of this work

Five million and then 20 000 years ago, global climates reached a climax of cooling and drying such as had not been seen for about 300 000 000 years (Linacre and Hobbs 1977). These events, called the Terminal Miocene Event (TME) and the Glacial Maximum (GM) respectively, heralded great changes in Australia's biota. The late Miocene and subsequent Pliocene saw the contraction towards the continental margins of the Tertiary rainforest which had covered most if not all of the continent, and the expansion of sclerophyll and grassy habitats in their place (Singh 1982, Martin 1997). These changes had a profound effect on Australia's mammalian biota, and many of our contemporary genera of mammals, including a Quoll, *Dasyurus dunmalli*, first appeared during this time in the early to mid-Pliocene. The Glacial Maximum (20 kya) resulted in the disappearance of much of Australia's megafauna, including several families, genera and species of marsupial carnivores. Meanwhile, in Africa, the Terminal Miocene Event resulted in the development of extensive grasslands which provided the impetus for the evolution of *Homo*, which nearly 5 million years later was to act as agent to even more drastic environmental changes than either of the climatically driven ice age events. Human activities, including land-clearing, road and dam construction, feral carnivore baiting and introduction of feral vertebrates now threaten the survival of the genus *Dasyurus*, with all four Australian species listed as Rare and Threatened or Near Threatened.

Spot-tailed Quolls, *Dasyurus maculatus*, have undergone a decline in their extent of occurrence throughout their mainland Australian range (Maxwell *et al.* 1996, Chapter 8), and are regarded as Threatened, Endangered or Extinct throughout their range (Stanger *et al.* 1998). Studies which examine patterns of faunal extinction and decline following European colonisation of Australia, have shown that *Dasyurus maculatus* is one of the first species to become locally extinct (or at least very rare) following colonisation by Europeans (Lunney and Leary 1988). *D. maculatus* is also one of the few wet tropical rainforest mammals that disappear from large patches of remnant vine forest following habitat fragmentation (Laurance 1989). The rarity and decline in distribution of *D. m. maculatus* in South Australia, New South Wales, Victoria, South

Australia and south-east Queensland (Mansergh 1984, Watt 1993), has led to this species being declared as Vulnerable or Endangered in all mainland states in which it occurs (Stanger *et al.* 1998).

Winter *et al.* (1984) gave north Queensland's disjunct population of *D. maculatus* a conservation prognosis of poor, rating it as the most threatened of the mammals of the wet tropics. The subspecies was first given an official conservation status by the Queensland Government in 1994 when it was classed as Rare under the regulations of the *Nature Conservation Act (Wildlife)* 1994 (Queensland Department of Environment and Heritage 1994). Based upon the results of the work presented below and using IUCN conservation criteria (IUCN 2000) for determining conservation status, north Queensland's *D. maculatus* is listed as Endangered by the Environment Protection and biodiversity Conservation Act 1999 (Commonwealth of Australia 1999).

The conservation status of any species is the outcome of the interaction between its ecology and its environment. In this thesis I document the ecology of the poorly known Northern Spot-tailed quoll, *Dasyurus maculatus*, with the aims of: (1) understanding why the species is endangered (*Nature Conservation (Wildlife) Regulation 1994*, *Environment Protection and Biodiversity Conservation Act 1999*), and; (2) assessing its conservation prognosis in the short and the long term. It was decided early on in this project that an hypothesis-testing approach was inappropriate for this study; the Endangered status of north Queensland's *D. maculatus*, and the extreme scarcity at which it occurs, preclude an experimental approach on practical and ethical grounds. I used a deductive approach, which I justify by the conservation importance of the species.

The aim of this thesis is to assess the short and long term conservation status of the Spot-tailed quoll, *D. maculatus*, by collection and analysis of ecological data, in particular, details of its life-history strategy (Chapter 5), diet (Chapter 6), ranging behaviour (Chapter 7), and distribution (Chapter 8). I then used this information to evaluate the potential impacts of human activities on, and the competitive significance of Eutherian carnivores for the subspecies in north Queensland and throughout its Australian range (Chapter 9). In order to obtain a longer term perspective on the conservation prognosis of the species and of Australia's marsupial carnivore guild in general, I review and search for patterns in the outcomes of the mixing of eutherian and marsupial carnivores from the fossil and historical records (Chapter 3). I conclude this thesis (Chapter 10), with a conceptual model for the conservation of the Spot-tailed Quoll in north Queensland, and discuss the implications of my findings for the long-term viability of marsupial carnivores in Australia.

Although this thesis focuses on the ecology and conservation status of the north Queensland population of the Spot-tailed quoll the results are applicable throughout the species' Australian range.

Definitional considerations

The taxonomy of *Dasyurus* has been contentious, with some authors (for example Kirsch and Archer 1982), proposing that the genus is polyphyletic and that it should be split into three genera, *Dasyurinus* (Eastern and Western quolls), *Satanellus* (Northern quoll) and *Dasyurops* (Spot-tailed quoll). None-the-less, most other recent texts (for example, Strahan 1995), retain all species within the genus *Dasyurus*, and I follow that convention here.

For the purposes of this thesis, I have considered only that guild of marsupial carnivores which are terrestrial, medium to large–sized (i.e. >500g), and which consume significant amounts of vertebrate prey during most seasons of the year. Two species of carnivorous mammals are excluded from this thesis because their inclusion would make the discussion unwieldy. These species include the Water Rat, *Hydromys chrysogaster* which occasionally consumes terrestrial mammals and birds as-well-as its usual prey of aquatic vertebrates and invertebrates (Woollard *et al.* 1978), and the Ghost bat, *Macroderma gigas,* which consumes birds, small mammals, bats and invertebrates (several sources listed in Churchill 1998). In addition, many species which are normally considered to be herbivorous or insectivorous are known to eat vertebrate material on rare occasions including: Sugar Glider *Petaurus breviceps* (Fleay 1947, McKenzie *et al.* 1977); Brush-tailed Phascogale *Phascogale tapoatafa* (Fleay 1929); Yellow-footed antechinus *Antechinus flavipes* (Menkhorst 1995); Agile antechinus *Antechinus agilis*

(Menkhorst 1995). These species are excluded from this thesis, except where they are discussed as prey species for *D. maculatus*.

Within the context of this thesis, the term "carnivore" is used to describe those species, which prey predominantly upon vertebrates. The capitalised term "Carnivore" is used throughout this thesis to describe members of the eutherian order Carnivora, which includes the families Felidae, Canidae, Ursidae, Mustelidae, Procyonidae and Viverridae.

The identification of carnivory (*sensu* this thesis) in Australian mammals is based on my own and others first hand knowledge and an accessible and familiar literature. Corresponding data for the other continents are based primarily on accounts in Nowak and Walker (1991). Species of the Order Carnivora, which do not qualify as trophic carnivores (as defined above) are excluded from further discussion, and are listed in Appendix 1.1.

Chapter 2.

Australia's mammalian carnivore fauna

In this Chapter I explore the species and communities of carnivorous mammals in Australia through a literature survey. The species richness of Australian marsupial carnivores is low compared to all other continents, at both a continental and a local scale. All extant marsupial carnivores have undergone range decline and three of the four species which occurred on mainland Australia at the time of European settlement are now extinct or Threatened.

Chapter 2. Australia's mammalian carnivore fauna

2.1. The history of Australia's carnivorous marsupials

The recorded history of Australia's marsupial carnivores begins in the late Oligocene/early Miocene (c. 25 mya). Fossil carnivores from this period are preserved in the Alcoota and Riversleigh fossil beds. The marsupial carnivore guild had evidently evolved sometime considerably earlier, because by this time it was represented by two very different lineages: the Orders Dasyuromorphia and Diprotodontia. Two families of Diprotodontians containing at least seven genera and 17 species developed carnivory over the intervening period (Appendix 2.1): (1) the now extinct family, Thylacoleonidae, which included cus-cus to leopard-sized marsupial "lions" (Fig. 2.1), most closely related to the Phalangeroid possums (Murray 1991), and, (2) an extinct subfamily (Propleopinae -"killer" potoroos (Fig. 2.2)) of the extant Family Potoroidae, which is today represented by herbivores and omnivores.

The Dasyuromorphian carnivores derive from at least two families containing at least ten genera and 24 species, including the recently extinct family Thylacinidae (Fig. 2.3), and the extant family Dasyuridae, which contains the Quolls and the Devil, *Sarcophilus harrisii* (Fig. 2.4), and a host of small insectivores. Extinct Miocene forms of Dasyuromorphian, which have generally been regarded as primitive Dasyurids (e.g. Archer 1982a), cannot be satisfactorily classified within the Order Dasyuromorphia due to the small amounts of material referable to them, and constraints on the use of morphological synapomorphies in elucidating their relationships (Wroe 1997a).

Fig. 2.1. An artist's reconstruction of the Pleistocene marsupial "lion" *Thylacoleo carnifex*, based on an almost complete skeleton (Source: Archer *et al.* 1991).

Fig. 2.2. An artists reconstruction of the "killer-potoroo" *Propleopus oscillans*.

These forms from Miocene deposits in central and southern Australia are superficially 'convergent' upon *D. maculatus* and *Dasyurus hallucatus* respectively (Archer 1982a). The number of known prehistoric carnivorous Dasyuromorphians will no doubt increase when other forms from the Oligo-Miocene deposits of Riversleigh (Archer *et al.* 1991a) are published.

The earliest known, unambiguous dasyurid (the family to which *Dasyurus maculatus* belongs) is a *Dasyurus*-sized carnivore (*Barinya wangala*) from the early to mid-Miocene Epoch (25 – 10 mya)(Wroe 1999). By the early Pliocene the Dasyuridae had already radiated to include a large, relatively specialised, but as yet unassigned Devil, *Sarcophilus* species from southern Australia (Tedford 1994), and *Dasyurus dunmalli* from north-eastern Queensland's Bluff Downs and later Pliocene deposits in southern Queensland, New South Wales and Victoria (Rich 1991, Wroe and Mackness 1998). Ambiguous material which may represent dasyurids has been found in many older deposits although their exact familial relationships are unknown (Archer 1982a, Rich 1991).

Post-Miocene fossil Dasyurids are, with few exceptions, referable to modern genera of the Family. The exception is the late Pliocene or early Pleistocene genus *Glaucodon* which Ride (1964) and later Wroe and Mackness (1998) consider, on the basis of dental morphology, to be part of a morphocline grading from *D. maculatus* through *Glaucodon* and thence to recent *Sarcophilus* species. Carnivorous dasyurid fossils are known from the Pleistocene as four species of Devils (*Sarcophilus* spp 1 & 2, *S. laniarus*-Pleistocene, *S. harrisii*-Pleistocene-recent)(Dawson 1982a, Tedford 1994) and all four contemporary species of Australian *Dasyurus*.

Fig. 2.3. The Tasmanian "Wolf", *Thylacinus cynocaphalus* (Source: Guiler 1991).

Fig. 2.4. The Tasmanian Devil, *Sarcophilus harrisii*, the largest member of the family Dasyuridae and the largest extant marsupial carnivore (Source: Strahan 1995).

There have been three significant developments in the composition of Australia's carnivorous mammal fauna over the period from which that fauna is known (approximately 25 million years). Two of these developments hinge upon the two Ice Age Events, which have affected Australia over that time, and the third involves the post-Glacial activities of humans. These post-glacial activities include the introduction of a new suite of carnivorous mammals (Eutherians) to Australia, and direct persecution and displacement of all *Dasyurus* species, the Devil *S. harrisii*, and the Thylacine as a result of agricultural activities.

Although no marsupial carnivore lineage became extinct following the Terminal Miocene Event, the subsequent Pliocene was characterised by a shift in patterns of diversity away from the Thylacinids and Thylacoleonids towards the Propleopines and the Dasyurids (Fig.2.5).

Marsupial carnivore faunas had re-evolved to pre-Pliocene levels of diversity and species richness by the time of the late Pleistocene Glacial Maximum. The Glacial Maximum resulted in the extinction of two lineages which had been consistent components of the Australian carnivorous mammal fauna during the previous 25 million years. Because it is only 20 000 years since the Glacial Maximum, there has been no subsequent radiation of marsupial carnivore faunas in Australia, although the sudden appearance of *Dasyurus maculatus* across south-eastern Australia suggests that there was significant faunal reassortment following the decline of these carnivore taxa.

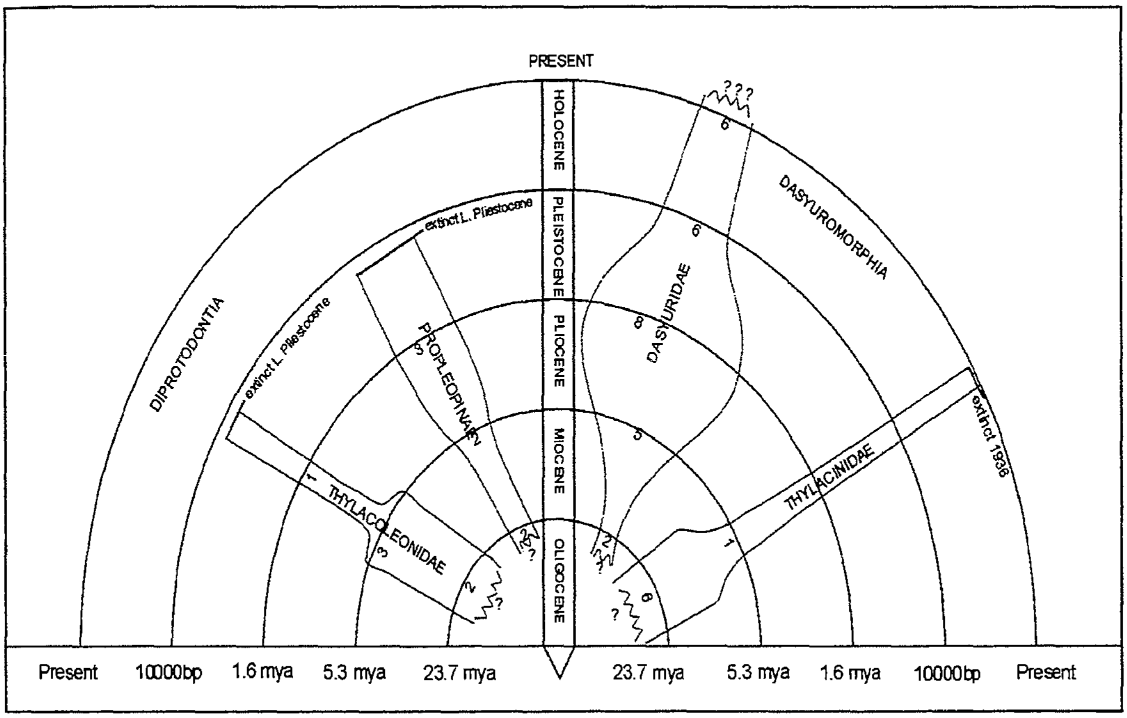
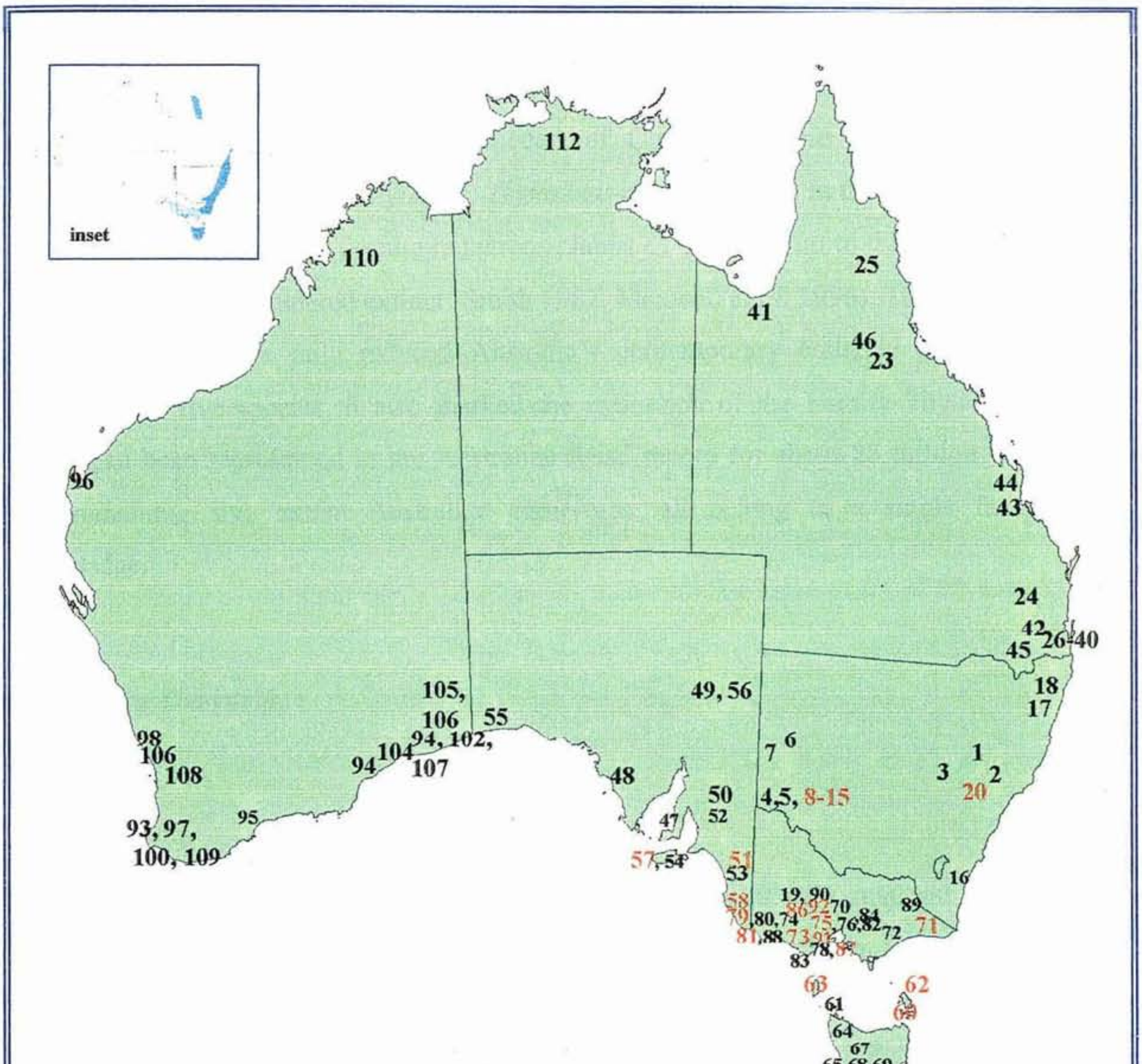


Fig. 2.5. The radiation and attenuation of Australian marsupial carnivores since their first appearance in the fossil record in the late Oligocene/early Miocene.

Numbers within each epoch for each family represent the number of species within that family which were known from that entire epoch.

The appearance of *D. maculatus* throughout southeast Australia (Map 2.1) at this time, suggests that the species may have experienced competitive release following the decline of the two Diprotondontian lineages, Thylacoleonidae and Propleopinae.

During the Holocene, three species of Eutherian carnivores became established in Australia. During the early to mid-Holocene, the Dingo was introduced. At about this time, the Thylacine became extinct on the mainland. Although the evidence is circumstantial, it is likely that Dingoes contributed to the Thylacine's demise on the Australian mainland (e.g. see arguments by Guiler 1985). Dingoes are more adaptable than Thylacines: they can take a greater range of prey through foraging alone or as a pack, they consume plant as-well-as animal material, and domestic dogs are well recorded in the anecdotal literature as frequently killing Thylacines (e.g. Woods 2001). During the past 200 years, Australia's carnivore fauna has been augmented by the introduction of a further two species of Eutherian carnivore bringing the Eutherian contribution to Australia's carnivore fauna to two families and three genera. These latter two carnivores (Domestic cat and Red Fox), have been implicated in the decline of members of the genus *Dasyurus* throughout Australia. The introduction of these species, which are now Australia's dominant carnivores, brings the Family and Generic diversity of Australian carnivores back to pre-Glacial levels. The actions of humans, in the form of direct persecution and habitat destruction have further altered the constituency of Australia's mammalian carnivore fauna through the extinction of the last of the ancient marsupial carnivore lineages, the Thylacinidae, and the near extinction of four of the remaining five marsupial carnivores (*Dasyurus*).



Map 2.1. The location of fossil and subfossil sites for *D. maculatus* (marked in red type). Inset, the contemporary distribution of *D. maculatus* (from Edgar and Belcher 1995).

Note: Other Pliocene - Holocene fossil sites which contain carnivorous marsupials are shown in black type. See Appendix 2.2 for carnivore assemblages from each numbered site.

2.2. Australia's contemporary carnivore fauna

2.2.1. Marsupial carnivores

At the time of European settlement in 1788, Australia supported a marsupial carnivore fauna of six species including four species of Quoll, *Dasyurus* spp., the Devil, *Sarcophilus harrisii,* and the Thylacine, *Thylacinus cynocephalus*. In the 1930s, the last known Thylacine died, and despite numerous claims of sightings up to the present day, the species is now considered extinct (Smith 1982, Maxwell *et al.* 1996). The extinction of the Thylacine not only reduced Australia's contemporary endemic mammalian carnivores to five species, it also marked the extinction of the Family Thylacinidae which had been represented in the Australian fossil record for about 25 million years. The remaining five extant Australian carnivores, all belong to a single family, Dasyuridae.

2.2.1.1. The Dasyuridae

The Spot-tailed quoll

The Spot-tailed Quoll, *Dasyurus maculatus* (Fig 2.6), owes its colloquial name to the cream or white coloured spots which occur on its tail as well as its body, a characteristic which sets it apart from all other species of *Dasyurus*. The colloquial term quoll, which is applied to all six species of *Dasyurus*, is derived from the Cape York Peninsula, Kuku Yimidirr word for the Northern Quoll, ja-quoll (Mahoney and Ride 1984) or de-kol (Roth 1901). The Spot-tailed Quoll is the largest of all the Quolls with adult males recorded weighing up to 7kg (Edgar and Belcher 1995), and the most specialised for carnivory (Wroe & Mackness 1998).

The Spot-tailed quoll (Kerr 1792) was amongst the first of the Australian mammals to be collected and described by Europeans. Arthur Phillip's party collected a specimen of *D. m. maculatus* at Port Jackson in 1788 (Walton 1988). Specimens from the disjunct north Queensland metapopulation, on which this thesis is based, were first collected almost 100 years later (Lumholtz 1888, Ramsay 1888). Based on variations in colour and size, the north Queensland meta-population was first considered to consist of two species, *Dasyurus maculatus* and *Dasyurus gracilis* (Ramsay 1888, Tate 1947). Troughton (1941) subsequently concluded that the north Queensland population represented a single subspecies of the Spot-tailed quoll, which he named *Dasyurus maculatus gracilis*. This convention was followed by all subsequent authors, with the exception of Tate (1947) who later revised his opinion to fall into line with the one species model (Tate 1952). A recent genetic study (Firestone *at al.* 1999), has shown that: (I) *D. m. gracilis* does not warrant sub-specific status, and (2), while the Tasmanian subspecies, which was previously considered a member of the nominate subspecies, should be considered a sub-species of *D. maculatus*. Firestone *et al.* (1999) also notes that there are significant differences in the variability of microsatellite loci between the Northern Spot-tailed Quoll, known as *D. m. gracilis* and Southern Spot-tailed Quolls, *D. m. maculatus* from the south-east mainland, and considers that the north Queensland population (formerly considered *D. m. gracilis*), should be considered as a distinct Management Unit (*sensu* Moritz 1994) of *D. m. maculatus*. There has not yet been any formal move to suppress the name *D. m. gracilis*, however in anticipation of such a move, I refer to the northern populations on which this study is based as the northern Spot-tailed Quoll where required for clarity.


Photo: S. Burnett

Fig. 2.6. The northern Spot-tailed Quoll *Dasyurus maculatus* (above) and the southern mainland *D. maculatus* (below). Note the profusion of pale spots which extend onto the animals' tails, a feature which distinguishes this species from all other *Dasyurus*. Note also the larger spots and darker background colour of the northern Spot-tailed Quoll compared to its southern mainland congener.


Photo: R. Jackson

Despite 200 years since the Spot-tailed quoll was first described, published ecological accounts have until recently been limited to accounts of the breeding biology of captive animals (Fleay 1940, Troughton 1954a & 1954b, Settle 1978, and Conway 1988), and brief anecdotal descriptions in general texts (for example, Le Souef and Burrell 1926, Troughton 1941, Ride 1970). It was not until the 1980s and 1990s that any autecological studies were undertaken on the species. These consisted of a summary of its distribution and conservation status throughout Australia, with particular emphasis on Victoria (Mansergh 1984); a summary of the species' ecology in Tasmania based on museum specimens (Green and Scarborough 1990); a description of latrine use in northern New South Wales (Kruuk and Jarman 1995); and a description of its diet in Victoria (Belcher 1995). The difficulties in acquiring specimens can be gauged from the fact that none of these autecological studies involved handling or even observing live individuals. In the early 1990s several studies on the species began. Doctoral research on niche partitioning among marsupial carnivores in Tasmania (Jones 1995a) and phylogeographic population structure across Australia (Firestone *et al.* 1999) has added greatly to our understanding of the ecology of this species. The state of knowledge of northern *D. maculatus* is even poorer than that of its congener, being represented by only seven museum specimens and only one 110 year old published illustration (Lumholtz 1888). In his book 'Furred Animals of Australia", Troughton (1941) referred to northern *D. maculatus (gracilis),* as "this mythical beast", and except for this study, that situation has not changed.

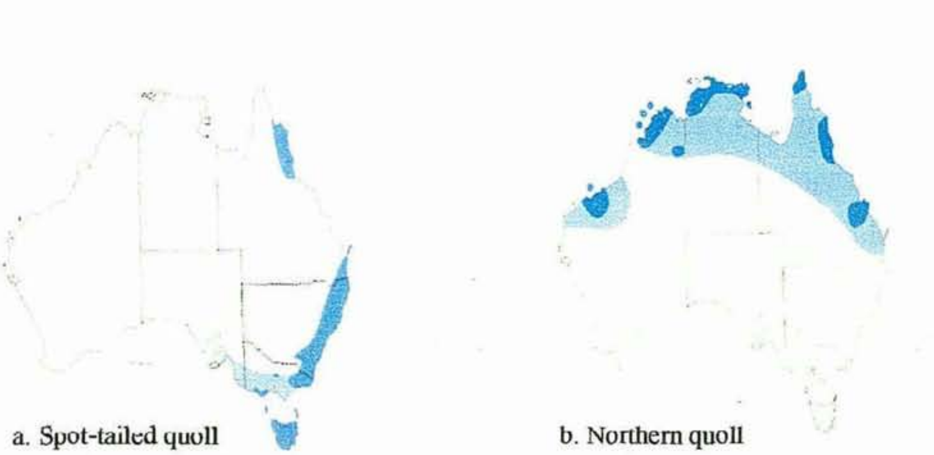
Spot-tailed Quolls have undergone a demonstrable decline in their extent of occurrence throughout their mainland Australian range (Maxwell *et al.* 1996, Chapter 8), and are regarded as Threatened, Endangered or Extinct throughout this range (Stanger *et al.* 1998). *D. maculatus* is one of the first species to become locally extinct (or at least very rare) following colonisation by Europeans (Lunney and Leary 1988). Similarly, *D. maculatus* is one of the few wet tropical rainforest mammals, which disappear from large patches of remnant vine forest following habitat fragmentation (Laurance 1989).

Other species of the genus *Dasyurus*

Apart from the Spot-tailed Quoll, five other members of the genus *Dasyurus* are known. These include three Australian species: the Western Quoll, *D. geoffroyi*, the Eastern Quoll, *D. viverrinus*, and the Northern Quoll, *D. hallucatus;* and two very poorly known New Guinean species: the Bronze Quoll, *D. spartacus* and the New Guinean Quoll, *D. albopunctatus*.

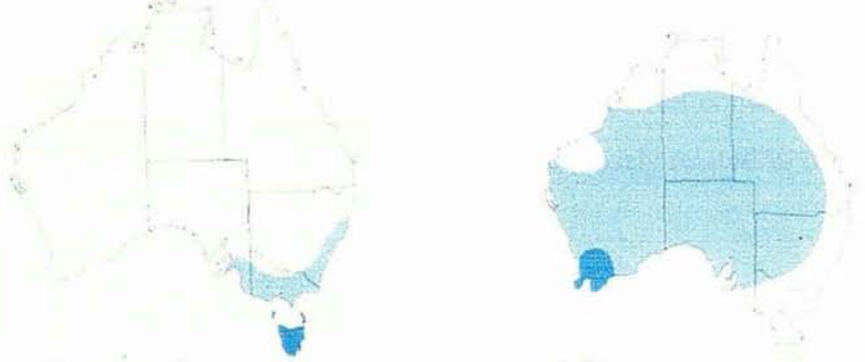
The diet and population ecology of the three smaller Australian species of Quolls have been more extensively studied than the diet of *D. maculatus*. The diet of the New Guinean species has been little documented. The three smaller species of Australian Quolls (the Eastern *D. viverrinus*, Western, *D. geoffroyii,* and Northern Quolls, *D. hallucatus*), consume seasonally large amounts of invertebrate and plant material, and lesser although regular amounts of vertebrate prey and carrion (Blackhall 1980, Soderquist and Serena 1994, Oakwood 1997). They produce a single litter of between six and eight young during their annual winter breeding season (Godsell 1982, Braithwaite and Begg 1995, Serena and Soderquist 1995). It is unknown whether the two New Guinean Quolls have a specific breeding season and knowledge of their diets is poor (Flannery 1995). An observation of *D. albopunctatus* killing an adult bandicoot, the Common Echymipera, *Echimipera kalabu,* (R. and M. McKay pers. comm.), and reports of *D. spartacus* raiding chicken coops (Van Dyck 1988) suggest that they include large vertebrate prey in their diets, although it is unknown whether they also consume invertebrates or plant material, or in what quantities.

All the species of Australian *Dasyurus* have undergone significant range contractions since European settlement (Map 2.2). The Eastern Quoll has disappeared from the mainland, and is now confined to Tasmania (Godsell 1995). The Western Quoll has disappeared from much of its former range throughout central Australia and is now restricted to the extreme south west of Western Australia (Orell and Morris 1994). The Northern Quoll has undergone significant range collapse and is now restricted to rocky and coastal areas within its once more widely spread tropical distribution (Braithwaite and Griffiths 1994). The Spot-tailed Quoll has disappeared from about 50% of its habitat in southern Australia (Mansergh 1984) although little is known of its pre-European distribution in north Queensland.



a. Spot-tailed quoll

b. Northern quoll



c. Eastern quoll

d. Western quoll

Map 2.2. The present and former ranges of Australia's four Quoll species (from Strahan 1995). Dark shading represents the current range of each species, pale shading represents areas of the former range from which each species has disappeared.

The Tasmanian Devil, *Sarcophilus harrisii*

The Tasmanian Devil *Sarcophilus harrisii* is the largest extant marsupial carnivore (Strahan 1995). Although now confined to Tasmania the species is common in fossil and sub-fossil deposits right around the coastline of Australia. The youngest sub-fossil age for this species on the mainland is 430 years (Paddle 2000), and so it is likely that the species may have occurred in very small numbers on mainland Australia at the time of European settlement.. The Tasmanian Devil occurs in a range of habitats in Tasmania but is most abundant in woodland and dry sclerophyll forest (Jones 1995b). It is exclusively carnivorous, preying upon a range of vertebrate species and consuming carrion. Little has been published on the population ecology of this species. Sexual maturity is thought to be attained at 2 years of age. Maximum litter size is four young. Tasmanian devils have a winter breeding season. The species underwent a decline in numbers in the early part of this century but is now considered common in Tasmania. Among living mammals, the Tasmanian Devil is most closely related to the Spot-tailed quoll (Wroe and Mackness 1998).

2.2.2. Introduced mammalian carnivores

During the Holocene (10 000 years before present (ybp) to present), three species of Eutherian carnivores belonging to two families; Canidae and Felidae, were deliberately introduced into Australia and became established as feral populations as described below. The Golden Jackal, *Canis aureus,* was also introduced into Australia in the 1860s, but failed to become established (Lever 1985).

The earliest evidence of Eutherian carnivores in Australia is of a fossil Dingo, *Canis familiaris dingo*, aged at about 7450 +/- 270 ybp (Archer 1974a). There is no palaeontological evidence of the species in north Queensland. However, given that the Dingo was certainly introduced from Asia, it seems reasonable to assume that Dingoes have occurred in north Queensland for thousands of years. Domestic dogs, *Canis familiaris familiaris,* arrived with the first settlers and probably became feral shortly afterwards. In Tasmania and New South Wales for example, feral dogs were reported as a problem by shepherds in the early 1880s (Rolls 1969). Dingoes/feral dogs are found throughout all habitat types in Australia including the central deserts, alpine areas and the thick forests of the Great Dividing Range and Eastern Escarpment (Corbett 1995). Because they hybridise readily in the wild (Corbett 1995) and because of a supposed similarity in ecology, I will, unless explicitly stated otherwise, refer to both subspecies from here on, as Dogs.

A second species of canid which was successfully introduced to Australia is the Red fox, *Vulpes vulpes,* which was first introduced into Victoria in 1845 and was subsequently introduced at various times and places throughout mainland Australia (Newsome and Coman 1989). Jarman (1986) suggests that Red Foxes had reached approximately to the Burdekin River, south of Townsville by the 1930s. It is unknown when foxes reached the wet tropics area, but they are now known from former rainforest pasturelands and dry sclerophyll forests adjacent to the region (Werren 1993 and Ch. 9).

Domestic Cats, *Felis catus*, were introduced with the first settlers and feral populations probably became established shortly afterwards. There is also a suggestion that cats colonised areas of north-western and inland Australia prior to European settlement, from shipwrecks on the Western Australian coast in the 1700s (Newsome 1991, Corbett 1995). Jones (1989) states that the major spread of feral cat populations occurred during the nineteenth century. This may have occurred later in north Queensland, in conjunction with European settlement in the mid and late 1800s. Feral Domestic Cats are known from all terrestrial habitats within Australia (Jones 1989). Little coordinated research into feral cats has been conducted in Queensland, and there are no published accounts of the distribution or diet of the species in the Wet Tropics Area of Queensland (Gordon 1991).

Introductions of different cat strains to Australia have continued throughout the European history of the continent. However, of particular concern is the recent introduction of Leopard Cat *F. bengalensis* x Domestic Cat *F. catus* F4 hybrids to Australia. *Felis bengalensis* is characterised by a love of water, and a strongly arboreal nature (Nowak and Walker 1991), both characteristics which are not found in *F. catus* but which are reported in the F4 hybrids (Roberts 1996). As such, the potential for supplementation of feral cat genes, especially over evolutionary time, must be high and is of major conservation significance, particularly to forest dwelling and aquatic fauna. The Queensland Department of Natural Resources (QDNR) recently assessed the pest potential of the F4 hybrid (Queensland Department of Natural Resources 1996). They concluded that they would not pose any threat to Australian ecosystems. However, their approach fails to consider the long-term implications of this introduction, which I discuss more fully in Chapter 9.

2.2.3. Australian Avian and Reptilian Carnivores

Australia is home to a large number of avian and reptilian carnivores for which mammals constitute a significant proportion of their diet (Table 2.1). These avian and reptilian predators are probably the predominant predators in most of Australia's ecosystems, in terms of diversity and biomass. I am not aware of any published studies, which estimate the biomass or impacts of vertebrate-eating carnivores in Australia.

Table 2.1. The number of non-mammalian Australian predators for which mammals are a predominant prey type.

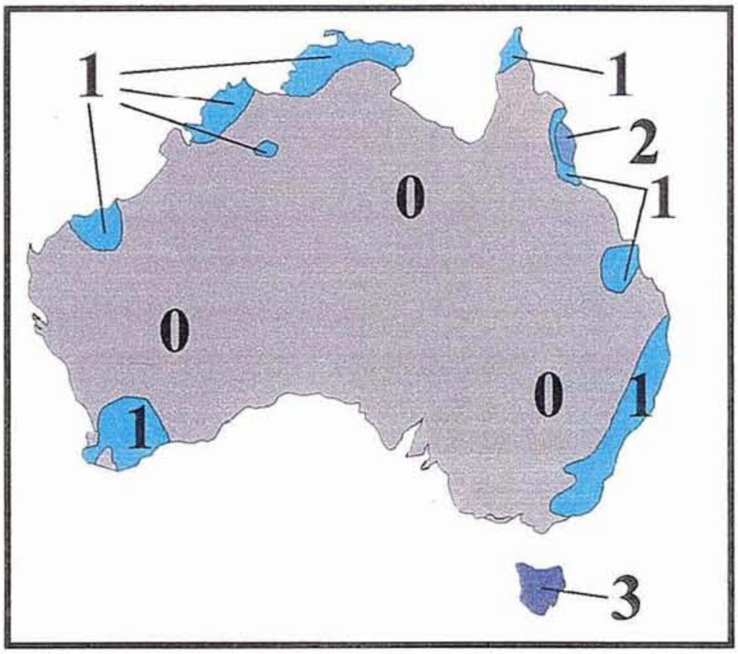
Family	Common name	Number of species	Vertebrates eaten	Source
Boidae	Pythons	11	Amphibians, reptiles, birds, and mammals	Shine 1991, Torr 2000
Colubridae	Rear-fanged snakes	1	Amphibians, reptiles, birds, and mammals	Shine 1991
Elapidae	Venomous Australian snakes	16	Amphibians, reptiles, birds, and mammals	Shine 1991
Varanidae	Goannas	8	Mammals, birds, reptiles amphibians	King and Green 1999, Vincent and Wilson & Knowles 1988, Cogger 2000
Strigidae	Owls	9	Mammals, birds, reptiles	Higgins 1999
Accipitridae	Falcons, Hawks and Eagles	13	Mammals, birds, reptiles, amphibians	Marchant and Higgins 1993
TOTAL		58		

2.3. Characteristics of Australia's mammal carnivore communities

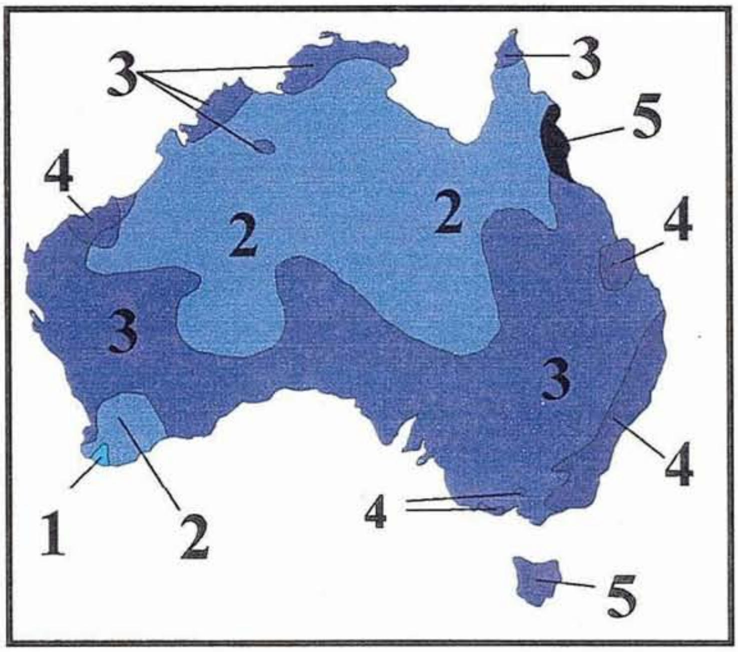
2.3.1. Species richness of Australian carnivore communities

At a local scale, contemporary marsupial carnivore species richness in Australia varies from zero to three species (Map 2.3). When eutherian carnivores are included, this species richness increases to between two and five species (Map 2.4). The species richness of marsupial carnivore communities is highest in Tasmania which has three species which occur in sympatry or narrow allopatry. The only other area of Australia with more than one marsupial carnivore species is the Wet Tropics Area which has two species of *Dasyurus* in narrow sympatry. Most of the Australian continent lacks any marsupial carnivore species. When eutherian carnivores are included in the calculations, the highest species richness is once again found in Tasmania and in the Wet Tropics Area, where five species of mammalian carnivore occur in sympatry or in narrow allopatry. Combined marsupial/eutherian carnivore species richness varies between two and four over the rest of the Australian continent, including at most only one marsupial endemic (*Dasyurus sp*) at any one site. The three introduced Eutherian carnivores are the three most widespread Australian mammalian carnivores (see distribution maps in Strahan 1995), and constitute the entire mammalian carnivore fauna over most of mainland Australia.

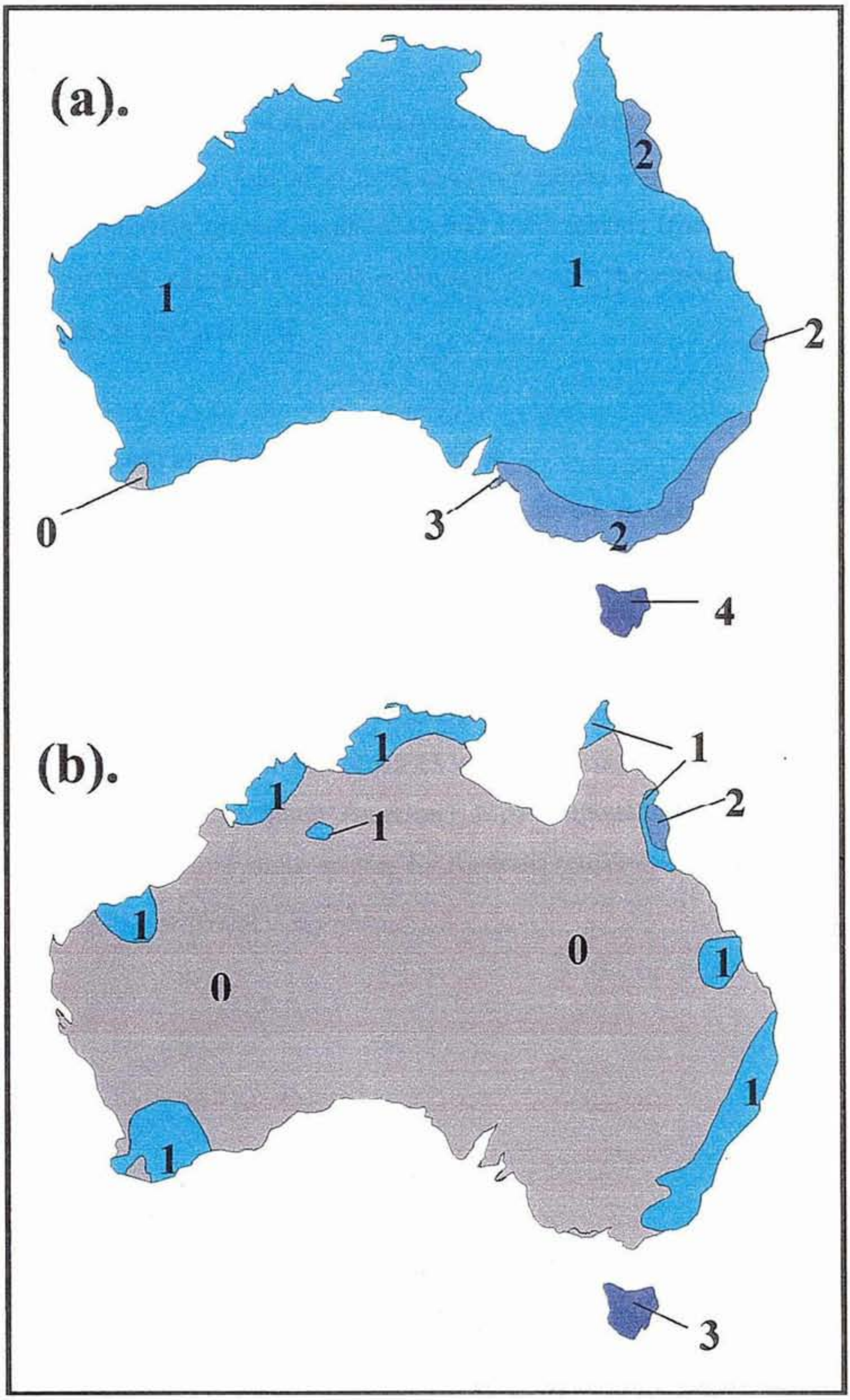
The areas of highest mammalian carnivore species richness (eastern seaboard, Tasmania and south-west Western Australia) are characterised by high and predictable rainfall (for example see Colls and Whittaker 1990). The areas in which endemic carnivore species richness is highest (Tasmania and Wet Tropics Area) are also characterised by extensive areas of inaccessible forested habitats and high topographic relief. It is evident from the patterns of distribution and from patterns of decline at the time of European settlement (Maps 2.5a & b), that the species of *Dasyurus*, which comprise the entire endemic mainland marsupial carnivore fauna, are adapted to mesic and predictable environments. The only *Dasyurus* which occupied the arid zone, *D. geoffroyii*, was the first to undergo range collapse (Orell and Morris 1994, Maxwell *et al.* 1996), and now survives only in the wettest and most climatically predictable part of its former range, in extreme south-western Western Australia.



Map 2.3. Species richness of contemporary Australian marsupial carnivore communities (Based on Strahan 1995). Numbers refer to the number of sympatric or narrowly allopatric carnivore species within each polygon.



Map 2.4. Species richness of contemporary Australian marsupial and eutherian carnivore communities. Numbers refer to the number of sympatric or narrowly allopatric carnivore species within each polygon



Map 2.5. The species richness of marsupial carnivore communities in (a) the 1880s, when declines in *Dasyurus* spp were first detected, and, (b) the 1990s (based on distributions shown in Strahan 1995).

Numbers refer to the number of sympatric or narrowly allopatric marsupial carnivore species within each polygon.

2.3.2. Australia's carnivorous mammal fauna in a global perspective

2.3.2.1. Species diversity of mammalian carnivore faunas

The species richness of Australian local carnivore faunas is much lower than that from within all continents (except Antarctica), and some islands (Map. 2.6). These values clearly show that Australia's carnivore fauna is not only depauperate at the continental level but also at the local level.

2.3.2.2. Ratio of carnivores to non-carnivores

Irrespective of whether intercontinental comparisons are based at the level of Family, Genus or Species, the ratio of endemic carnivorous to non-carnivorous mammals is less than that of the African, North American or South American faunas (Fig. 2.7). The addition of Australia's introduced carnivores and non-carnivorous species to the data modifies the comparison (Fig. 2.8) in that it renders the ratio of Australian carnivore families almost equivalent to that of Africa while rendering the ratio of carnivore genera almost equal to that of South America. Most importantly however, the ratio of carnivorous to non-carnivorous species for Australia remains much lower than that of all other continents compared (Fig. 2.8).

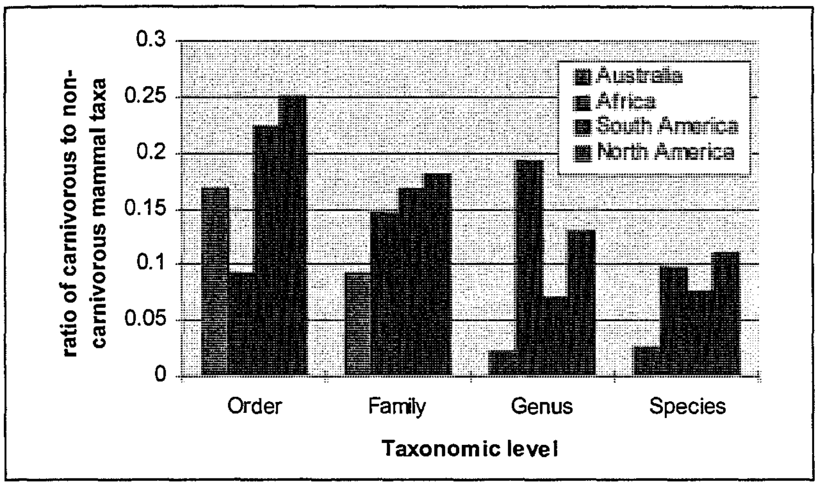


FIG. 2.7. THE RATIO OF CONTEMPORARY ENDEMIC CARNIVOROUS TO NON-CARNIVOROUS MAMMAL TAXA AT FOUR LEVELS OF TAXONOMIC RESOLUTION IN FOUR CONTINENTS.

Sources: Hall and Kelson (1959), Keast (1972), Eisenberg (1989), Redford and Eisenberg (1992), Strahan (1995) and sources listed in Appendix 2.2.

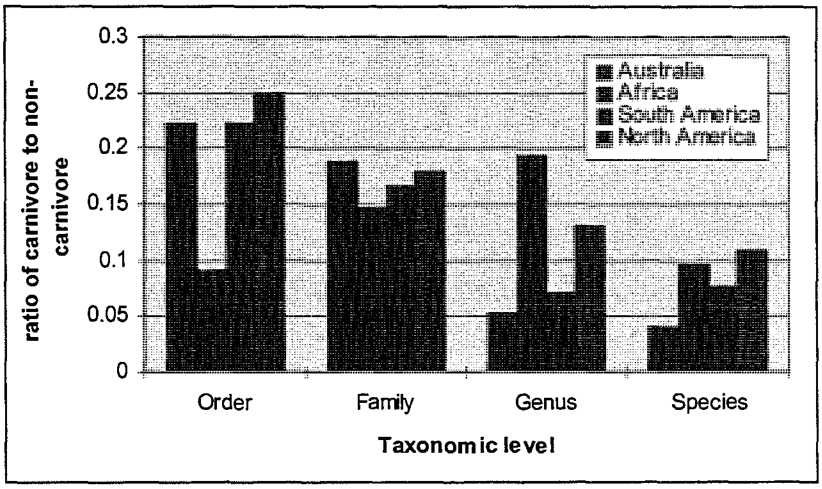
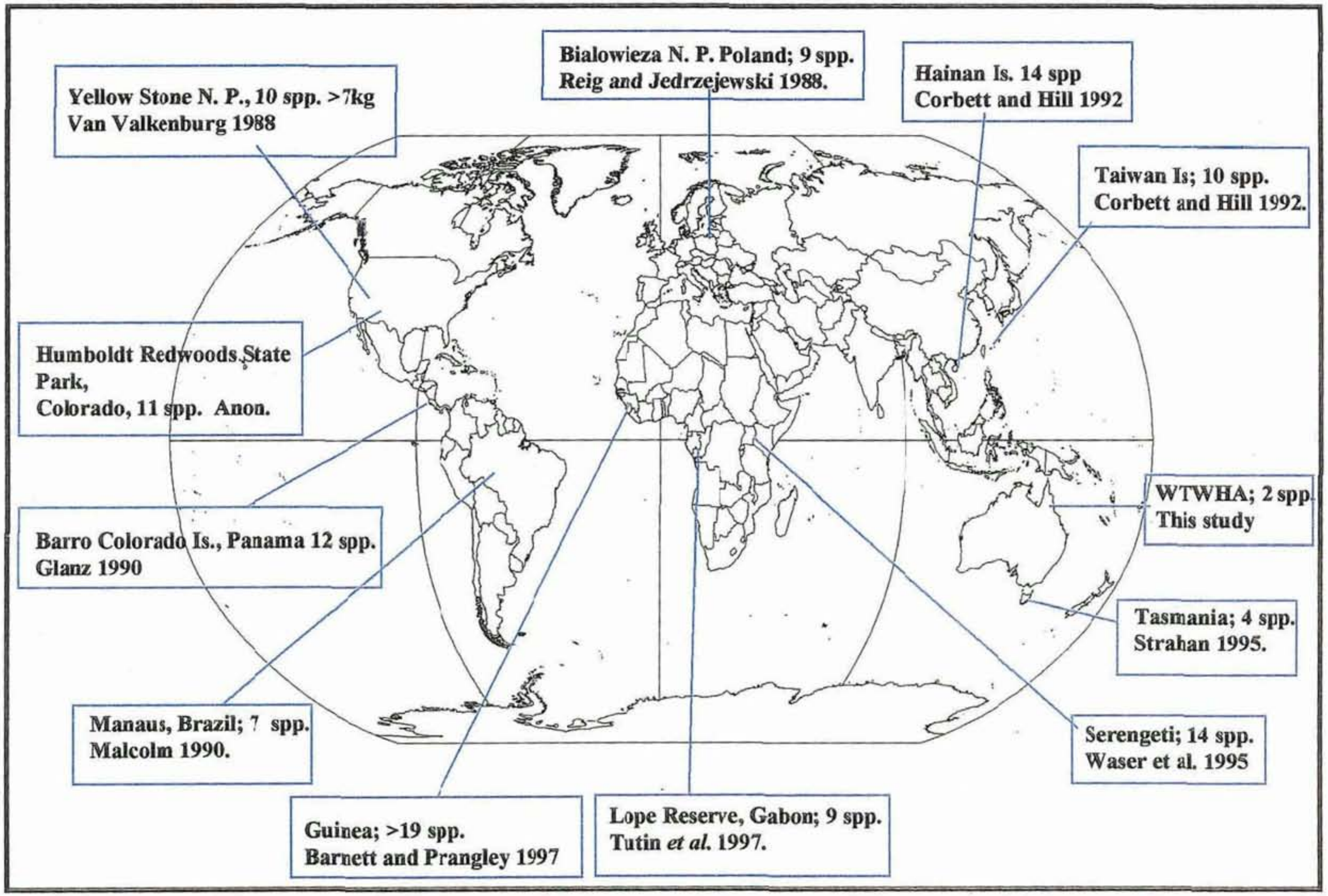


FIG. 2.8. THE RATIO OF CONTEMPORARY CARNIVOROUS TO NON-CARNIVOROUS MAMMAL TAXA AT FOUR LEVELS OF TAXONOMIC RESOLUTION, AND INCLUDING AUSTRALIA'S EXOTIC CARNIVORES.

Sources: Hall and Kelson (1959), Keast (1972), Eisenberg (1989), Redford and Eisenberg (1992), Strahan (1995).



Map 2.6. The species richness of selected *mammalian* carnivore faunas from around the globe.
Those species noted in Appendix 1.1 are not included in local faunal values, nor are Australia's introduced eutherian carnivores included in Australian values. The Thylacine is included in the Tasmanian value for carnivore species richness.

2.4. Summary

- Australia supports a depauperate mammalian carnivore fauna at both the continental and local scale, compared to all other continents except Antarctica.

- At the time of European settlement, Australia supported six species of terrestrial mammalian carnivore; the Thylacine, the Tasmanian Devil, and four species of Quoll, *Dasyurus*. At that time, terrestrial carnivorous mammals occurred in all habitats and across the entire continent.

- Two hundred and thirteen years later, these species are either extinct (Thylacine), or their distributions have been greatly reduced. Marsupial carnivores are now absent from most of the Australian continent. Sympatric or narrowly allopatric marsupial carnivore communities now only survive in Tasmania, and Wet Tropical northeastern Queensland.

- During the past 213 years three species of Eutherian carnivore have become established in Australia and have extended their distributions throughout most of the continent. These species are now the dominant and in most areas, the only terrestrial mammalian carnivores on mainland Australia.

Chapter 3.

Changing the Guard: the history of replacement of Marsupial carnivore communities by Eutherian carnivores

Even if we can secure populations of *D. maculatus,* this species' ultimate survival relies its capacity to radiate in the face of pressure from a new suite of Australian mammalian carnivores, the Eutherians. In this chapter, I review the history of marsupial carnivore faunas when they mix with other carnivore faunas. I also attempt to tease out the environmental and historical determinants of Australia's mammalian carnivore fauna on the premise that environmental limits to carnivory imply that any introduced carnivore species will have to displace existing species or vice versa. In contrast, a soley historical explanation for Australia's depauperate carnivore fauna may suggest that introduced species can fill niches left vacant by extinction without replacement.

I conclude that marsupial carnivores are susceptible to exclusion by Eutherian carnivores, and that the long-term future of Australian marsupial carnivores is tenuous.

Chapter 3. Changing the Guard: the history of replacement of Marsupial carnivore communities by Eutherian carnivores

3.1. Introduction

The subsequent chapters of this thesis are concerned primarily with the immediate conservation status of the Spot-tailed Quoll *Dasyurus maculatus*, culminating in an integrated discussion of the interactions between its various ecological attributes and its conservation status. However, even if human activities were to be ameliorated and habitat and ecosystems restored to pre-European status, the evolutionary survival of Australian marsupial carnivores relies on their capacity to radiate in the face of competition from a new suite of mammalian carnivores, the Eutherians (see Chapter 2). While the conservation significance of the Eutherian carnivores has been discussed in terms of the past and immediate conservation status of Australia's marsupials (e.g. Cats: Potter (1991), Dickman (1996), Risby *et al.* (1999); Foxes: Risby *et al.* (1999), NSW National Parks and Wildlife Service 2001.) I am not aware of any published discussion of the longer term implications of the presence of the Eutherian carnivores in the Australian fauna. In this review, I evaluate the evolutionary potential of marsupials as carnivores in Australia by drawing on the palaeontological and ecological literature. I compare patterns of marsupial and eutherian carnivore community richness within each epoch for which data are available. By reviewing the history of radiation and extinction of marsupial carnivore faunas in isolation and when they mix with other carnivore faunas, I also attempt to tease out the environmental and historical determinants of Australia's mammalian carnivore fauna on the premise that environmental limits to carnivory imply that any introduced carnivore species will have to displace existing species or vice versa. In contrast, a solely historical explanation for Australia's depauperate carnivore fauna may suggest that introduced species can fill niches left vacant by extinction without replacement.

Biases in the fossil record (discussed below), and problems with separating cause and effect in contemporary ecological systems (let alone prehistoric ones), preclude definitive answers to the questions posed here. However, the data presented below strongly suggest that, for whatever reasons, the radiation and diversity of marsupial carnivores are constrained compared to Eutherian carnivores. When marsupial and Eutherian carnivores mix, marsupial carnivore diversity suffers. I conclude that marsupial carnivores are susceptible to exclusion by Eutherian carnivores, and that the long-term future of Australian marsupial carnivores is tenuous.

3.2. The nature and biases of Australia's fossil mammal record

This section draws largely on data provided by the mammalian fossil record, which is inherently biased in some respects, as discussed below. While these biases are significant in some regards, they are not sufficient to disregard the general trends outlined below.

The fossil record is an inherently biased source of data. Very specific sets of conditions are required for the preservation of biological material. These conditions are not distributed evenly across space or time. Nor are species "captured" evenly within depositional environments. For example gigantic herbivores such as *Palorchestes* are much more likely to become trapped in bogs around receding water sources than are *Dasyurus* species which are light enough to escape being trapped in deep soft mud. Similarly, because of its arboreality, *D. maculatus* is more likely to be able to escape sinkhole depositional environments than is a terrestrial Thylacine.

Accurate dates for most Australian fossil deposits are problematic given that many have been deposited as undatable cave fills and reworked sedimentary deposits (McNamara (1990)). Because there has been so little volcanic activity, there are few convenient dating benchmarks and there has been little uplift and exposure of fossil bearing sediment (Archer *et al.* 1994). There is a scarcity of temporal sequences from any single locality which limits the usefulness of the fossil record for interpreting evolutionary change within lineages. Only two localities in Australia have produced stratigraphically interpretable Miocene deposits: late Miocene Alcoota and Ongeva Local Faunas of the Waite Formation, in the central Northern Territory (Megirian *et al.* 1996), and the five local faunas from the late Oligocene - mid Miocene Ettadunna Formation in the Lake Eyre Basin (Rich *et al.* 1991). Within the Pliocene period, Tedford (1994) notes that only in the Murray and coastal basins of Victoria is there a relatively complete sequence of sites which span the Plio-Pliestocene. Although early Pliocene sites are also known from northeastern Queensland (for example, Bluff Downs-Charters Towers area), there is a large temporal gap in the fossil record there, until the Pleistocene records from the same area (Tedford 1994).

Australia has the temporally and numerically most depauperate fossil record of land mammals, of any continent except Antarctica (Rich 1991). Very few undoubted pre-Miocene mammal fossil sites are known from Australia (Table 3.1), and with the exception of the Alcoota site in the Northern Territory (Rich 1991), they are as yet poorly described. In addition to Alcoota, these sites include Murgon in southeastern Australia, Lightning Ridge in New South Wales, and Dinosaur Cove in Victoria. Some Riversleigh, (Queensland) sites may yet prove to be of this age but are presently classed as Miocene (Archer *et al.* 1991a). Miocene vertebrate fossil sites are distributed in northern Western Australia, central Northern Territory, north-western Queensland, central and southern South Australia, eastern New South Wales, Victoria and Tasmania (Rich 1991). Pliocene sites are more numerous and widely distributed (Table 3.1). In addition to those regions listed above (with the exception of Tasmania), Pliocene sites are known from northeastern and southern Australia (Rich 1991). As might be expected from their much greater numerical abundance (Table 3.1), Pleistocene and Holocene sites are much more widely distributed than those from earlier epochs, being found in all Australian states, including abundant deposits from south-western Western Australia, southern and central South Australia, Victoria and eastern New South Wales and Queensland (Horton 1984). Throughout the Miocene there is a general bias towards sites from central and northern Australia, while subsequent epochs are characterised by biases towards sites from the southern basins and coastlines.

Another important bias in Australia's post-Miocene faunal record is the paucity of fossil deposits which accumulated in rainforest or dense forest habitats. This may be particularly important when attempting to interpret the evolutionary history of *Dasyurus maculatus*, as discussed below. While many Miocene fossil deposits are thought to have accumulated in either rainforest or gallery forest environments, only a single Pliocene fauna, the Hamilton local fauna in south-western Victoria (Archer *et al.* 1994) and no Pleistocene sites (Flannery 1990), are known from these environments.

Similarly, and even more importantly with respect to a discussion of the origins of *D. maculatus*, no fossil assemblage has been recorded within the Wet Tropics Area, although some locations such as the peat deposits on the Atherton Tablelands may provide vertebrate fossils if examined systematically.

Table 3.1. The number of Australian vertebrate fossil faunal assemblages from each epoch from which carnivorous mammals are known.

Epoch	Number of vertebrate fossil assemblages
Oligocene	1*
l. Oligocene-Miocene	24 (including oldest Riversleigh sites)
Pliocene- e. Pleistocene	28
l. Pleistocene- Holocene	>158

Sources; Rich *et al.* (1991) (pre-Pleistocene sites), Merrillees (1979a & b) (Pleistocene sites in Western Australia), Williams (1980) (Pleistocene sites in South Australia), and Molnar and Kurz (1997) (Pleistocene sites in south-eastern Queensland).* more precise dating of the local faunas from Riversleigh may well increase the known Oligocene representation of Australian mammal fossils.

3.3. Australia's depauperate mammalian carnivore fauna: environmental constraint or historical artefact?

3.3.1. Species richness of prehistoric carnivore communities

The most speciose marsupial carnivore communities known in Australia contained five species. Three such communities are known: one from the early Miocene and two from Pleistocene southeastern Australia (see Appendix 2.2). The Miocene site (Riversleigh System B) contains at least two genera and species of Thylacinid, two genera and species of Thylacoleonid and one genus and species of Propleopine. In addition, three genera and five species of undescribed Dasyuromorphian are known from this system (Archer *et al.* 1991), some of which probably preyed upon vertebrate prey, although descriptions of these species have not yet been published. Thus five species is probably an under-representation for this Miocene site. Both Pleistocene sites containing five species (Wellington Caves and Henshke's Cave), contain a fauna which includes a single Thylacinid, a single Thylacoleonid, a single Propleopine and two species of Dasyurid. A third site at the eastern Darling Downs has been described as containing five carnivorous mammal species (Bartholomai 1976) however a detailed review by

Molnar and Kurz (1997) shows that none of the individual sites within the general area of the eastern Darling Downs, contain more than four carnivore species. By contrast, no fossil assemblages containing five or more carnivorous mammals are known from any of the 13 Pliocene or 26 Holocene sites which I have reviewed and which contain carnivore fossils (Appendix 2.2). Further evidence for a temporal decline in mammalian carnivore community richness following each glacial maximum is provided by the data which show that the proportion of sites from the Holocene which contain only one species of carnivore is higher than for any other epoch and that the proportion of sites with four or more carnivores is lowest for the Holocene (Fig. 3.1). These findings are especially significant given the bias of larger samples from progressively more recent epochs (Table 3.1).

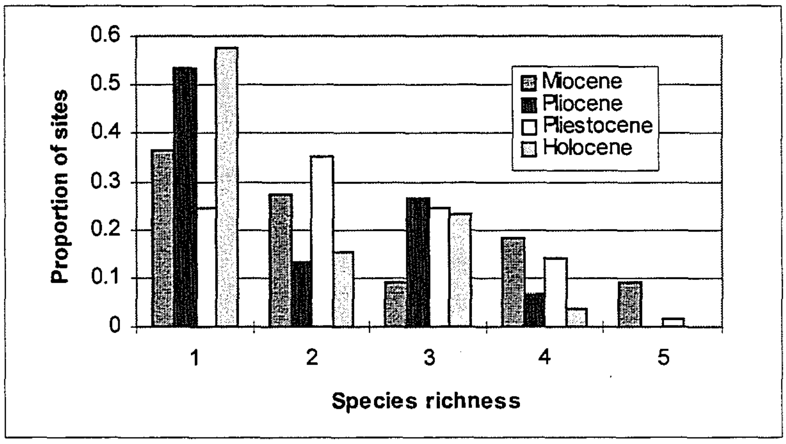


FIG. 3.1. THE PROPORTION OF AUSTRALIAN SITES CONTAINING BETWEEN ONE AND FIVE MAMMALIAN CARNIVORE SPECIES IN THE MIOCENE, PLIOCENE, PLEISTOCENE AND HOLOCENE (SOURCES AND DATA LISTED IN APPENDIX 2.2).

Australia's ratio of carnivorous to non-carnivorous mammals has not always been low compared to other continents (Fig 3.2). The Australian value (at the generic level) was within three percentage points of that of Africa during the Miocene, and was greater than that of South America during all epochs until the Pleistocene and Holocene. These ratios peaked in Africa, South America and North America (which has always had a higher ratio value than that of Australia) following the formation of land connections between each of the continents (Fig. 3.2)(Briggs 1996). It should be noted that generic diversity provides only a rough guide to species diversity, as evidenced by the changes in the proportional values in Figs. 2.7. and 2.8 (Chapter 2), when different taxonomic levels are used. The low generic diversity from South America compared to Australia can perhaps be attributed to the fact that South American carnivorous marsupials belonged to only one Order and Family compared to two orders and four families of Australian carnivorous mammals.

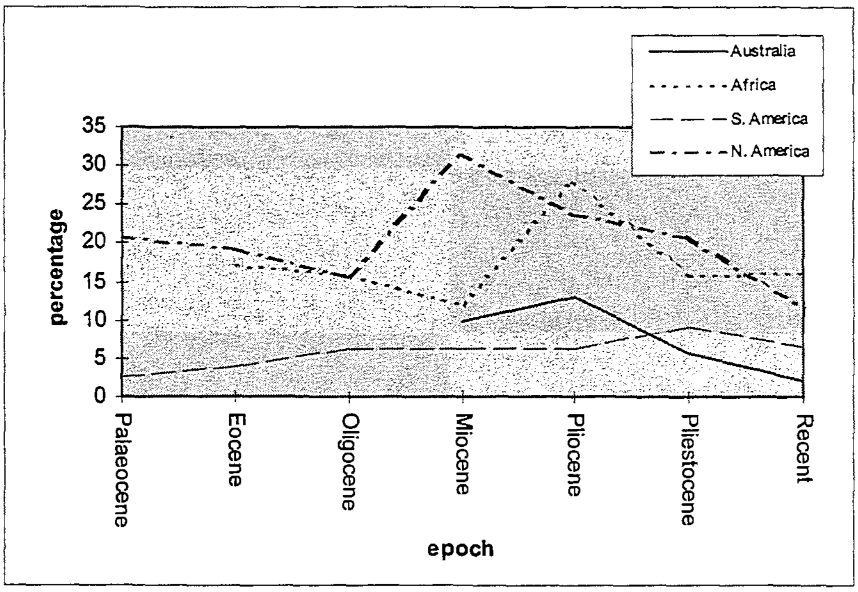


FIG. 3.2. THE RATIOS (EXPRESSED AS PERCENTAGES) OF CARNIVOROUS TO NON-CARNIVOROUS MAMMAL GENERA IN THE AMERICAS, AFRICA AND AUSTRALIA FROM THE PALAEOCENE TO THE PRESENT. Sources: Hall and Kelson 1959, Keast 1972, Patterson and Pascual 1972, Marshall 1976, Maglio 1978, Eisenberg 1981, Simpson 1980, Rich and Thompson 1982, Redford and Eisenberg 1992, Strahan 1995, Rich *et al.* 1991.

3.4. Why is Australia's endemic mammalian carnivore fauna depauperate?

Several hypotheses can be put forward to explain the pattern of low mammal carnivore diversity in Australia. These hypotheses are not mutually exclusive. For convenience these can be grouped into biogeographic and phylogenetic hypotheses. Biogeographic hypotheses include characteristics of Australia's geology and climate, and geographic isolation. Phylogenetic hypotheses pertain to constraints placed upon radiation of marsupial carnivores by their unique system of tooth replacement, and as I will propose, encephalisation and aspects of their life-history strategy including longevity.

3.4.1. Environmental constraints

Australia's geology and climate is characterised by soils of very low nutrient content (Specht and Specht 1999) and low, irregular and unpredictable rainfall (Linacre and Hobbs 1977). Murray (1991), and Molnar (1991) propose that Australia's low nutrient, low rainfall environment is not conducive to the evolution of mammalian carnivores. They argue that the patchy and sparse distribution of resources in Australia favours the evolution and success of reptilian carnivores which have lower energy demands than their mammalian counterparts. Carnivorous reptiles included the terrestrial crocodiles, giant goannas and giant snakes in the pre-Holocene epochs, and 58 species of contemporary Australian carnivorous reptiles.

Changes in the spatial distribution of the most diverse palaeo- and contemporary carnivore assemblages provide evidence for a link between wet environments and high marsupial carnivore diversity. The highest prehistoric carnivore community species richness is known from northern Australia (Riversleigh) during the Miocene, when that area consisted of closed forests and a presumably much wetter environment than at present (Martin 1997). Today, Riversleigh, which receives an annual average rainfall of between 600 and 800mm (Commonwealth of Australia 1986) hosts no endemic carnivores and at the time of European settlement, only a single species, the Western quoll. Later, during the Pleistocene, when much of northern and inland Australia had undergone significant desiccation, the most species rich sites are known only from the south-eastern region of Australia, Wellington Cave and Henschke's Cave (Appendix 2.2). Australia's contemporary marsupial fauna also reflects the link between high and predictable rainfall and carnivore community diversity. Marsupial carnivores are found only in coastal and near-coastal environments that receive high and predictable annual rainfall. No marsupial carnivores are now known from arid Australia.

However, despite the regions low rainfall and poor soils, Australia's three Eutherian carnivore species have successfully colonised the arid zone suggesting that environmental factors alone do not control the low diversity of marsupial carnivores in Australia.

3.4.2. Historical artefacts

Marsupial phylogeny

Although the depauperate nature of Australia's marsupial carnivore fauna can be explained solely on the basis of biogeography it is likely that phylogeny, (aspects of "marsupialness") also contributed to this continent's depauperate mammalian carnivore fauna as outlined below.

Molar morphology

Werdelin (1987) contends that marsupial carnivores have a much narrower adaptive zone, and thus less opportunity for speciation than Eutherian carnivores, because of the marsupial pattern of molar and jaw development. In marsupials, each erupting molar functions as the carnassial and is subsequently shunted forward in the jaw as the next molar erupts. This pattern places restrictions upon the specialisation of molar morphology and thus on diet. In eutherians, the molars erupt *in situ*, and so there is a much greater scope for specialisation of the dentition. Werdelin (1987) proposes that this explains the much lower diversity found in marsupial, as opposed to Eutherian carnivores, as it limits the differentiation of feeding niches between marsupial species.

Reproductive system

Lee and Cockburn (1985) attribute the relatively low morphological diversity of marsupials to the limitations imposed on morphological divergence by the accelerated early development necessary for marsupial neonates to survive extrauterine existence, specifically the early development and acquisition of function in the upper half of the body. The reverse side of this hypothesis is that eutherians, with their greater time spent in the womb, are more able explore the evolutionary possibilities of heterochrony.

Brain development

There has been a general trend towards evolution of larger brains within the eutherian carnivores (Jerison 1973, Savage and Long 1986), suggesting that larger brains are competitively superior. Encephalisation quotients (EQ), (a ratio of brain to body weight), of the Dasyuromorphian carnivores are low relative to their eutherian counterparts (Jerison 1973, Eisenberg 1981), and are lower than most of their non-carnivorous marsupial cohabitants (Nelson and Stephan 1982). This is in startling contrast to the Eutherian mammals in which carnivorous species have amongst the highest EQ values of any mammals (excluding the primates). Jerison (1973) also noted that the brains of the Neotropical ungulates, which were replaced by north American ungulates when the Panamanian Ismuth was formed in the Pliocene had smaller brains than their northern counterparts. Eisenberg (1981) notes that low encephalisation quotients seem to involve maximum pre-programming of information and a reduced capacity to store and retrieve information. Thus learning capacity is curtailed. Additionally, low EQ's correlate with specialisation of only one or two sensory modes, compared to higher EQ values which correlate with three or more modes.

An example of competitive advantages that might be gained by greater brain power in carnivores include evolution of complex social behaviour which increases hunting success. For example group hunting which is so important for Dingoes in the arid zone where they prey on large prey (Corbett 1995), is unknown amongst the extant marsupial carnivores. Larger brain size is also correlated with increased visual perception. Australian Eutherian carnivores have well developed vision; a domestic dog can catch an object thrown through the air towards it and a domestic cat can capture birds and small bats on the wing. Among the extant Dasyuromorphian carnivores the Spot-tailed Quoll at least, appears to lack this visual acuity. The secondary nature of vision as a prey finding sense was illustrated to me by my experiences with a wild *D. maculatus* that had become accustomed to scavenging around my field shelter on the Windsor Tableland. On one occasion I offered this animal a raw, whole egg out of curiosity of whether it would recognise it as food. The Quoll grabbed the egg in its jaws, but it slipped out almost immediately. It was obvious to me while watching the Quoll trying to relocate the egg that it was using smell and not vision to find the object which it subsequently broke open and ate.

Vision may confer advantages in terms of capture of small prey such as invertebrates, small reptiles and birds, thereby facilitating a broader prey base. The Dasyuromorphians on the other hand rely on smell to track prey which may be advantageous in cluttered environments such as rainforests where smelly prey (mammals) are common, but may confer a competitive disadvantage in more open habitats where Dingoes/Dogs, Red Foxes and Cats can use their sight more effectively than in those cluttered environments.

Life Span

Marsupials are shorter-lived than eutherians of similar trophic niches (Montali 1980). Annual recruitment is not assured in environments in which climate is stochastic and all else being equal such environments should favour the longer-lived Eutherian carnivores. The history of the Australian arid zone suggests that this is indeed the case. The single marsupial carnivore extant throughout the arid zone at the time of European settlement (*D. geoffroyi*), rapidly became extinct there, and three eutherian carnivores are now widespread throughout the zone. A greater longevity may also confer advantages in the ability to acquire complex behaviours that in turn may provide a competitive advantage to the Eutherian carnivores over the marsupials.

Whether by an accident of biogeography or phylogeny, and quite possibly as a result of both, marsupial carnivores do appear to be competitively inferior compared to Eutherian carnivora. This is evidenced by: (1) the small maximum size attained by contemporary marsupial carnivores compared to eutherians in both Australia and South America, (2) the inability of marsupial carnivores to maintain their distributions in marginal habitats in Australia while Eutherian carnivores have expanded, and, (3) by the repeated patterns of replacement of marsupial carnivores by eutherian carnivores in the fossil records of both Australia and South America.

It is impossible to quantify the relative impacts of phylogeny and biogeography on the diversity of Australia's mammalian carnivore fauna. It is likely that both types of constraints have played an important role in determining the nature of our Marsupial carnivore fauna. Poor soils and unpredictable rainfall create conditions in which resources are low, and phylogeny imposes constraints on the ability of marsupial carnivores to evolver into new niches.

Geographic history

Geographic isolation

Australia is unique among all of the world's continents in its unbroken physical isolation from all other landmasses. The first major exchanges of mammals between Africa and Eurasia and Asia and North America occurred in the Miocene, and between South and North America in the late Pliocene (Briggs 1996). Each of these biogeographic contacts provided a boost to the carnivore diversity of the relevant continents (Fig. 3.2). In contrast, Australia has always had to rely upon "in house" evolution to replace losses incurred during Ice Age induced and other extinction events. Contact with other continents also results in a greater pool of genetic material, with theoretically greater potential for diversification and speciation especially in the face of changing environmental conditions.

Land mass

The global fossil record indicates that when continental faunas mix, those from the larger continents invariably predominate (e.g. Briggs 1996). This trend has been attributed to the greater role of competition in the evolution and survival of species in more speciose faunas such as usually occur on larger landmasses. Australia is the smallest of all the continents, and thus whatever the mechanism, our fauna would be expected to be competitively inferior compared to those from the large land masses.

3.5. Conclusions: Replacement and augmentation of Australian marsupial carnivore communities by the Carnivora

Patterns in the vertebrate fossil record of Australia and South America suggest that marsupials are inherently susceptible to exclusion by Eutherian and other carnivores with similar ecological niches. However, it is difficult to tell whether this is due to an inherent susceptibility to competitive exclusion of marsupial carnivores by Eutherians, or by an accident of biogeography in which marsupial carnivore faunas inhabit(ed) the two smallest continents. Faunas from larger landmasses invariably dominate over those of smaller landmasses when faunal interchange occurs (Briggs 1996).

Circumstantial evidence of the exclusion of marsupials by Eutherian equivalents in Australia comes from Australian fossil sites and from the history of marsupial carnivore replacement by Eutherian carnivores in Australia (see Chapter 2). Dingoes replace Thylacines in younger strata from fossil sites in southern and northern Australia (Archer 1974a), and Thylacines survived until recent times only in Tasmania, where Dingoes were absent. In South America, two separate incidences of apparent marsupial replacement by Eutherian equivalents, and one case of marsupial replacement by Avian equivalents are discussed below. The persistence of gigantic reptilian and terrestrial avian carnivores in the two continents which contained only marsupials among their mammalian carnivore fauna provides further circumstantial evidence of marsupials faring poorly in competition with Eutherian and other carnivores.

As with the Australian carnivorous marsupials, those of South America were apparently susceptible to exclusion by other carnivore lineages. In South America, three circumstantial cases of marsupial carnivore replacement by other carnivore lineages are discernible from the fossil record (e.g. Marshall 1976, Savage and Long 1986). In the early Pliocene, Procyonids (racoons) and Ursids (bears) invaded South America and took over the niches of the medium to large omnivorous-carnivorous marsupial carnivores. Later in the Pliocene, Mustelids (weasels) and Canids (dogs) took over the niches of the small to medium omnivore/carnivorous marsupials. Commencing in the Miocene and culminating in the Pliocene, the large to very large marsupial carnivores were replaced by large terrestrial carnivorous birds, the Phoracorhoids.

As in Australia, the highest carnivore diversity in South America was attained only after the arrival and diversification of eutherian Carnivores beginning in the mid-Pliocene (Fig. 3.2, Simpson 1980). Interpretation of this trend in species richness must be tempered by consideration of the geographic effects of isolation of the South American continent including the possibility that eutherians filled niches which became vacant through marsupial extinctions caused by other agents.

Within the contemporary Australian fauna, Eutherian carnivores now form more species rich communities than marsupial carnivores over almost the entire continent. For example, three Eutherian carnivores co-exist at many sites (e.g. Triggs *et al.* 1984, Brown and Triggs 1990, Catling and Burt 1994, 1997). In contrast, a single marsupial carnivore (a *Dasyurus* species) occurs in some of these sites, although at the majority of sites no marsupial carnivores exist. Even before the arrival of Europeans, and before the Eutherian carnivores were established, marsupial carnivore species richness was no more than two at any site on mainland Australia (see Map 2.5a, Chapter 2).

Because of their probable roles in limiting species richness and competitive abilities, geographic isolation and small geographical extent might be expected to predispose the faunas of Australia and South America to replacement by immigrant taxa from less isolated and spatially more extensive faunal provinces. Based on the global pattern of extinction and radiation of continental faunas (Briggs 1996), this should apply irrespective of whether this fauna is eutherian or marsupial. Because of the coincidence of Australia and South America's small areas relative to those of other continents and the marsupial nature of their carnivore faunas, it is thus impossible to separate the effects of biogeography and phylogeny on the selective extinction proneness of their marsupial faunas. None-the-less there are reasons of life-history for supposing that marsupial carnivores might be competitively inferior and prone to displacement by Eutherians, as discussed below.

This pattern of competitive inferiority of marsupial carnivores is cause for great concern for their future in Australia. With Eutherian carnivores now well established in virtually all habitats in Australia, the evolutionary potential of the Dasyuridae for radiation into the carnivorous guild, and the re-evolution of non-dasyuromorphian marsupial carnivores appears to be limited.

3.6. Summary

- Despite the constraints and biases of Australia's fossil mammal record, it is evident that the local community richness of carnivorous mammals has declined since the Miocene.

- Like Australia's contemporary fauna (see Chapter 2), our prehistoric mammalian carnivore fauna was depauperate compared to that of all other continents for the Oligocene, Miocene, Pliocene and Pleistocene.

- Historically, when marsupial carnivore faunas have met eutherian carnivore faunas, the Eutherians have thrived and the marsupials have disappeared. This pattern is seen in the fossil records of South America and Australia. Recent trends in the abundance and distribution of marsupial and eutherian carnivores also demonstrate the replacement of marsupial by eutherian carnivore communities in Australia.

- Aspects of the geography and phylogeny of Australia's marsupial carnivores place them at risk of replacement by Eutherian carnivores including: (1) the history of isolation and the depauperate nature of Australia's prehistoric mammalian carnivore fauna which has resulted in an evolutionary environment of low competition compared to that in which Eutherian carnivores have evolved; (2) the short life-span of marsupials, and; (3) developmental constraints imposed by marsupial phylogeny and by the marsupial reproductive mode.

Chapter 4.

Study Site and General Methods

In this Chapter I describe the study area and methodologies that are relevant to multiple chapters of this thesis including: live-trapping, scat surveys and scat analysis.

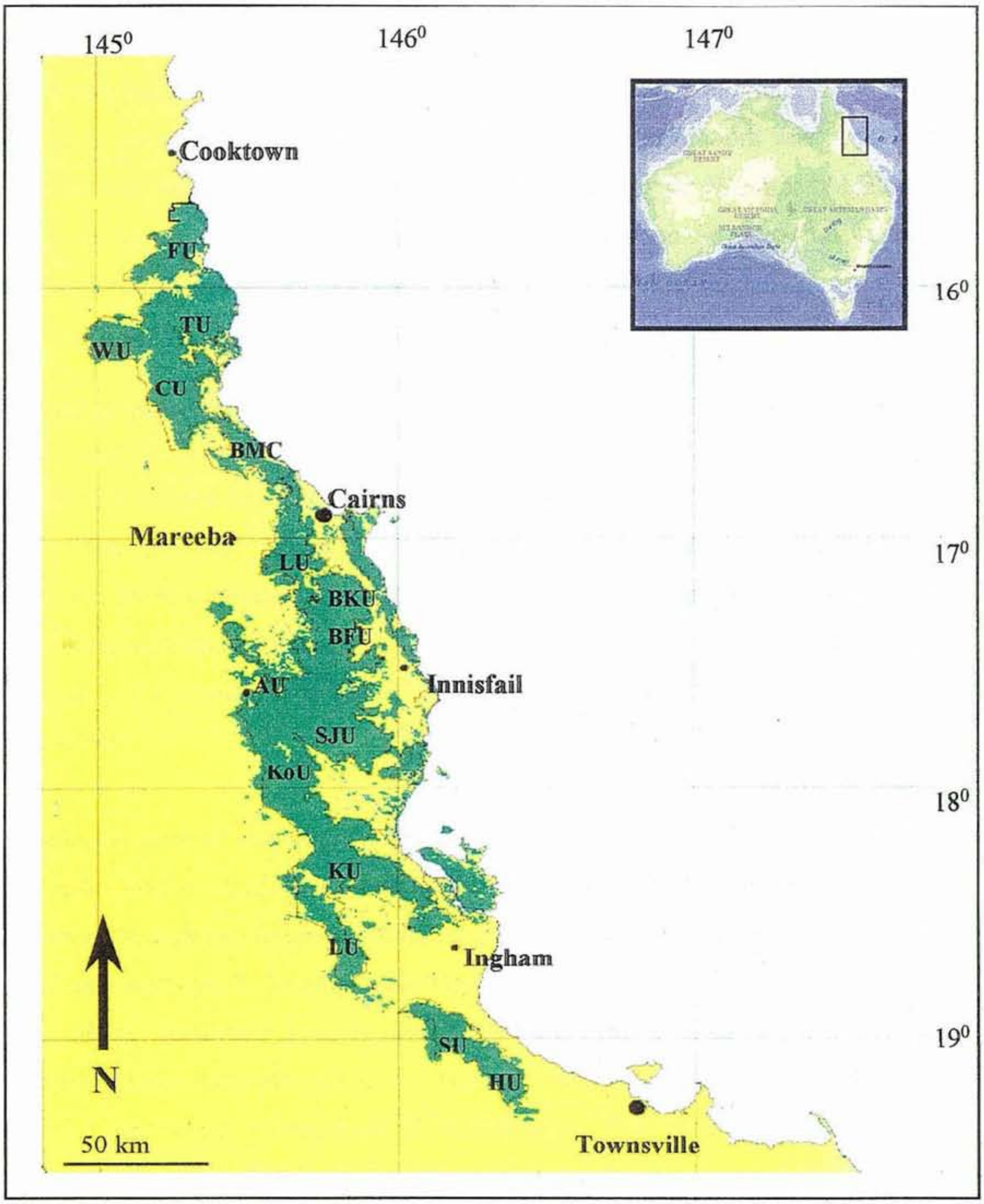
Chapter 4. Study Site and General Methods

4.1. Study Site

4.1.1. The Wet Tropics World Heritage Area

This study was conducted solely within the Wet Tropics World Heritage Area (WTWHA) in north Queensland (Map 4.1). The WTWHA covers most of the eastern escarpment which stretches almost unbroken from just south of Cooktown to just north of Townsville. The highest point of the escarpment is the main summit of Mt Bartle Frere (1622m asl). Much of the area lies above 600m asl and is covered by closed forest with limited areas of various Eucalypt forest communities. The narrow coastal plain to the east of the escarpment lying outside of the WTWHA has been largely cleared for agriculture. In the 1880s, Lumholtz (1888) noted that large areas of the Herbert River Valley had already been turned to agriculture. While this wet tropical coastal plain and the higher altitude basalt tablelands of the WTWHA support high human population densities compared to other areas of north Queensland, the vast majority of the WTWHA above 300m asl supports no human habitation although the more accessible regions have been selectively logged since late last century (Winter *et al.* 1984).

Winter *et al.* (1984) developed the first biogeographic framework for the WTWHA, in which they recognised three altitudinal zones and 27 biogeographic regions. The altitudinal zones were: lowlands, 0-300m above sea level (asl); highlands, 301-900m asl; and uplands, 901-1622m asl. In a reappraisal of this biogeographic scheme, Williams *et al.* (1996) confirmed all of Winter's regions and identified a further two regions, the Lamb Uplands and the Kirrama Uplands, which they split from Winter's Atherton Uplands. In this study, I have further modified Williams *et al's.* (1996) model by: (1) splitting their Bellenden Ker unit into separate Bellenden Ker and Bartle Frere regions, and (2) splitting their Atherton Uplands unit into three: the Atherton Uplands, Koombooloomba Uplands and South Johnstone Uplands (Map 4.1). These changes reflect the patterns of discontinuity between the upland forests of these geographical areas, which are separated by low altitude forest or high altitude cleared habitats which are probably impermeable to *D. maculatus*.



Map 4.1. The Wet Tropics World Heritage Area (WTWHA). Dark shading represents rainforest, the thin dark line marks the boundary of the WTWHA.

Note: Upland biogeographic regions recognised in this study are labelled as follows. FU, Finnegan Uplands; WU, Windsor Uplands; CU, Carbine Uplands; BMC, Black Mountain Corridor; LU, Lamb Uplands; BKU, Bellenden Ker Uplands; BFU; Bartle Frere Uplands; AU, Atherton Uplands; SJU, South Johnstone Uplands; KoU, Koombooloomba Uplands; KiU, Kirrama Uplands; LU, Mt. Lee Uplands; SU, Spec Uplands, HU, Halifax Uplands.

Two strands of field work were pursued during this study. One on the Mt Windsor Tableland consisted of intensive studies of the ecology of *D. maculatus*, including capture-mark-recapture, radio-telemetry, prey species abundance and diet, as outlined below, or in the relevant chapter(s). The second strand of field work was performed throughout the uplands of the Wet Tropics Area (including Mt Windsor Tableland), where I conducted distribution surveys and dietary studies on *D. maculatus*, and its potentially sympatric eutherian carnivores, Dingoes, Cats and Red Foxes.

4.1.2. Mt Windsor Tableland

The Mt Windsor Tableland (16^{0}15'40"S 145^{0}02'30"E), lies approximately 75 km north west of Cairns (Map 4.1). The Tableland is an isolated granitic massif roughly ovoid in shape, which rises very steeply from 500m asl to 900-1000m asl on the northern, western and southern faces and less steeply up from 300 to 800m on the eastern face. The resulting tableland area occurs as a broadly domed area reaching an altitude of over 1300m asl. The Tableland is part of the watershed for the Daintree, Mitchell and Palmer Rivers.

The tableland area of the massif consists of approximately 13200ha of continuous closed forest (Winter *et al.* 1984), primarily simple and complex notophyll vine forests and microphyll vine fern forests and thickets (Types 8 and 9, Tracey 1982) and 17990ha of highland sclerophyll forest, consisting of wet sclerophyll forest dominated by Flooded Gum, *Eucalyptus grandis,* and Turpentine, *Syncarpia glomulifera,* and dry sclerophyll forests dominated by Lemon-scented Gum, *E. citriodora,* Bloodwood, *E. intermedia,* and White Stringy-bark, *E. acmeniodes.* The open forest communities occupy the western third of the tableland, while closed forest communities occupy the remainder. The ecotone between the two broad vegetation types occurs just west of the high point of the tableland. The only physical connection between the closed forest communities of the Windsor Tableland and other biogeographic units of the WTWHA is a tenuous connection via a narrow saddle at about 600m asl which joins it to the Carbine Uplands to the east. The rainfall of the summit area of the Tableland, where most of my study was conducted, is estimated to exceed 2500mm annually (Nix and Switzer 1991).

Apart from some tin mining on its northern and western periphery in the late 1800s and early 1900s, the Mt Windsor Tableland was pristine when first opened up to logging in the early 1970s. Logging operations ceased with the implementation of World Heritage Listing of north Queensland's Wet Tropics Area in 1988. Access to the Tableland is limited to one serviceable road and public access is restricted by a locked gate some 30km from the foothills of the Tableland.

The rainforest areas within the Tableland are accessible via two serviceable roads which traverse the Tableland (A and B-roads), and numerous, now overgrown roads and logging tracks which feed off these roads.

The Tableland is notable in that, presumably because of its high altitude, very dry and steep northern, western and southern ramparts, and pristine forested eastern grade, it is the only rainforest unit in the Wet Tropics area which has been disturbed by humans but which has not been invaded by the introduced Cane toad, *Bufo marinus* (unpublished data).

4.2. General Methods

Any methods which were fundamental to collecting data for more than one chapter of this thesis are listed here as general methods. Methods specific to particular chapters are described within that chapter.

4.2.1. Quoll capture and handling

Live-trapping was used to gather morphological, demographic, ranging, and sex-specific dietary data for *D. maculatus* on the Mt Windsor Tableland. Live-trapping was also used to capture Spot-tailed quolls for radio-collar attachment. *D. maculatus* were caught in wire "cat-traps" (Mascot Wireworks, Sydney), operated by a treadle mechanism and measuring 30cm x 30cm x 60cm (Fig. 4.1). Up to 45 traps were set 250m apart along an 11 km stretch of the single trafficable road which traverses the Tableland. Traps were set along that part of the road which traverses rainforest habitats from 1000m to 1300 m above sea level. Traps were set one metre in from the roadside and were baited with beef bones, usually one vertebral segment per trap. In most cases, the bait did not need to be changed during each trapping session even when quolls were caught. All trapping was conducted within the rainforest habitat and each trapping episode consisted of four consecutive days.

Trapping was conducted between April 1992 and December 1994. I attempted to set traps during each month within the period of November 1991 to February 1994. However, because of restrictions on access to the Tableland during periods of wet weather, this was not possible. Similarly, access along the entire road was not always possible because of inclement weather and so not all traps could be set on each trapping occasion. Traps were checked each morning and afternoon.

Initially, quolls were transferred from traps to a conical calico restraining bag (Fig. 4.2) which allowed me to access their hind end and ears only. From mid-1993, I decided to lightly anaesthetise each captive once it was within the calico restraining bag, in order to reduce the stress involved with handling the animals. This also allowed me to make a more thorough examination of each animal. Quolls were anaesthetised with the inhalation anaesthetic Forthane (Isofluorane) which was applied to the animal while it was within the restraining bag. The top of a cut-off plastic bottle (Fig 4.2) into which several drops of Forthane were added to a piece of cottonwool, was fitted over the quoll's snout. The anaesthetic applicator was removed when the quoll showed no signs of involuntary reflex, such as in response to manipulation of the pes or light touching of the area around the eye, and when its breathing became deep and slow.

Each new quoll was individually numbered by tattooing its ear pinnae. Information gained from live-trapping included for each capture: location along the transect; sex; reproductive status including number of pouch young and pouch characteristics; weight; trap site; time of day; and testes width, length and depth in males.

Fig. 4.1. A cage trap set to capture Spot-tailed Quolls alongside the Mt Windsor Road, Mt Windsor Tableland. Plastic sheeting was used to weatherproof the traps.

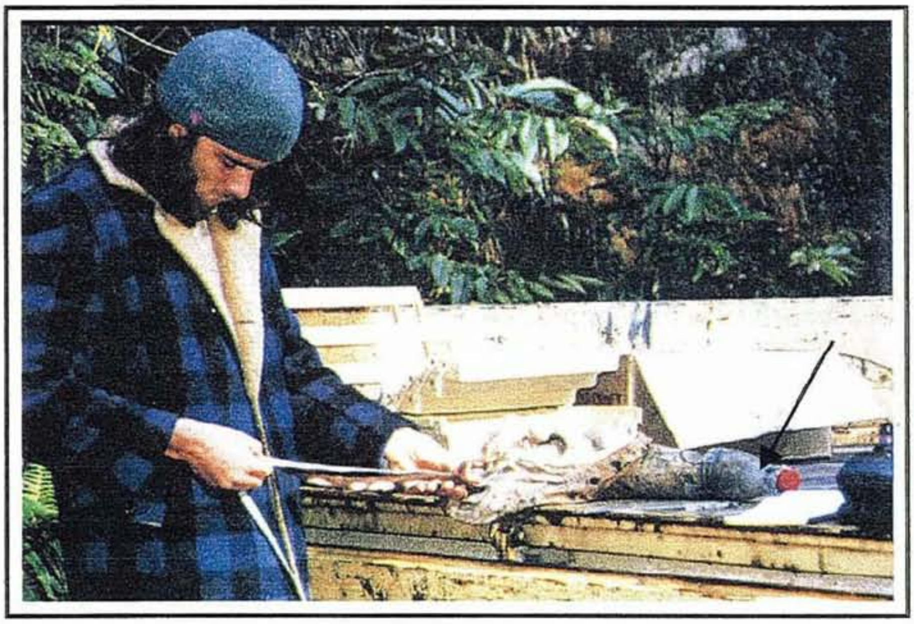


Fig. 4.2. Method of handling Quolls using a conical calico restraining bag. The body of the animal is restrained within the bag while it is anaesthetised. Note the anaesthetic applicator (arrowed), over the snout of the Quoll which is within the bag.

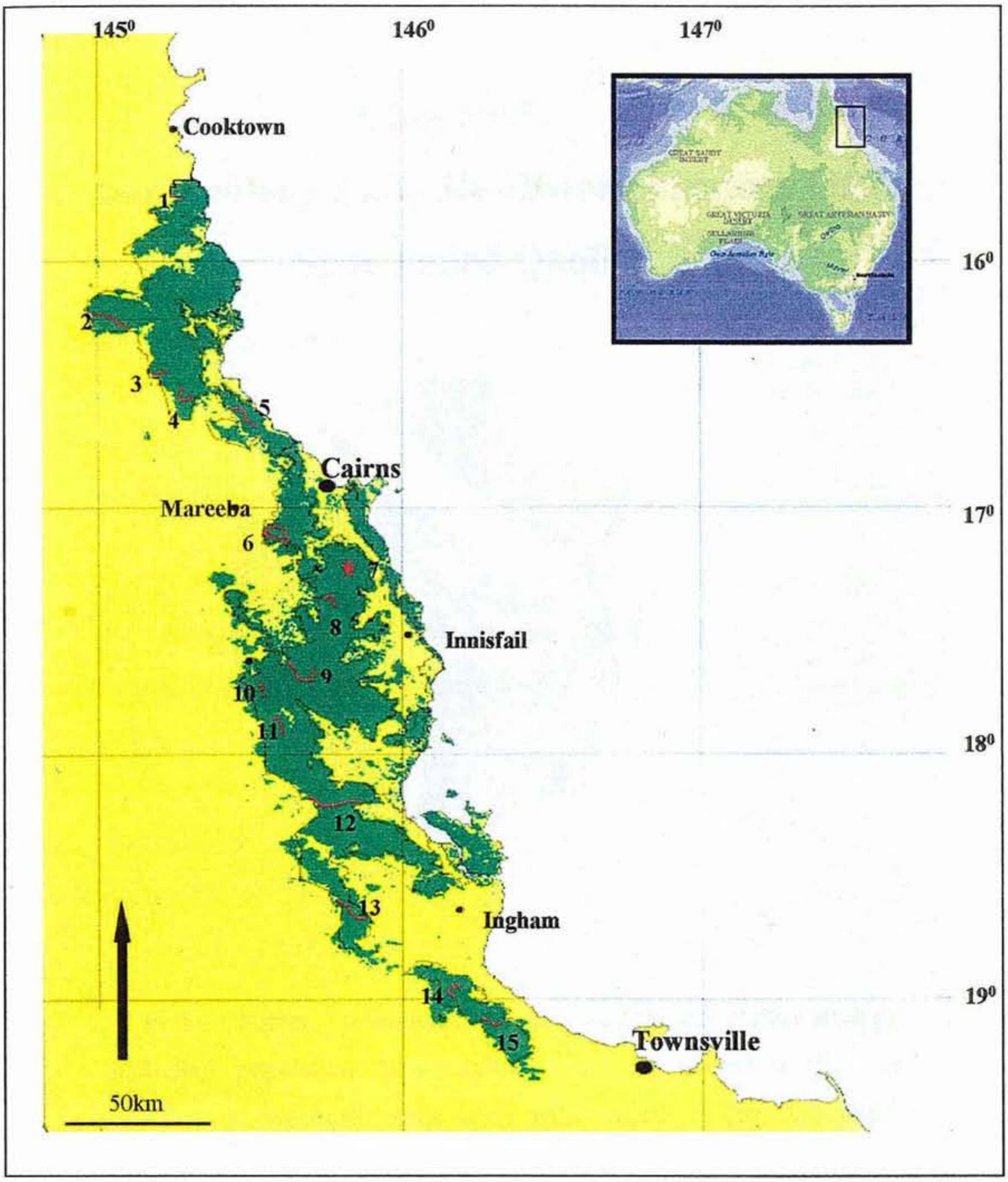
4.2.2. Scat collection and analysis

Scat collection was used to gather distributional and dietary data for Spot-tailed Quolls, Dingoes (*Canis lupus dingo)*, Cats (*Felis catus),* and Foxes (*Vulpes vulpes).* Scats were collected from set transects throughout the Wet Tropical Uplands (Map. 4.2), and were opportunistically collected from throughout the Mt Windsor Tableland. Quoll scats in particular are highly visible on maintained gravel roads (see Chapter 7), and were easily detected by a person sitting on the bonnet of a slowly moving car. Dingo scats tend to be placed off to the side of roads and so, when I began systematic scat collection from transects in 1993, I changed my methodology and walked the length of each transect.

Scat surveys were conducted in October 1993 and November 1994 in each of the upland bioregions accessible by vehicle. Additional surveys of areas not visited by me during these times (that is, Bartle Frere, Bellenden Ker and Big Tableland), were conducted in September 1996. Where vehicular access was possible, these surveys took the form of a scat census along 15-km-long stretches of road within each bioregion. Transects were conducted on a mountain bike fitted with an electronic odometer and pedalled at approximately 5 km/h. Scat census in the Bartle Frere, Bellenden Ker and Big Tableland were different from other transects because of the different access available at each site. In the Bartle Frere unit, I walked a scat transect that followed the western Bartle Frere walking track from start of the walk on the Atherton Tablelands (Wooroonooran National Park), to 1 km beyond the summit. On Bellenden Ker I collected scats from around the television transmitting station and down to the third cableway tower from the summit. On the Big Tableland, I searched for scats along a disused road leading up to the dam from Mungumby Lodge, and signs were searched for in soft mud around the dam on that Tableland.

During surveys, mammalian carnivore prints were identified in dried mud around puddles and in the dried surface of the dirt roads which constituted each transect. Predator scats were recognised by the predominance of hair and/or feathers and bones within them. Scats were identified as being either Dingo/dog, *Canis* spp., Feral domestic cat, *Felis catus*, or Spot-tailed quoll, *D. maculatus*, on the basis of: (1) identification of accidentally ingested grooming hairs and (2) scat size and general appearance. Dog scats are greater than 1.5 cm in diameter, while both quoll and cat scats are smaller. Quoll scats can be distinguished from cat scats by their ropy appearance which cat scats lack. No fox scats were found.

Prey were identified from scats by identification of hair, feathers, scales or exoskeleton. Prey hairs were identified from Spot-tailed Quoll and Dingo scats by Barbara Triggs, (Dead Finish, Genoa, Victoria), using the cross-sectional and casting techniques employed by Brunner and Coman (1974). Non-mammalian material was simply classified as bird, reptile, invertebrate or plant.

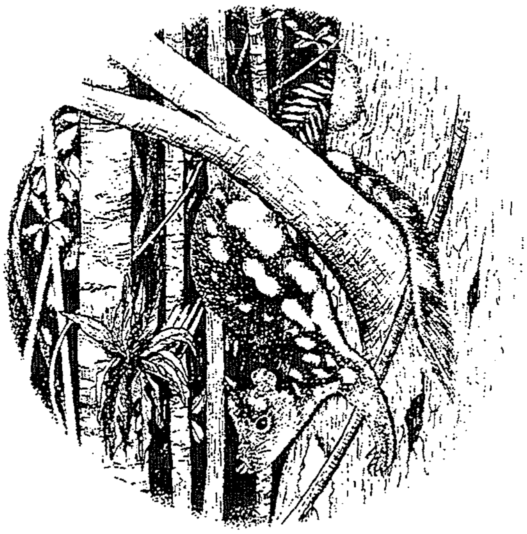


Map 4.2. Numbered scat survey transects used in this study. Transects marked by thin red lines.

Note: Numeric code: 1, Big Tableland track (Finnegan Uplands); 2, Mt Windsor Forestry Rd (Windsor Uplands); 3, Spurgeon transect (Carbine Uplands); 4,, Lewis transect (Carbine Uplands); 5, Black Mountain Forestry Rd (Black Mountain Corridor;6, Mt Edith and Mt Haig Rds (Lamb Uplands); 7, Point location, Bellenden Kerr summit area (Bellenden Ker Uplands); 8, Bartle Frere walking trail (Atherton Uplands); 9, South Johnstone Forestry Rd (Atherton Uplands); 10, Tully Falls Rd (Atherton Uplands); 11, Koombooloomba Road (Atherton Uplands); 12, Kirrama Forestry Rd (Kirrama Uplands); 13, Wallaman Falls Rd (Lee Uplands); 14, Paluma Dam Rd (Spec Uplands); 15, Bluewater Forestry Rd (Halifax Uplands).

Chapter 5.

Population Ecology And Life-History Strategy Of The Spot-Tailed Quoll



In this Chapter, I investigate and document the life-history strategy including population demography of the Spot-tailed quoll. In addition, I investigate these traits with respect to the Spot-tailed quoll's phylogeny and its ecological niche as a medium-sized carnivore. I show that the species life-history strategy is constrained within the small insectivore type from which it has evolved, the major adaptation of the species being a dependence upon predictably productive and wet environments in which extrinsic mortality is minimal. The interface between the species' life-history strategy, resultant habitat requirements and its conservation status are also discussed.

Chapter 5. Population Ecology and Life-History Strategy Of The Spot-Tailed Quoll

5.1. Introduction

Darwinian evolution dictates that the primary measure of evolutionary success for an individual is to produce as many viable offspring as possible within the energetic and phylogenetic constraints of its environment and evolutionary past. Species achieve this end via the evolution of life-history strategies which are tailored to the environmental conditions in which they evolved. For simplicity's sake, these life history strategies can be reduced into individual life history traits which include body size, age at maturity, age at senescence, brain size, number of young per litter, number of litters per season and per year, seasonality and timing of births, and innumerable other subtleties of morphology, physiology, and behaviour (for example Eisenberg 1981). The combination of these features leads to an environmentally dependent and predictable pattern of birth and death. A life-history strategy can be considered to have failed when a species goes extinct through its inability to replace mortality with recruitment.

Australia's environment is characterised by aridity, seasonality and unpredictability. It is within this context that I compare the Spot-tailed quoll to other members of its class (Metatheria), and to medium-sized members of the Eutherian order Carnivora.

Several trends are evident in the evolution of life-history strategies in mammals. For example, larger animals are typically longer-lived than smaller ones (Eisenberg 1981), carnivores are progressively shorter lived than omnivores and herbivores respectively (Gittleman 1993), and marsupials are generally shorter-lived than their Eutherian ecological counterparts (Eisenberg 1981). Within this context, Spot-tailed quolls would be expected to be shorter-lived than either; (I), non-carnivorous marsupials of equivalent body mass and, (2) their Eutherian counterparts.

In this Chapter, I investigate and document the life-history strategies, including population demography, of the Spot-tailed quoll. In addition, I investigate these traits with respect to the Spot-tailed quoll's phylogeny and its ecological niche as a medium-sized carnivore. I show that the species life-history strategy is constrained within the small insectivore type from which it has evolved, the major adaptation of the species being a dependence upon predictably productive and wet environments in which extrinsic mortality is minimal. The interface between the species life-history strategy, resultant habitat requirements and its conservation status are also discussed.

5.2. Methods

5.2.1. Animal capture and processing

I collected data for this chapter by live-trapping on the Mt Windsor Tableland between April 1992 and December 1994. Full details of the study site and of the trapping methodology are presented in Chapter 4.

5.2.2. Data treatment and mathematical methodology

5.2.2.1. Abundance data

I estimated the abundance of Spot-tailed quolls on the Mt Windsor Tableland by a combination of live-trapping and radiotracking data which provided an estimate of relative abundance, and from published information on the area of suitable habitat (as defined in Chapter 8) on the Mt Windsor Tableland (Winter *et al.* (1984)). The latter was multiplied by the relative abundance estimate (0.3 quolls of each sex/km^2) to provide a crude estimate of the absolute abundance of the species. This is a "ball-park" approach only, and is underpinned by the following assumptions:

- that all quolls within one-kilometre of the trap line were captured (Chapter 7),
- that quolls occur in all closed forest habitats but at very low numbers if at all, in sclerophyll habitats (Chapter 8),
- that on the Windsor Tableland, quolls are evenly dispersed throughout closed forests above 900m asl,
- that in closed forests below 900m asl, quolls occur at a density an order of magnitude less than above that altitude (Chapter 8).

5.2.2.2. Morphological data

Because of possible statistical bias' associated with repeated measurements on the same individuals, I used only one set of morphological measurements from each individual in the analysis of body-size. For animals which were recaptured in more than one trapping trip, I used the data from the last capture of that animal. Measurement data from juveniles (weight < 500g) were not used in the analyses of external morphology. When a juvenile was captured repeatedly those data were used to examine growth rates.

Pouch young were sexed when possible (very young joeys cannot be sexed), and aged by comparison with the growth curve for Tasmanian *D. m. maculatus*, presented by Green and Scarborough (1990). This method might be expected to underestimate the age of joeys given that adult northern *D. maculatus* are approximately 50% of the size of their Tasmanian counterparts (Green and Scarborough 1990). How this difference applies to pouch young and juvenile sizes is unknown.

I could estimate the age of individuals which were initially caught when they were less than one year old. Females less than one year old were identified by the cream or ginger coloured hairs of the pouch. Females greater than one year old were identified by red staining of the hairs in the pouch, which is indicative of having had a litter. The pouch hairs of one older female which never produced a litter likewise remained unstained.

In males, age of greater than one year was indicated by a body mass of greater than 900 grams and by a dark coloured, bald ventral surface of the scrotal sac, similar to that described in *Antechinus* by Inns (1976).

5.2.2.3. Life-history data

I calculated the nett reproductive rate R_0 and intrinsic rate of increase r_m as per Krebs (1985) with one important variation. I calculated r_m using overall mean annual survivorship (l) and overall mean birth rate (b) rather than age specific data, as the latter were not available. Following convention (Krebs 1985), female values only are used in these calculations.

I compared the life-history strategy of *D. maculatus* with Eutherian carnivores, (Dasyuromorphian, Ameridelphian, Peramelemorphian and Diprotodontian marsupials, rodents, insectivorans and primates), by collation of longevity and fecundity data for each family. The actual species used in these comparisons and the sources in the analyses are listed in Appendix 5.1.

Lifespan was compared among families by plotting mean recorded longevity in captivity +/- 2 standard errors. Given the positive relationship between body-size and longevity in mammals (Lindstedt and Calder 1981, Gittleman 1993), I have only used data from species in which females weigh less than the maximum weight of *D. m. maculatus*, (6 kg, Green and Scarborough 1990). I would expect this approach to underestimate the mean life-span of those other families (the Diprotodont marsupials, the Eutherian carnivores, the Rodentia, the Xenarthuria, the Insectivora and the Primates), because of the range of smaller species included in the data set.

For each species, the potential annual fecundity (PAF) was calculated by multiplying the maximum litter-size known for that species by the maximum number of litters per year. Means and standard errors were calculated for each family.

I calculated extinction probabilities for 24 hypothetical populations of *D. maculatus*, in which all parameters were held constant except: (1) adult longevity, which ranged from 1- 6 years, and, (2) initial population size which included values of 50, 100, 150, and 250 individuals, (that is 6 x 4 = 24 populations). I calculated extinction probabilities using the VORTEX Population Viability Analysis Program (Lacey 1993). The values of the fixed parameters used in these analyses are presented in Appendix 5.2. A full description and list of assumptions underpinning the program is made by Lacey (1993).

5.3. Results

5.3.1 Trapping statistics and population demography

I captured a total of 24 individual female and 26 individual male *D. maculatus* (Table 5.1). These captures were made over 1688 trap nights over 18 field trips between April

1992 and December 1994. This equates to an average capture success of approximately 11% per trip (range 2.2% to 27.9% per trip, SE=5.95%) and an average density of females and males per km of transect over three years, of 0.68 (SE=0.07) and 0.6 (SE=0.04) respectively. The highest number of individuals known to be alive (ktba) for any trapping trip during this study was 15 individuals which were trapped along a 10km transect over a period of four nights in August and September 1993 and December 1994 (Fig. 5.1). During 1992 and 1993, the number of females ktba plateaued in July, the time of the annual peak in births. Despite a high annual population turnover (see below), this ktba value was maintained until the following breeding season by an influx of the previous years' young in March. During the same two years, the number of males ktba peaked during the breeding period but then declined during the latter months of the year.

Based on quoll density estimates collected throughout this study, and on the extent of available habitat on the Mt Windsor Tableland, I estimate that the numerical size of the Mt Windsor quoll population in each of 1992, 1993, and 1994 was 86 (s.e +/- 20), 85 (s.e +/- 28) and 81 (s.e +/- 11) individuals respectively. Based on these figures, the overall average number of quolls on the Windsor Tableland based on trapping figures from each trapping session (Fig. 5.2) is 85 (s.e +/- 13).

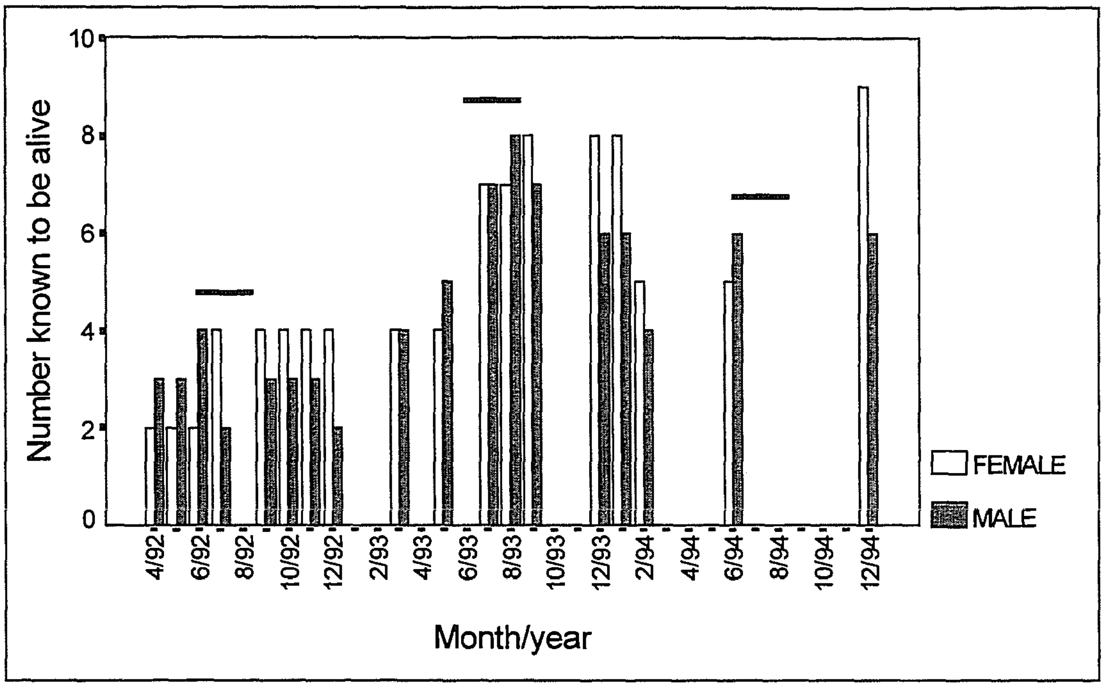


Fig. 5.1. The number known to be alive (KTBA) of male and female D. maculatus within the Windsor Tableland trapping transect during each trapping trip.

The horizontal bars delineate the mating period.

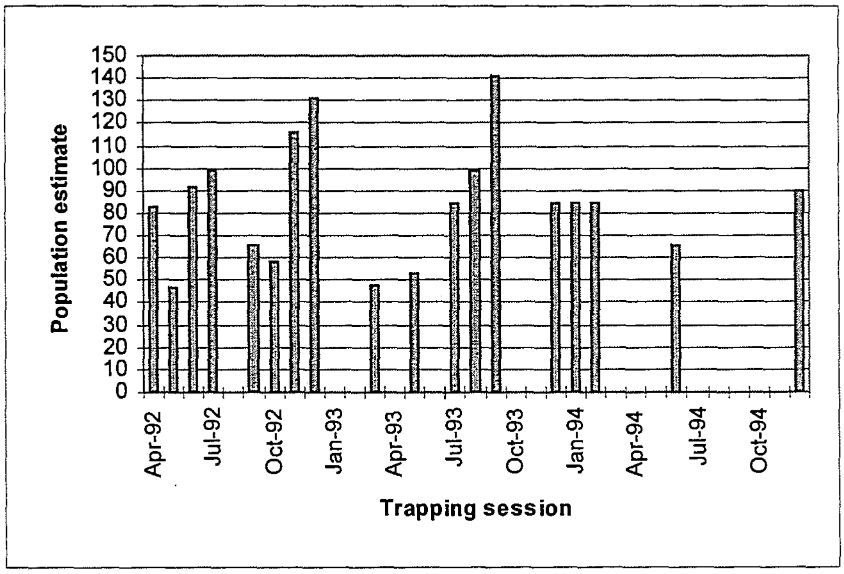


Fig. 5.2. The estimated number of quolls on the Mt Windsor Tableland based on trapping figures from all months.

The average estimated population size over all sessions is 85 (s.e +/- 13).

Table 5.1. Summary of capture data of Spot-tailed quolls from the Mt Windsor Tableland between April 1992 and December 1994.

Trapping period[1]	# trap nights[2]	km trapped[3]	# captures		# individuals		Ktba[4]		density/km trap transect	
			female	male	female	male	female	male	female	male
4/92	45	4	2	3	2	3	2	3	0.5	0.75
5/92	87	7	4	5	2	3	2	3	0.28	0.43
6/92	60	4	3	4	1	2	2	4	0.4	1
7/92	60	4	3	2	2	0	4	2	1	0.5
9/92	60	7	8	3	4	2	4	3	0.57	0.43
10/92	53	7	2	3	1	2	4	3	0.5	0.38
11/92	116	8	6	4	3	2	4	3	1	0.75
12/92	26	4	2	0	1	0	4	2	1.33	0.66
Total 1992	**507**	**8**	**30**	**24**	**10**	**7**	**10**	**7**		
Mean 1992									**0.69**	**0.61**
S.E 1992									**0.13**	**0.07**
3/93	87	11	2	8	2	3	4	4	0.36	0.36
5/93	123	11	1	5	1	3	4	5	0.36	0.45
7/93	60	11	6	4	5	3	7	7	0.64	0.64
8/93	135	10	8	13	5	5	7	8	0.7	0.8
9/93	68	7	10	9	4	5	8	7	1.14	1
12/93	112	11	10	4	6	5	8	6	0.73	0.55
Total 1993	**585**	**11**	**37**	**43**	**12**	**13**	**12**	**13**		
Mean 1993									**0.65**	**0.63**
S.E 1993									**0.12**	**0.1**
1/94	230	11	10	6	9	4	8	6	0.73	0.55
2/94	92	7	2	0	2	0	5	4	0.71	0.57
6/94	146	11	4	8	3	4	5	6	0.45	0.55
12/94	128	11	13	9	7	6	9	6	0.82	0.55
Total 1994	**596**	**11**	**29**	**23**	**14**	**11**	**14**	**11**		
Mean 1994									**0.68**	**0.56**
S.E 1994									**0.08**	**0.01**
Grand Total	**1688**		**96**	**90**	**24**	**26**	**24**	**26**		
Grand Mean									**0.68**	**0.6**
Total S.E									**0.07**	**0.04**

Note. (continued over)

1. Trapping period refers to the month and year of each trapping trip.
2. # trap nights refers to the number of nights x number of traps set during each trapping period.
3. km trapped refers to the length of road over which traps where set during each trapping period.
4. ktba refers to the number of quolls known to be alive and density/km of road refers to quoll density per kilometre of road over which traps were set.

There was a high population turnover of *D. maculatus* between years (Table 5.2). The average survival of females from calendar year to year was 56% (s.e. of binomial 3.35%). Twenty-five percent (s.e. of binomial 2.2%), of females were known to be alive in two consecutive breeding seasons and 13% (s.e. of binomial 1%) were known to be alive in three. The comparative figures for males were 32% (s.e. of binomial 2.58%), 5.5% (s.e. of binomial 1%) and 0% respectively. Male survival from year to year was lower than that for females and no male was known to be alive in three consecutive years.

Table 5.2. The proportion of male and female D. maculatus known to be alive at the start of each breeding season over three seasons at the Mt Windsor Tableland, north Queensland.

For example five out of nine males ktba during the 1991 breeding season were ktba during the 1992 breeding season and one out of nine males ktba during 1991 were ktba during the 1993 season *et cetera.*

	Male			Female		
	1992	1993	1994	1992	1993	1994
1991	5/9	1/9	0/9	4/8	2/8	1/8
1992	------	1/7	0/7	------	13/20	4/20
1993	------	------	4/12	------	------	11/18

The sex ratio of individual adult males: adult females captured over the duration of the study was 1:1.08, which does not differ significantly from parity (χ^2=0.080, d.f=1, p=0.777).

Females exhibited greater residency times on the transect than males and were generally recaptured more often (Fig. 5.3). Approximately half of the animals caught during this study were captured on fewer than three trapping trips. These animals could include transients, trap shy individuals or individuals whose home ranges barely intercept the transect. Forty-two percent of all captures were of animals which were captured only once (Fig. 5.3).

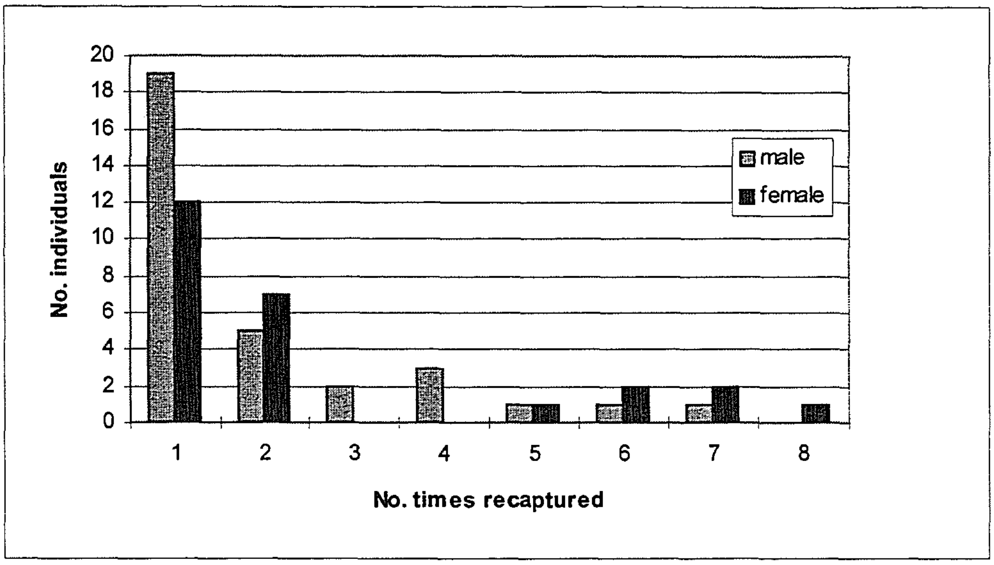


Fig. 5.3. The number of recaptures of male and female *D. maculatus*, captured between one and eight times during this study.

I recaptured females more often than males; six females were recaptured on five or more trips, compared to only three males (Fig. 5.3). Conversely, animals caught only once included 19 males and only 12 females which were captured only once. Females also exhibited a greater residency time on the transect than males (means: 17 and 10 months respectively; t=2.14, d.f= 17, $p<0.05$). Implicit in my interpretation of these results is the assumption that all individuals are equally capturable, both before and after each capture. This assumption may be violated by different degrees of trap shyness in some individuals and by the peripheral location of the trapping transect relative to some home ranges.

5.3.2. External Morphology

Male Spot-tailed quolls are significantly larger than females for all the external measurements I made (Tables 5.3 & 5.4). *D. maculatus* from the Mt Windsor Tableland are much smaller than their counterparts from southern Australia. On average, adult male and female *D. maculatus* are 51% and 31% lighter respectively than their Tasmanian counterparts (M. Jones unpublished data), and are 51% and 47% lighter respectively than their Barrington Tops, New South Wales counterparts (Karen Firestone unpublished data).

Table 5.3. Summary statistics of the external measurements of male and female *D. maculatus* from the Mt Windsor Tableland, north Queensland.

Measurement	Sex	Mean+/-2s.e.	Range	n
Weight(g)	male	1624+/- 82	850-2540	30
	female	1115+/ 34	800-1600	27
Head-body(mm)	male	413 +/- 8	330-510	25
	female	385 +/- 6	310-440	24
Tail-vent(mm)	male	388 +/- 6	310-440	25
	female	357 +/- 4	285-410	24
Pes(mm)	male	72 +/- 0.7	65.5-79.8	22
	female	65.4 +/- 0.7	58.6-71	20
Head-vol(cm^3)	male	80.5 +/ 5.8	50-109	23
	female	54 +/- 2.2	37-66	20

Table 5.4. Results of 2-tailed t-tests to test for sexual dimorphism in various body measurements for *D. maculatus* on the Mt Windsor Tableland, north Queensland.

Body feature	t	p	d.f	Conclusion	DR ratio[1]
Weight	8.0464	<0.0001	126	reject Ho	1.38
Head-body	-3.9009	0.0001	108	reject Ho	1.07
Tail-vent	-5.1001	<0.0001	106	reject Ho	1.07
Pes	-10.2259	<0.0001	92	reject Ho	1.09
Head-vol	-8.4773	<0.0001	62	reject Ho	1.49

Note.

1. **D.R. is the dimorphism ratio (mean male value/mean female value).**

5.3.3. Reproduction

In north Queensland, Spot-tailed quolls have a well defined annual breeding season. Between July 1991 and December 1994, pouch young were only observed between the months of June and September, inclusive (Fig. 5.4). Based on Green and Scarborough's (1990) pouch young growth line for Tasmanian *D. maculatus*, most births are estimated to have occurred in June and July of each year in the Mt Windsor population.

With one exception, the 24 females that I examined had six nipples. The exception had seven nipples although two of her litters for which I obtained data, contained five and six joeys respectively. I observed litter sizes ranging from two to the full complement of six pouch young. The mean number of joeys per litter was 5.3, (69 joeys/13 litters, S.E=0.09). The average number of joeys weaned each year, which is crudely represented by the number of enlarged nipples in each female's pouch after weaning, was 4.6 (104 nipples, 22 litters, s.e= 0.05), representing a pre-weaning mortality of 13%. When the fate of known litters was followed, this pre-weaning mortality rate was higher at 27.2% (six litters, s.e. = 5.5%).

The overall sex ratio of male to female pouch young was 1.24 which did not differ significantly from 1 (χ^2 homogeneity = 0.446, d.f=1,0.5> p < 0.25) or from the adult sex ratio of 1.08, (χ^2 goodness-of-fit = 0.02257, d.f=1, 0.9 > p < 0.5). However, the male:female sex ratio of individual litters varied from 3 to 0.5.

Females raised a single litter per year although a second litter may be born if the first failed. I observed one female which had five pouch young, estimated to have been born in early June 1993. In early December 1993 she was retrapped with six, 14-mm-long nipples and was lactating. Had her first litter survived she would have been expected to have ceased lactating and to have only five elongate nipples in December. I monitored thirty six breeding opportunities (i.e., no. females x no. breeding seasons) during this study. Three different females failed to breed in four (11%) of these breeding opportunities. Only one female was known to have never had a litter during her lifetime (2 years).

Recapture data were too scanty for detailed analysis of growth patterns, however, all three females that I recaptured over a greater than one year period, showed an annual cyclic pattern of weight loss of between 10% and 20% (mean=15.5%, S.E=4.49) over the last five months of the calendar year in both 1992 and 1993 (Fig. 5.5). Notably, two of these females which failed to give birth during the 1993 breeding season, showed a concomitant weight decline during that season. Despite losses in weight during the litter rearing season, two of these females were heavier at the onset of their second breeding season than at the onset of their first. The third female was lighter at the onset of her second breeding season. Females appeared to reach maximum weight by the start of each breeding season (Fig. 5.5). Male recaptures were too irregular to enable any detailed determination of annual growth patterns.

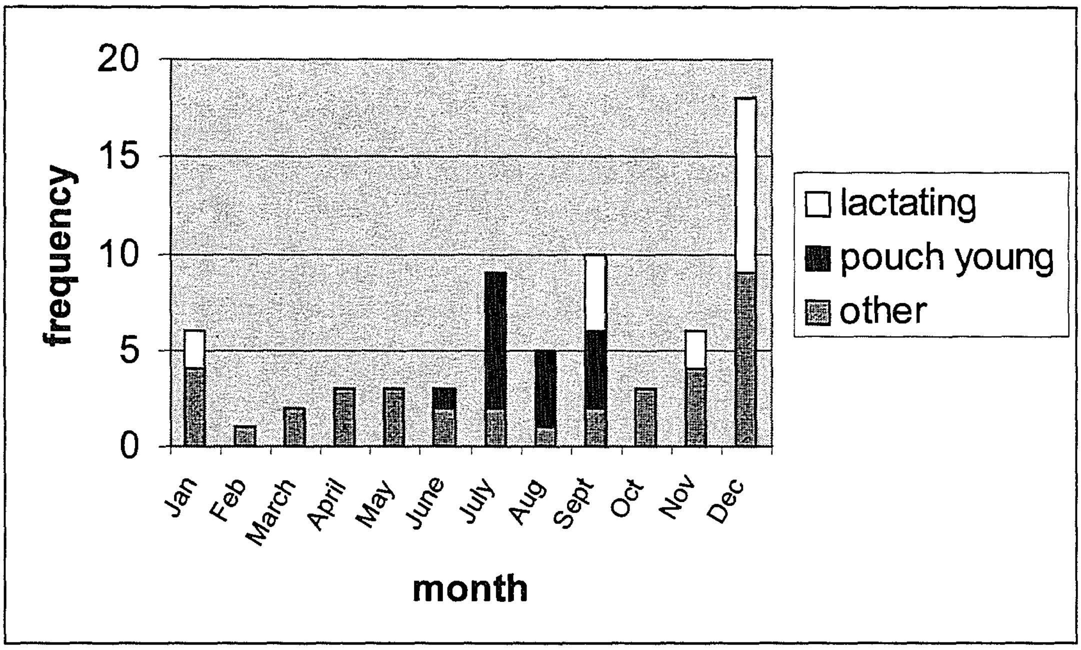


Fig 5.4. Monthly reproductive condition of female *D. maculatus* from the Windsor Tableland, north Queensland, summed over three years.

Key to legend: Lactating, no pouch young but milk able to be expressed from teats; pouch young attached; other, all other pouch states.

I calculated the overall nett reproductive rate R_0 and the overall intrinsic rate of increase r_m, for the population of *D. maculatus* on the Mt Windsor Tableland as 1.49 and 0.17 respectively.

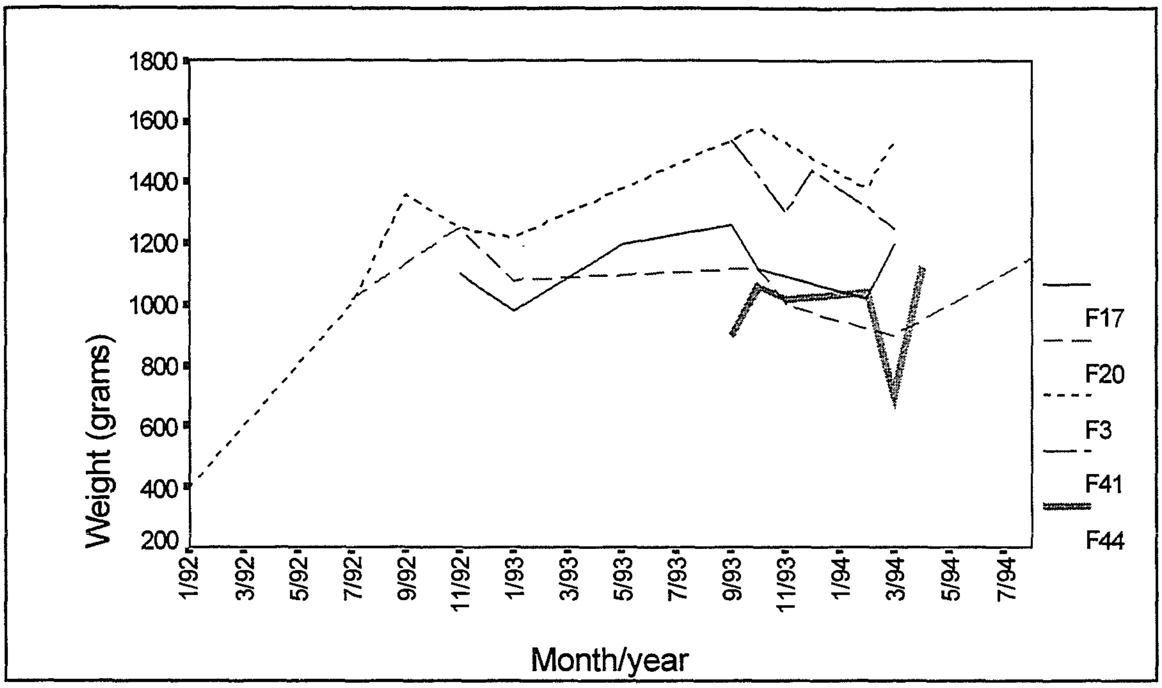


Fig. 5.5. Changes in body weight of five female *D. maculatus* which were recaptured over periods greater than 12 months, on the Mt Windsor Tableland, north Queensland.

5.3.4. Longevity

Based on minimum age at first capture, only one of the 50 individuals that I trapped between April 1992 and December 1994 was known to have been alive for the duration of the trapping study (36 months). Only seven of the 25 individuals that I trapped more than once were recaptured in successive years and only two of these individuals, both females, were captured in three successive years. Based on their minimum age when first captured, these two females were estimated to have been alive for 36 and 30 months respectively, when last captured, ten months and two trapping trips before trapping was discontinued.

5.3.5. Comparative life-history strategy

Comparative life-history data are presented in Appendix 5.3.

5.3.5.1. Longevity

All three polyprotodont marsupial families of comparable body-size and for which I was able to gather data (quolls, opossums and bandicoots), have significantly shorter mean lifespans in captivity than any of the 27 species belonging to five Eutherian carnivore families (Fig 5.6). Longevity of marsupial carnivores was also significantly lower than for eight comparatively sized species belonging to two families of Rodents and compared to 13 species in three Diprotodontid marsupial families (Fig 5.6). The only order of mammals in which similarly sized species have similarly short life-spans are the Insectivora, although the number of species which are of comparable size to *Dasyurus* and for which data are available is very small (Fig 5.6). The mean longevity in captivity for each of the groups Polyprotodonta, Diprotodonta, and Carnivora are;

Polyprotodonta	4.5y (range 3-6y),
Diprotodonta	11.5y (range 5-18y), and,
Carnivora	12.5y (range 8-17y).

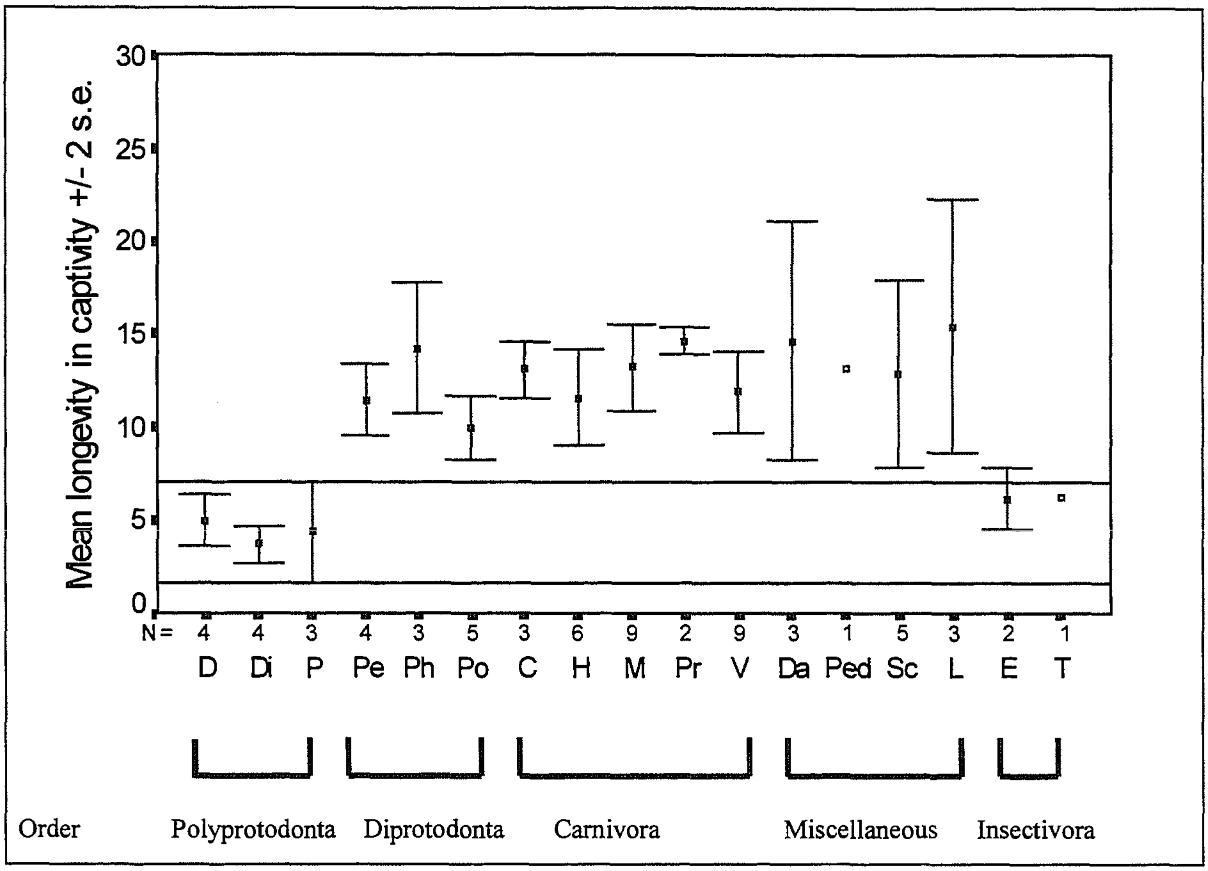


Fig. 5.6. Mean longevity +/- 2 s.e. in captivity of 67 species belonging to 18 families of metatherian and eutherian mammals of equivalent or lower body mass than female *D. maculatus*.

Family codes are: D, Dasyuridae, (marsupial 'mice' & 'cats'); Di, Didelphidae, (Opossums); P, Peramelidae, (marsupial Bandicoots); Pe, Petauridae, (gliding possums); Ph, Phalangeridae, (Brushtail possums, Cuscus); P, Potoroidae, (Potoroos); C, Canidae, (Dogs and foxes); H, Herpestidae, (Mongoose); M, Mustelidae, (Martens, stoats, weasels); Pr, Procyonidae, (Linsangs); Viverridae, (Civets); Da, Dasypodidae (Ant-eaters); Ped, Pedarthuridae (Aardvark); Sc, Sciuridae, (Squirrels); L, Lemuridae, (Lemurs); E, Erinacae, (Hedgehogs); T, Tenrecidae, (Tenrecs); V,). N refers to the number of species within each family. Horizontal reference lines delimit the upper and lower 95% confidence limits for polyprotodont marsupial values.

Note: N refers to the number of species within each family used in this analysis.

5.3.5.2. Fecundity

The mean potential annual fecundity (MPAF), (i.e. maximum litter size recorded/ number of litters per year) of the large predatory Dasyuridae (*Dasyurus* species) is not significantly different from that of their Eutherian carnivore counterparts including members of the families Mustelidae, Herpestidae, Viverridae, Canidae and Procyonidae, nor from that of the polyprotodont marsupial family Didelphidae (Fig. 5.7). The MPAF of the third family of polyprotodont marsupials, the Peramelidae, is significantly greater than that of all others. The Bandicoots have long been recognised as being among the most fecund of the medium-sized mammals (for example, Gordon and Hulbert 1989).

The mean potential annual fecundity of Dasyurids is not significantly different from that of the Eutherian carnivores (Fig. 5.7). The median age at first reproduction is not significantly different between the Dasyuridae and their Eutherian counterparts, the Canidae, Mustelidae, Herpestidae, Viverridae and Procyonidae (Non-parametric ANOVA, χ^2=5.0512,df=5, p=0.4097).

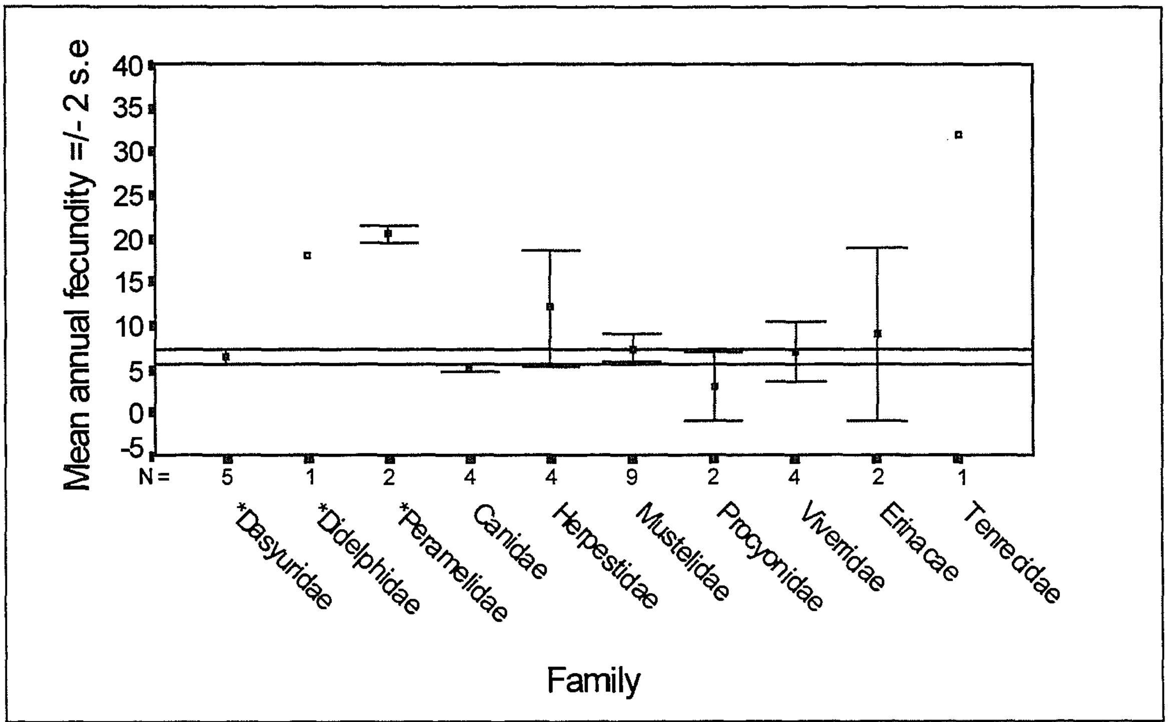


Fig. 5.7. Mean annual fecundity +/- 2 s.e. of the Dasyuridae, two other families of Polyprotodonta , five families of Carnivora and two families of Insectivora.

Note: N refers to the number of species within each family used in this analysis.

Fig 5.8, illustrates the role of longevity on population persistence, species with shorter maximum longevity's show a lower population persistence than species with greater longevity's.

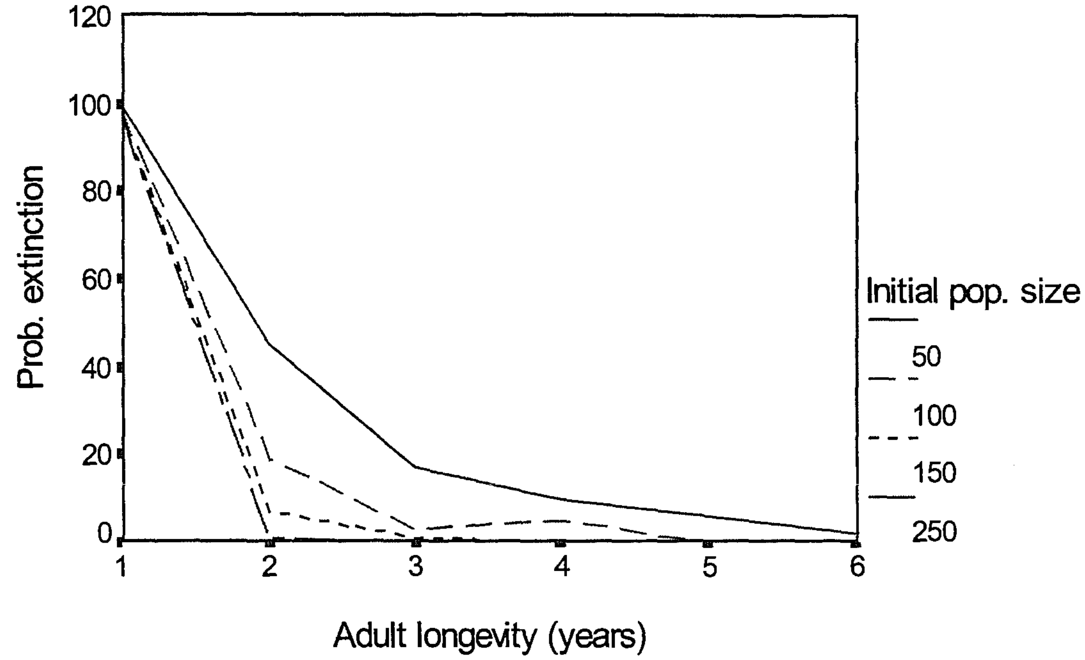


Fig. 5.8. Effects of maximum adult longevity on extinction probabilities of four theoretical populations of *Dasyurus maculatus* of different initial numerical sizes, as modelled by VORTEX.

VORTEX parameters based on the findings of this study and summarised in Appendix 5.2.

5.4. Discussion

5.4.1. Trap statistics and population demography

My trapping data suggest that *D. maculatus* occurs in higher densities on the Mt Windsor Tableland than in any other sites for which information is available. South-east Queensland: (Watt 1993); Cradle Mt/Lake St Clair, Tasmania: (Jones 1995a); Barrington Tops, N.S.W: (Firestone 1995 pers. comm); other sites in N. E. Queensland: this study Chapter 8). The high density of quolls on the Mt Windsor Tableland compared to other sites in southern Australia can at least partially be explained by the smaller size and hence smaller home range requirements of *D. maculatus* from the wet tropical rainforests of north Queensland compared with *D. maculatus* from southern mainland Australia and Tasmania. The dimensional complexity of tropical rainforest, the relatively low climatic seasonality (Nix and Switzer 1991), and high productivity of this habitat, and presumed higher prey-base density may also account for the relative high population density of *D. maculatus* at the Mt Windsor Tableland. Differences in densities of *D. maculatus* between populations within north Queensland are discussed in Chapter 8. Despite their relatively higher abundance at my study site than elsewhere within the Wet Tropics (Chapter 8), Spot-tailed quolls are, none-the-less, much less abundant than other medium-sized mammals of different trophic roles at the study site, for example ring-tailed possums (Family Pseudochieridae), pademelons (F. Macropodidae), and *Uromys*, (F. Muridae) (Chapter 6). The sparsity of quolls in comparison to other medium-sized mammals at the site is in keeping with trends described for the various eutherian trophic groups in which increasing carnivory is correlated with increasing home range size and decreasing density (Mace and Harvey 1983).

Monthly variation in the number of quolls ktba can be attributed to changes in behaviour associated with the annual breeding season. Females become more trappable during months when they are bearing pouch young and are lactating. Presumably this occurs as a result of their greater energetic requirements at this time (see Green and Eberhard 1983 for comparative data for *D. viverrinus*), and their accordingly greater need for food. The number of males ktba, which peaks at the beginning of the breeding season, probably increases as a result of the postulated greater tendency of males to roam in search of mates at this time. Similar behaviour has been observed in males of the Northern quoll, *D. hallucatus,* (Begg 1981) and the Western quoll, *D. geoffroii,* (Serena and Soderquist 1989). Mansergh (1983) also noted that the number of male Spot-tailed quolls collected from a variety of sources in Victoria, peaked during the breeding season. Numbers of females ktba remained high between breeding seasons because of the replacement of females by new females from February onwards.

The density of quolls on the Mt Windsor Tableland was extrapolated from the density of quolls per kilometre of transect and based on radio-tracking observations which suggested that the transect collected animals from within one kilometre on either side (see Chapter 7). This figure provides a rough guide only, as some individuals probably were not trapped and because all potential habitat is possibly not occupied. The greater number of individuals ktba in 1993 and 1994 can be attributed to greater trap coverage during these years (Table 5.1), rather than to any increase in quoll numbers *per se,* as the value for densities of males and females per kilometre of transect does not differ significantly between years.

Annual adult mortality was higher for males than for females. This trend was also noted in populations of *D. hallucatus* and *D. viverrinus* (Begg 1981, Godsell 1982). While this may be attributable to greater physiological stress placed upon males of these polygamous species during the breeding season, the possibility that males exhibit less attachment to a particular home range or are otherwise less retrappable than females, can not be definitively precluded from either of the above studies or from this one.

The sex ratio of total captures and of individuals in this study were not significantly different from 1:1. This is in contrast to Mansergh (1983) who, on summarising all available records of the species in Victoria noted a sex ratio of 1 female to 11 males, while Green and Scarborough (1990) calculated a sex ratio of 1 female:3.5 males from a variety of sources in Tasmania. Similarly, Fleay (1940) bemoaned the difficulties he had in capturing females. None-the-less, Settle (1978), Fleay (1940) and Green and Scarborough (1990) found that pouch young sex ratios were close to 1:1, leading Mansergh (1983) to conclude that the extremely skewed sex ratio of Museum and other collections was the result of the greater trappability of males compared to females. In the population under study on the Mt Windsor Tableland, the numbers of males and females trapped is similar. As such, I suggest that the high proportions of males to females in these prior studies may reflect real population structure, and provide an indication of the interaction between landscape use and demography in these areas as follows.

Within any population of Spot-tailed quolls, I would expect that the distribution of individual females is more restricted than that of males. Females are restricted to optimum habitat because of denning and nutritional requirements associated with litter rearing. Males, with their greater size and their correspondingly greater ranging and fasting abilities (Lindstedt and Boyce 1985), and apparent lack of responsibility for litter rearing, occupy a greater range of environments and are more likely to be detected in habitats which cannot support permanent breeding populations of the species. Such habitats include agricultural and artificial forest mosaic habitats. As these are habitats most frequently traversed by humans and contain the highest human densities in rural areas, it would be expected that most museum records are from these areas and so the preponderance of males in collections may reflect the actual demography of quoll populations in those landscapes, rather than a behavioural tendency towards greater trappability of males. This contention is further supported by my observations that for half of the year, females are actually more trappable than males on the Mt Windsor Tableland.

5.4.2. External morphology

The sexual size dimorphism (SSD) ratio for body weight is 1.38 for *D. maculatus* from the Windsor Tableland, and is comparable to that of their Barrington Tops (New South Wales) congeners which is 1.51 (Karen Firestone pers. comm. 1995). The SSD for body weight from a population in the Cradle Mountain area of Tasmania is much higher at 1.93 (Jones 1995a). The Tasmanian figure is well above Ralls' (1977) definition of extreme dimorphism at a ratio of 1.6. Interestingly, body weight data provided by Green and Scarborough (1990) for *D. maculatus* from throughout Tasmania give a body weight ratio of only 1.31, which is very close to that observed during this study. I suggest that the smaller body-size of females results from the shorter growth season available to them each year. One hundred and thirty days of the female year are committed to rearing young. During this time and particularly during late lactation, energy which might otherwise be put into self growth is diverted into their offspring. In effect then, the growth season for females is the period from about January to June whereas that of males is year round.

Secondary selection may also operate towards smaller females and larger males due to the different roles which each sex plays in reproduction. Erlinge (1979) demonstrated that in weasels, the energetic costs associated with litter rearing result in a smaller optimum body-size for females than for males. In addition, the larger optimum body-size of males also confers sexual advantages to that sex in a polygynous mating system, including greater ranging potential and greater competitive advantage in male/male conflicts (Erlinge 1979).

Sexual-size dimorphism may also be secondarily driven by selection towards minimisation of intersexual competition as has been suggested in the case of mustelids (Brown and Lasiewski 1972, Moors 1980). In the case of quolls, small adult female body size may allow access to smaller prey refuge areas including tree hollows and hollow logs, than in the case of the larger males which in turn are able to subdue larger prey.

5.4.3. Reproduction

In north Queensland, *D. maculatus* has a well defined annual breeding season from June to August. Fleay (1940) noted that in Victoria, the species has a well defined breeding season during June and July while Le Souef and Burrell (1926) state that young are born in May in southern Australia. No births have been recorded in August in southern Australia which could reflect the opportunistic, and hence presumably incomplete nature of records from that region or a real difference in breeding season between the two subspecies. Watt (1991) for example, found that *Antechinus* subspecies from the tropics had longer breeding seasons than their conspecifics in temperate climes. Latitudinal differences in timing of annual breeding season are also known to occur in *Antechinus* species, for example *Antechinus flavipes* and *A. stuartii* (Van Dyck 1982). The mating season of *D. maculatus* held in captivity under natural photoperiod in north America, coincided with the Northern Hemisphere winter with births recorded between December and March (Conway 1988). It is clear then that despite discrepancies of a month or so between northern and southern populations, *D. maculatus* is a winter breeder. The significance of winter breeding is that young become independent in late Spring/early Summer which is a time of high food availability, resulting from the increased activity by invertebrates (Frith and Frith 1985, Watt 1991, Jansen 1993), and reptiles and peaks in juvenile dispersal of rodents and possums (Chapter 6). This timing confers advantages onto the newly independent young which no doubt benefit from the abundance of easily subdued prey. Similarly, this is also the best time of the year for females to recoup the body weight which they have lost during the course of rearing their offspring.

As suggested by Settle (1978) and by my observations, *D. maculatus* is polyoestrus although functionally monoestrus. Juvenile independence is inferred to occur from October to December based on the distribution of the capture of juveniles in this study and ages at independence identified by previous authors (Settle 1978, Green and Scarborough 1990).

Data on weight changes in three adult females show that their body weight declines from the commencement of the breeding season and reaches a low at about the time of juvenile dispersal at the end of the calender year (Fig. 5.5). Two individuals which did not breed showed a concomitant loss of weight of the same magnitude as that shown by females with litters. Although female weight changes may reflect hormonal changes and the stresses associated with litter rearing, a decline in prey availability in the late dry season may be the underlying cause of this weight change. Males were recaptured too infrequently to provide comparative data.

Data on longevity (see below) suggest that failure to breed in a single season may represent a loss of 33- 50% of an individual's life-time reproductive potential and thus, as expected, failure to breed was rarely encountered during this study. I observed only four cases out of 36 in which a female failed to breed in a single season. Three of these cases represented what would have been the first, second and third breeding seasons for three individuals respectively. The age and reproductive history of the fourth individual is unknown. The causes of failed breeding are unknown although one animal which was in her third potential breeding season was suffering from mange, from which she subsequently recovered. Another had a below average body weight for females at that time of the year.

My findings that only two animals were recaptured over periods greater than 2.5 years are probably confounded by poor recapture rates. None-the-less, the fact that only 20% of animals which have been recaptured more than once have been captured in successive years, suggests that either animals live for only one or two breeding seasons, or that their home ranges shift between years. Population turnover data (Table 5.2.) further illustrate the low survivorship (be that because of mortality or immigration) of quolls from year to year on the transect.

Support for the case of a life-span as short as that observed from the trapping data, comes from captivity data. Captive animals would be expected to have greater lifespans than wild animals, yet quolls lived for only four years in the National Zoological Park in Virginia, U.S.A (Conway 1988), and for this length of time or less in other non-Australian parks (Collins 1973). Featherdale Wildlife Park in New South Wales, Australia, has bred and raised dozens of litters over more than 20 years. Very few of these animals live for more than five years and very rarely do females breed beyond their third year (Brad Walker, pers. comm 31/5/94). Similarly, female Spot-tailed quolls held in captivity in the United States never bred beyond their third year, although males bred at up to five years of age (Collins *et al.* 1993). The single female which I knew to be in her third breeding season at the Windsor Tableland failed to give birth and appears to have died during the next Summer.

5.4.4. Comparative life-history

Comparatively speaking, the life-history strategy of *D. maculatus* and indeed all comparably sized polyprotodontine marsupials, can be summarised as lying more towards the *r* end of the *r-K* life history spectrum than that of their Eutherian counterparts amongst the Order Carnivora, and compared to members of other Eutherian and Marsupial Orders including the Rodentia and Diprotodonta respectively.

Compared to their Eutherian counterparts and similarly sized members of other mammalian orders (including Metatheria), *D. maculatus* and other members of the polyprotodontid group on average

- are significantly shorter lived in captivity and presumably in the wild (Fig 5.6),
- breed at a lower median age, and,

On the other hand, maximum potential litter size and number of litters per year are not significantly different between quolls and similarly-sized Eutherian carnivores and probably represent limits imposed by body-size and nutritional ecology.

Lindstedt and Calder (1981) suggest a negative relationship between longevity and metabolic rate including heart rate. The fact that the metabolic rate and heart rate of marsupials are generally lower than those of eutherians (Kinnear and Brown 1967, Hume 1982) suggests that this trend does not apply to comparisons between polyprotodont marsupials and their Eutherian counterparts and that some other, possibly phylogenetic or ecological factor causes early biosenescence in these species.

I speculate that short-life span, which is apparently a legacy of a polyprotodont heritage, is the driving factor in the evolution of these other life-history traits which result in maximisation of reproductive output during the very short lifespan of these Polyprotodont species. Indeed, work by Promislow and Harvey (1990) and Gittleman (1993) suggest that mortality schedules (which are in part a reflection of longevity) are key driving forces in the evolution of mammalian life histories.

5.4.5. Life history strategy: ecological and evolutionary implications

The life-history strategy of the Spot-tailed quoll is relatively inefficient for the species' ecology. Ecological forces, in particular energetic constraints imposed by the relatively large adult female body-size and by the high order trophic niche of the species (Chapter 6), limit the annual fecundity of the species in terms of both the number of litters able to be reared in a year, and the size of those litters. Phylogenetic constraints which are imposed primarily at the Order level, impose a low maximum attainable longevity. For what-ever reason, be it phylogenetic or ecological, the longevity of the polyprotodontid marsupials is shorter than that found in similarly sized mammals in all terrestrial, quadrupedal orders of equivalent size for which data are available, including other marsupial orders as discussed above (Fig. 5.6). Concomitant with this short longevity is the imperative to produce close to the optimum number of young at each birth and to breed in every season starting with that following the season of birth.

Interestingly, the only Eutherian order in which similarly sized animals have a comparably short life-span are members of the Order Insectivora (Fig. 5.6). As Eisenberg (1981) demonstrated, insectivory/carnivory somehow selects for short-lived species, either directly or indirectly. The highly seasonal nature of many invertebrate resources (Frith and Frith 1985, Jansen 1993, Dennis and Marsh 1997) may induce a reliance upon hormonally activated and intense breeding seasons, which in turn may result in either complete or partial post-mating mortality such as seen in its extreme form in species of *Antechinus* (see Dickman 1993 for a review of semelparity and sperm competition).

While all polyprotodont marsupials are short-lived by Eutherian standards, the ecological problems associated with short longevity are circumvented in most species by their: (1) being very small, (2) being opportunistically insectivorous and omnivorous, and (3) producing relatively large litters and/or several litters per year. *Dasyurus maculatus* flaunts all of these circumventions. It is by Australian carnivore standards, a relatively large (greater than 1000g), strictly carnivorous and solitary marsupial, which because of its ecology, has a limited annual reproductive potential. In this context, its very short reproductive life span is hard to explain, however the answer may lie in its subfamilial phylogeny. Character-state and electrophoretic studies of dasyurid phylogeny (Baverstock and Archer 1982, Kirsch *et al.* 1990) invariably place *D. maculatus* (and other *Dasyurus*) in a group which includes *Dasycercus*, *Dasyuroides*, *Dasykaluta*, and *Pseudantechinus*, most of which exhibit a similar life-history strategy to that elucidated for *D. maculatus* (Lee *et al.* 1982). This broad group is in turn most closely related to the semelparous genera, *Antechinus* and *Phascogale*. Perhaps then, the high plasma corticosteroid levels associated with intense mating behaviour, and post-mating male mortality in the latter two genera is an ancestral condition in *D. maculatus*. In support of this contention is Bradley's (1982) findings that male *D. maculatus* have higher plasma corticosteroid levels than any other of the 16 dasyurids which he tested.

Further pressure against *D. maculatus* escaping from the hypothetical, high steroid concentration, short life-span scenario, may lie in the role of sperm competition in the breeding system of the species, as in *Antechinus*. Mating in quolls is a protracted affair, with pairs remaining mounted for 12 hours or more (Settle 1978, Collins *et al.* 1993) and if given the opportunity, females mate with several males during their short oestrus period each year (Collins *et al.* 1993). Both of these features are indicative of sperm competition and, as Dickman (1993) propounds, may lead to the evolution of steroid induced, extremely intense mating behaviour. Thus, the disadvantages of a biochemically induced short-life span in *D. maculatus* may be offset by the advantages of heightened male mate searching activity which ensures that all, or most females within the small and sparse populations in which this species occurs (Chapter 8), are mated and preferably by more than one male thus ensuring genetic heterogeneity within litters.

The life-history strategy which I have described here for the Spot-tailed Quoll offers insights into the evolutionary history of the species in particular its relationships with the Devil, *Sarcophilus*. The dentition of *D. maculatus* is near the more specialised end of a clade leading from the other species of *Dasyurus* and culminating in *Sarcophilus*. So too are its life-history parameters. In body size and longevity, *D. maculatus* is intermediate between the other *Dasyurus* and *Sarcophilus*, while in litter size and age at maturity, it has the same values as the other *Dasyurus* (except the most primitive species *D. hallucatus* which has a larger litter size). These comparative life-history data add to the body of evidence which suggests that *D. maculatus* is indeed ancestral to *Sarcophilus*, placing its age of origin as much older than the 35 000 ybp, which is the age of its oldest known fossil. If this is so, this raises the compelling question of where was the species hiding all of this time? This question has yet to be answered with information from the fossil record.

Irrespective of the precise geographical region where *D. maculatus* evolved, its life-history strategy dictates that all else being equal, *D. maculatus* exists closer to a hypothetical viability/extinction threshold than any other of the extant polyprotodont marsupials. Also, Fig. 5.8 demonstrates that all else being equal, a difference of one or two years can make an enormous difference to the survival of quoll populations, and by inference must render the species relatively more prone to extinction than the longer-lived, and equally fecund members of the Order Carnivora. Generally speaking, *D. maculatus'* short life-span and limited breeding potential forces upon it a requirement for a relatively more stable, predictable and productive environment than is required by its Eutherian counterparts and Diprotodontid marsupial cousins. In effect, it is limited to environments in which a high recruitment rate is assured each year. The present distribution of the species within relatively undisturbed, highly productive and predictable environments in Australia (Mansergh 1984, Jones and Rose 1996, Chapter

8) reflects this requirement. The relatively rapid disappearance of the species from areas perturbed by human activities which impinge on these habitat requirements (Lunney and Leary 1988, Bennett 1990) also support my theory that the life history strategy of *D. maculatus* renders the species vulnerable to population extinction from relatively minor increases in extrinsic mortality. Population viability analyses conducted here (Fig. 5.8) also support this view and even though the results are not absolute, the effect of relative changes to the longevity which I modelled, demonstrate a threshold above which the probability of extinction declines dramatically. I contend that the short life span of *D. maculatus* places the species on or very near to that threshold.

The ecological niche occupied by quoll populations is further narrowed, relative to most other marsupials in Eastern Australia, by the naturally low density of the species due to its large size and the relictual nature of its habitat within Australia. The habitat of *D. maculatus* is threatened by a trend towards greater aridity and seasonality in Australia's climate, and further forest fragmentation caused by humans.

5.5. Summary

- Spot-tailed Quolls occur at a very low abundance on the Windsor Tableland, of about one individual of each sex per $3km^2$.

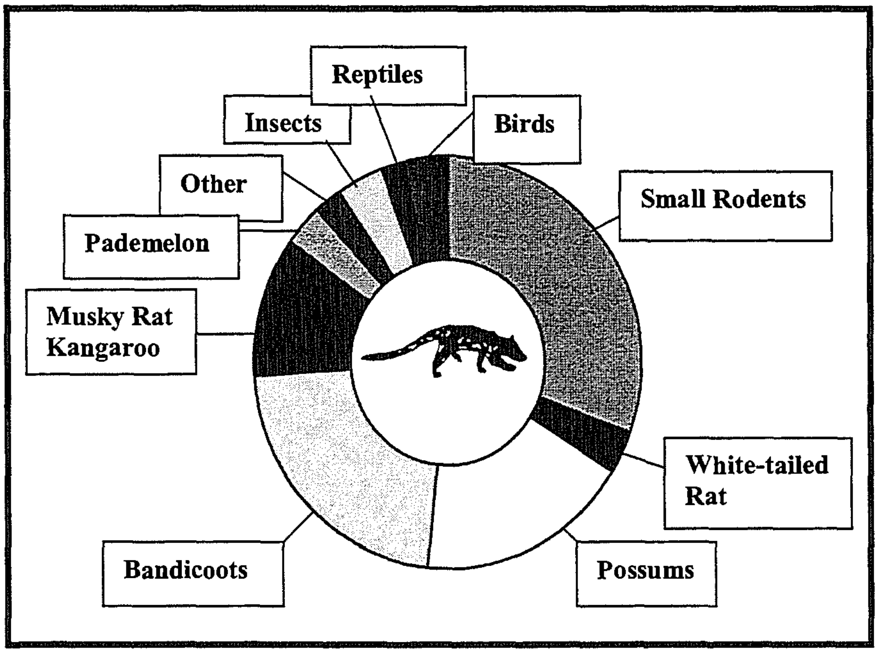
- The life-history strategy of the Spot-tailed Quoll is characterised by its short breeding life-span (3yrs), by a single annual breeding season (June-September), a mean litter size close to the maximum of 6, and by only one litter per year.

- The low abundance at which Spot-tailed Quoll populations occur translates to a numerically low population within the spatially restricted habitat that they occupy in north Queensland.. The small population paradigm suggests that this renders populations susceptible to extinction from demographic and environmental stochastic events.

- The life-history strategy of the species, especially its short life-span and its restricted breeding opportunities, renders populations of the species relatively more susceptible to extinction through relatively minor increases in mortality, especially compared to equivalent-sized Eutherian carnivores. This places a requirement on the species for productive and predictable environments in which mortality is low and recruitment high in each and every year. This explains the species distribution patterns (see Chapter 8).

Chapter 6.

The Diet of the Spot-tailed Quoll in north Queensland's Wet Tropics Area



In this chapter, I present the results of scat analyses including comparisons of quoll diets between north Queensland and Victoria, between different seasons on the Mt Windsor Tableland, and between different biogeographic units within the Wet Tropics Area. I also examine quoll diet with respect to prey preferences and variation in other dietary measures between these sampling units. I conclude that the Spot-tailed quoll is a mammal specialist, which prefers medium-sized prey over small or large prey. Although specialising in mammals, quolls are also opportunistic predators upon carrion, birds, reptiles and invertebrates, behaviour which brings them into conflict with humans.

Chapter 6. The Diet of the Spot-tailed Quoll in north Queensland's Wet Tropics Area.

6.1 Introduction

Most studies of the diet of the Spot-tailed quoll have been limited to passing references to its predilection for raiding the contents of hen houses and unqualified reports of its food preferences which include: insects, birds, bandicoots, small tetrapods, cockroaches, rabbits and rats (for example: Le Souef & Burrell 1926, Troughton 1941, 1954b, Gould 1974, Settle 1978, Mansergh 1984). Green and Scarborough (1990) published the first quantitative description of quoll diet and the only study based on gut content analysis. This list which was based on 33 individual prey records from the stomachs of an undisclosed number of Tasmanian quolls included a wide range of large, medium and small mammal species, birds, reptiles and frogs. In 1995, Belcher published the results of a study of the diet of the species in Victoria. His study was based on the analysis of 319 scats which were collected from two latrine sites in Gippsland. He found that, *D. maculatus* was primarily a vertebrate-eater. A wide range of mammals contributed to the bulk of its diet although invertebrates, reptiles and birds also occurred as minor dietary items (Belcher 1995). In contrast to the small number of studies of quoll diet, the diets of Australia's three species of Eutherian carnivores, the Dingo (*Canis lupus dingo*), the Red Fox (*Vulpes vulpes*), and the Feral Cat (*Felis catus*), have been the subject of several quantified studies each including thousands of prey records (for example, Brunner *et al.* 1975, Jones and Coman 1981, Triggs *et al.* 1984, Robertshaw and Harden 1985, Brown and Triggs 1990, and Lunney *et al.* 1990 to name a few).

Because of the relatively high density of *D. maculatus* in some areas of north Queensland, and because of its habit of depositing scats in latrines on roads (Chapter 7), it has been possible to collect large series of scats in seven of the upland biogeographic regions of the Wet Tropics Area. The Endangered status ascribed to northern populations of *D. maculatus* (considered an endemic subspecies *D. m. gracilis* at the time of legislative listing), under Queensland's *Nature Conservation (Wildlife) Regulation (1994)* and the Commonwealth's, *Environment Protection and Biodiversity*

Conservation Act (1999), places greater requirements upon an understanding of the ecological requirements of the species and this dietary study serves to describe the diet and prey selection of the subspecies.

In this chapter, I present the results of scat analyses including comparisons of quoll diets between north Queensland and Victoria, between different seasons on the Mt Windsor Tableland, and between different biogeographic units within the Wet Tropics Area. I also examine quoll diet with respect to prey selection and variation in other dietary measures between these sampling units. I conclude that the Spot-tailed quoll is a mammal specialist, which prefers medium-sized prey over small or large prey. Although specialising in mammals, quolls are also opportunistic predators upon carrion, birds, reptiles and invertebrates, behaviour which brings them into conflict with humans.

6.2 Methods

6.2.1. Scat collection and analysis

I collected Quoll scats from roads, walking tracks and around human infrastructure within seven of the upland biogeographic units of the Wet Tropics Area (described in Chapter 4). All scat collections were made between 1992 and 1994 inclusive. The mammalian contents of scats were identified by prey hair and skeletal analyses using the method described by Brunner and Coman (1974). Non-mammalian material was not identified beyond class level.

6.2.2. Prey species census

I conducted censuses of prey species in order to obtain information on the relative abundance of mammalian prey for comparison with their abundance in the diet of *D. maculatus.* I used capture-mark-recapture and spotlighting surveys to census the fauna of the study site. These surveys were executed on the Mt Windsor Tableland (see Chapter 4). The spotlighting surveys were carried out, along a 4km length of road, which was also surveyed for scats which provided information on the relative abundance of mammal species in the diet of *D. maculatus*. I recorded the following eight of the 29 mammal species known from the Windsor Tableland, frequently enough for estimates of their abundance to be calculated:

Bush/Cape York Rat	*Rattus* spp (*R. fuscipes* and *R. leucopus*)
Fawn-footed Melomys	*Melomys cervinipes*
Long-nosed Bandicoot	*Perameles nasuta*
Sugar Glider	*Petaurus breviceps*
Striped Possum	*Dactylopsila trivirgata*
Daintree River Ringtail	*Pseudochirulus cinereus*
Green Ringtail	*Pseudochirops archeri*
Red-legged Pademelon	*Thylogale stigmatica.*

Because of difficulties in distinguishing between the remains of the two *Rattus* sp. in quoll scats, these species have been combined for all analyses.

I utilised six live-trapping sites located at 800m intervals along the 4km spotlighting and scat collection transect to census small terrestrial and scansorial mammals. I ran each live-trapping site for three consecutive nights in each of the three seasons of the year in 1993 for a total of 1080 trap nights (see below for a definition of those seasons). Each of the six live-trapping sites consisted of 15 Elliott traps and 5 wire cage traps. Elliott traps were set in a 40 x 80 m grid with each trap placed 20-m-apart. Wire cage traps were regularly spaced on this grid.

I calculated the densities of prey species using the minimum number known to be alive (KTBA) method for each site. The KTBA value for each species was averaged over the six live-trapping sites for each season. The effective area covered by each grid, and thus the density of each prey species, differed depending upon its ranging behaviour as revealed by index line trapping. I established an index line for one night at each site, on the second night after live-trapping was finished there in each season. The index line consisted of a two hundred metre line transect of Elliot traps, spaced 10-m-apart, commencing at the centre of each trapping grid and radiating outwards. The incidence along the index line, of recaptures from the previous trapping session, gives an indication of the area from which each grid effectively collects each species.

I censused arboreal and other non-trappable mammals by spotlighting along the same 4-km-long transect along the Mt Windsor Road. I conducted spotlighting on 29 nights during 1993 for a total of 40 hours. Because of differences in behaviour and general detectability, the effective sampling width of the spotlighting transect was expected to be different for each species. I assessed this using the equation,

$$A_i = 2.(\text{mean}X_i).Y_i \qquad \text{equation1}$$

where A_i is the sampling area (hectares) of the transect for species i,
X_i is the perpendicular distance (m) of each sighting of species i, and,
Y is the length of transect searched (m).

The density of each of the above species was then calculated using;

$$D_i = N_i/A_i \qquad \text{equation 2}$$

where N_i is the number of sightings of species i, and, A_i is the effective transect width for each species i.

6.2.3. Data treatment

6.2.3.1. Quantification of diet

I analysed Quoll diets as contingency tables of the frequency of occurrence of each prey type for each time, place or sex. The classification of prey type varies depending on the temporal and spatial treatments being compared, and includes analyses based at the prey species, prey-size and prey ecomorph levels.

All mammal remains in scats were identified to species. I made no attempt to identify bird, reptile or invertebrate species from Quoll scats. For comparisons of diet between areas within north Queensland, percent occurrence data for allopatric sister species are combined, i.e. Bennett's and Lumholtz' Tree Kangaroos, *Dendrolagus bennettianus* and *D. lumholtzii*, and Daintree and Herbert River Ringtails, *Pseudochirulus cinereus* and *P. herbertensis*. The hair of two sympatric sibling species, the Bush rat *Rattus fuscipes* and the Cape York rat *R. leucopus* could not be discriminated from scats and so these two species are included together as *Rattus* spp. in all analyses. The common and scientific names of mammals follow those used in Strahan (1995).

To facilitate comparisons of diets between areas with different prey communities I categorised mammalian prey into ecomorphic groups based on size and spatial niche. I created a scatter plot of the mean weights of all wet tropical mammal species (Fig. 6.1), and visually delineated small, medium and large species as follows;

- nineteen small species, ranging in size from 10g (Feather-tailed glider *Acrobates pygmaeus*) to 200g (Masked Uromys *Uromys hadrourus*),
- eighteen medium-sized species ranging in size from 425g (Striped Possum *Dactylopsila trivirgata*) to 2000g (Brushtail Possum *Trichosurus vulpecula*), and,
- seven large-sized mammals ranging from 4000g (Echidna *Tachyglossus aculeatus*) to over 50 000g (Feral pig *Sus scrofa*).

Dasyurus maculatus is among the largest of the medium-sized mammals.

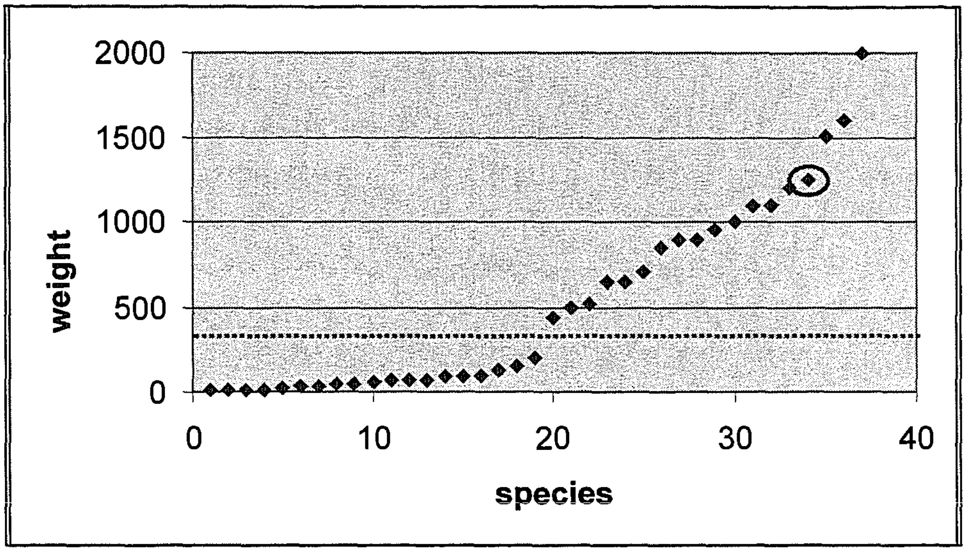


Fig. 6.1. The size distribution of the 37 species of small and medium-sized mammals in the Wet Tropics Area.

The point representing *D. maculatus* from the Mt Windsor Tableland is circled. The horizontal dashed line delineates small and medium-sized mammals. In order to facilitate high resolution of these data points, the nine species of large wet tropical mammals (i.e. >4kg) are not shown. Size data from Strahan (1995) and unpublished data.

I categorised mammalian spatial niches as terrestrial, scansorial and arboreal. This results in nine different ecomorphic categories; small terrestrial, small scansorial, small arboreal and so on for medium and large prey. No large arboreal species are found within the wet tropical study area, the Koala, *Phascolarctus cinereus* being the sole Australian mammal that fits this category. Spatial niche data were gathered from my own unpublished information and/or from that provided by Strahan (1995).

In order to assess the minimum number of scats required for a representative sample of quoll diet, I graphed the cumulative diversity H_k for k scats from the Windsor Tableland following the method of Hurtubia (1973) and where:

$H = \Sigma(p_i)(\log p_i)$ equation 3

where p_i is the proportion of prey in the ith class.

The resultant line graph (Fig. 6.2) plateaus at about 80-85 scats. Only scat collections from the Windsor, Carbine and Lamb units were therefore considered to provide representative information. Data from the four other biogeographic units were not used in the following comparative analyses.

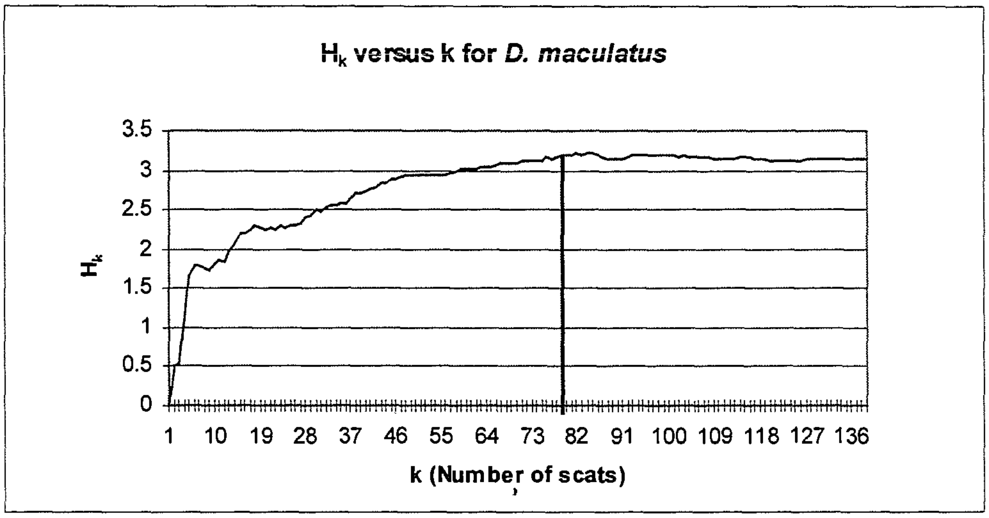


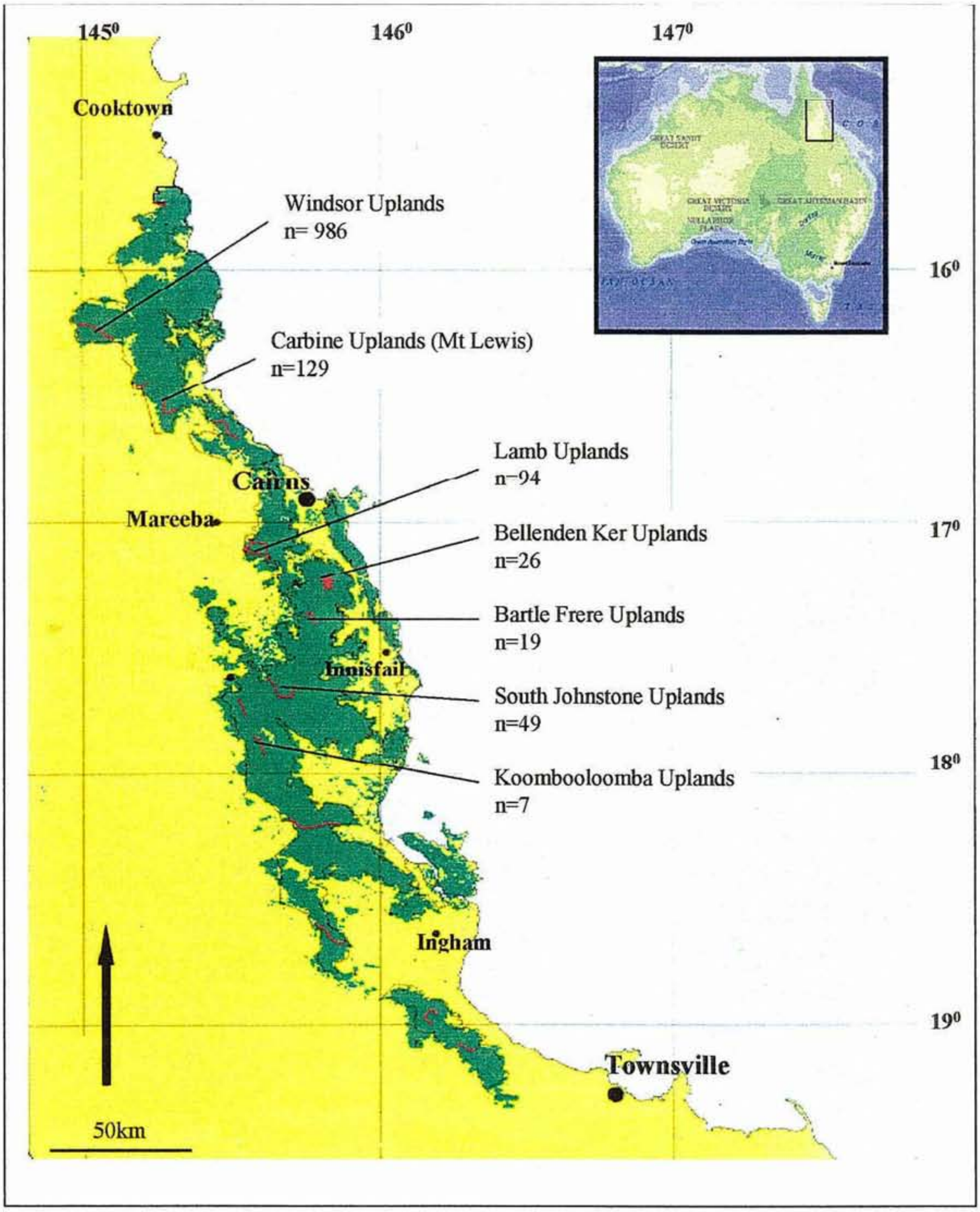
Fig. 6.2. Cumulative dietary diversity (H_k) vs number of scats analysed (k) from Spot-tailed quolls on the Mt Windsor Tableland, north Queensland.

The vertical red line marks the approximate point of the plateau in H_k

6.2.3.2. Geographical differences in diet

As explained above, although I collected Quoll scats from seven of the biogeographic units of the Wet Tropics Area, series large enough for reliable analyses (see Fig. 6.2) were collected from only three: the Windsor unit, the Carbine unit, and the Lamb unit (Map 6.1). I analysed these data by a χ2- homogeneity test using prey ecomorphic categories. Significant results were explored by reference to the residual values of each cell. Residual values of greater than 2 (or less than -2) indicate a significant departure from expected values for each cell (SPSS Base Manual).

One Victorian study of the diet of *D. maculatus* is available for comparative study (Belcher 1995). This comparison was facilitated using a Split-plot ANOVA (SPSS) and mammalian data classified according to size (see above). Analyses at the level of prey species were inappropriate given the different prey species assemblages in each area.



Map 6.1. The Wet Tropics Area showing scat survey transects (red lines) and the number of Spotted-tailed Quoll scats (n) analysed from each. Transects which are not labelled returned no Quoll scats.

See Map 4.1 for labelling of all bioregions.
Bellenden Ker search area was limited to the cleared summit area and is marked with a star.

6.2.3.3. Prey selectivity

I calculated prey selectivity for mammalian prey of *D. maculatus* on the Mt Windsor Tableland in 1993 only, as this was the only year in which prey abundances in the wild were assessed. Selectivity was calculated for each of the three annual seasons recognized in this study;

Wet season	January-April,
Dry season	May- August,
Storm season	September-December.

I calculated prey selectivity using Vanderploeg and Scavia's (1979a) electivity index (E*), which provides a rank order abundance rating for each prey species for which proportional abundance data are available in the field and in the diet. E* is calculated as

$$(W-1/n)/(W+1/n) \qquad \text{Equation 3}$$

where, n is the number of prey species available (i.e., 28 for the Windsor Tableland), and, W is Vanderploeg and Scavia's selectivity coefficient (Vanderploeg and Scavia 1979b), which is defined by;

$$(r_i/p_i)/\Sigma(r_i/p_i) \qquad \text{Equation 4}$$

where, r_i is the proportion of prey species i in the diet, and,
p_i is the proportion of that same prey species in the wild.

Prey selectivity indices range from zero to either 1 or –1. Negative values indicate that the prey item is avoided, and positive values indicate that the prey item is selected for.

6.2.3.4. Sexual differences in diet

I assessed sexual differences in diet from 17 male and 22 female scats. Scats of known origin were collected from the floors of cage traps in which quolls had been captured, on the Mt Windsor Tableland. Only a single scat, the first collected from each individual, was used in this analysis in order to avoid problems of repeated measures.

Because of the small sample size, I conducted comparative analyses at a coarse level of prey identification, namely small, medium and large mammal, and non-mammal prey, using a Chi-square homogeneity test. Values for medium and large mammals were combined due to low frequencies of the latter. Trends in the occurrence of particular species were examined graphically.

6.3. Results

A total of 1310 Spot-tailed quoll scats were collected and analysed, from which I tallied 1568 individual prey records. Including all phyla, 79% of scats contained one prey species, 18% contained two, 2.5% contained three and a single scat (0.1%) contained four species.

As in south-eastern Victoria (Belcher 1995), *D. maculatus* feeds primarily on mammals in the Wet Tropics Area (Fig 6.3). Ninety-eight percent of scats contained mammalian prey. In comparison only 4% of scats contained bird remains (1% consisted entirely of birds), 2.6% contained reptiles (0.5% contained only reptile), 5.4% contained invertebrates (0.3% contained only invertebrates). No plant material was detected.

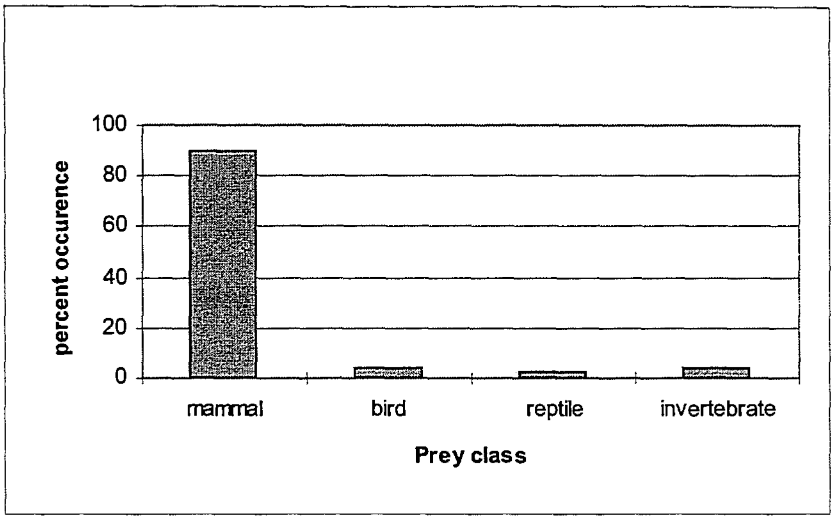


Fig 6.3. Frequency occurrence of mammal, bird, reptile and invertebrate remains from 1310 Spot-tailed Quoll scats collected from throughout the Wet Tropics Area.

Twenty-nine species of mammals were identified from the 1310 scats analysed (Appendix 6.1). Despite the fact that all quoll scats were collected within rainforest habitats, the 1568 records included seven records of three non-rainforest species (Northern Brown Bandicoot, *Isoodon macrourus*, Common Ringtail Possum, *Pseudocheirus peregrinus* and the Swamp Wallaby, *Wallabia bicolor*). In addition to mammalian prey, unidentified birds, reptiles (including unidentified skinks, snakes, and the Forest Dragon, *Hypsilurus boydii*), and invertebrates, primarily coleopterans and hemipterans were found in scats.

When results from scats are pooled across the Wet Tropics area, only three non-volant rainforest mammals are absent from the diet of *D. maculatus,* including the Atherton Antechinus, *Antechinus godmani*, the Rusty Antechinus, *Antechinus adustus*, and the White-footed Dunnart, *Sminthopsis leucopus*. Despite the broad representation of mammal species, only five species contributed more than 10% of total prey occurrences each (Fig 6.4). When data from each of the three individual geographic units with enough scats (i.e. >80), are examined, a subset of the same species always predominates (Table 6.1). Non-mammalian taxa (birds, reptiles, invertebrates) combined, also contribute greater than 10% occurrence in two of these sites, one each on Mt Lewis and the Lamb Range.

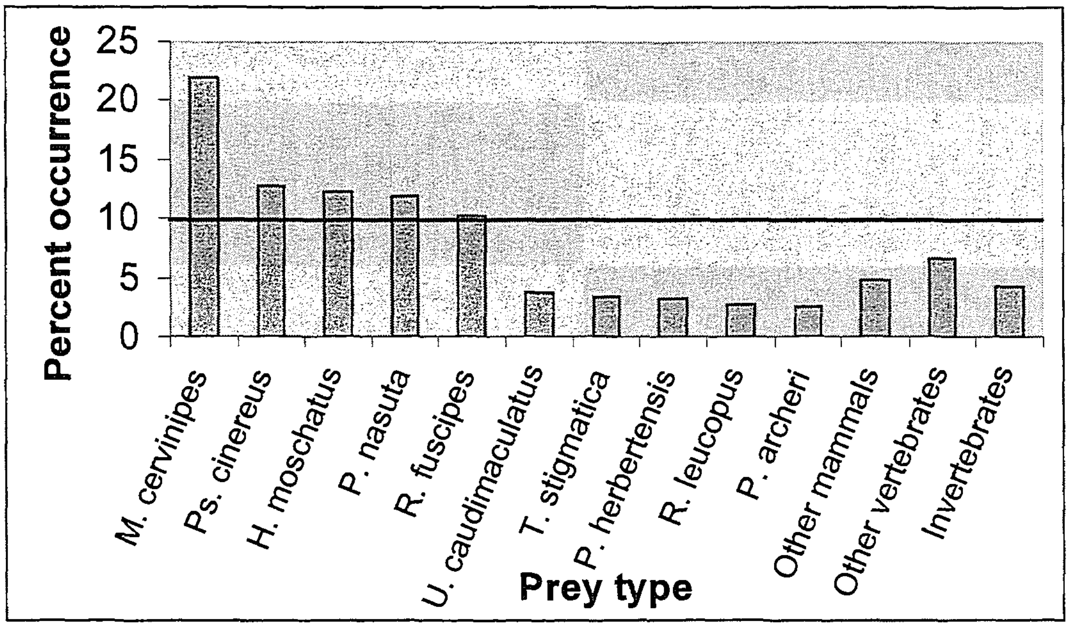


Fig 6.4. The percent occurrence of all prey species detected in 1310 scats from *D. maculatus* in the Wet Tropics Area.

Other mammals include; *O. anatinus, T. aculeatus, D. maculatus, A. flavipes, I. macrourus, C. caudatus, D. trivirgata, H. lemuroides, P. peregrinus, T. vulpecula, W. bicolor, D. bennettianus, D. lumholtzi, P. mollipilosus, U. hadrourus, H. chrysogaster, Pteropus sp, C. familiaris,* and *S. scrofa.* Other vertebrates include reptiles and birds only.

Table 6.1. Prey species1 occurring as greater than 10% of all prey records in the diet of D. maculatus in three biogeographic regions of the Wet Tropics area.

Windsor	**%^{2}**	**Lewis**	**%^{2}**	**Lamb**	**%^{2}**
M. cervinipes	25.3	*M. cervinipes*	20.4	*P. herbertensis*	32.7
P. cinereus	15.3	*P. cinereus*	16.9	*H. moschatus*	25.5
P. nasuta	11.4	*P. nasuta*	16.2	*M. cervinipes*	10.9
R. fuscipes	10.9	*P. archeri*	12.7		
H. moschatus	10.5	*H. moschatus*	10.6		
Total Prey Items	1104		142		110

Note.

1. Prey species are listed in descending order of abundance for each region.

2. % refers to the percent occurrence of each prey species. Total refers to the total number of prey items identified for each region.

Based upon the proportional occurrence data for all scats analysed, medium-sized mammals made the greatest contribution to the diet of *D. maculatus* (47.9%), followed by small mammals (37.6%), non-mammalian taxa combined (10.5%) and finally, large mammals (4.4%) (Fig 6.5).

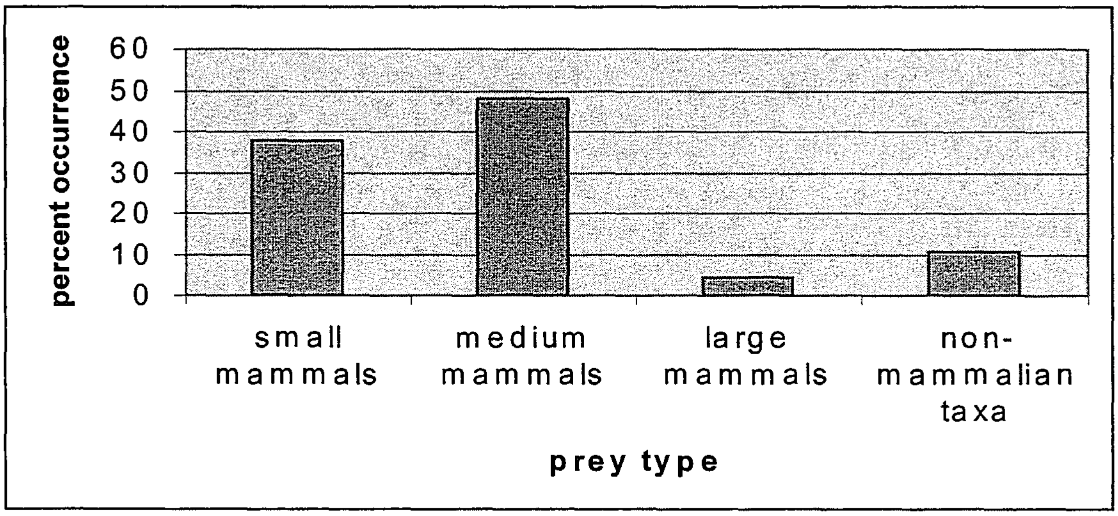


Fig. 6.5. The contribution of small (<200g), medium (400 – 2000g) and large (>4000g) mammals, and non-mammalian prey, to the diet of the Spot-tailed quoll in the wet tropics area.

Non-mammalian prey include birds, reptiles and invertebrates.

6.3.1. Geographic variation in diet

6.3.1.1. Wet Tropics populations

Based on frequency of occurrence, the composition of the diet of *D. maculatus* between the three Wet Tropical biogeographic regions from which adequate numbers of prey records were collected, varied significantly at the ecomorphic ($\chi 2=71.85$, d.f=10, $p=0.01^{-9}$), prey-size ($\chi 2=6.97$, d.f=2, p=0.03) and taxonomic ($\chi 2=55.47$, d.f=4,$p=0.03^{-9}$)

levels of prey classification. Residual values show that significant differences in diets at the prey ecomorphic level, are attributable to;

- more possums in the diet from the Lamb unit (residual value (r.v.) = 3.9),
- fewer *Rattus* spp. in the diet from the Carbine unit (r.v. = -3.1), and
- fewer *Rattus* spp. and *Melomys cervinipes* in the diet from the Lamb unit (r.v. = -2.9 each), than expected.

Differences in diets at the prey size level are attributable to;

- fewer small mammals in the diets from the Lamb and Carbine units (r.v. = -4.2 and -2.7),
- fewer medium mammals in diets from the Lamb and Carbine units (r.v. = -3.1 and -2.5), and,
- more small mammals in the diet from the Windsor unit (r.v. = 2.4).

Differences in the diets at the prey Class level were less significant than the other tests. The only statistically significant difference was that fewer than expected non-mammalian prey were included in the diet from the Carbine unit (r.v. = -2).

6.3.1.2. Regional Australian differences

There are no significant differences between the diets of quolls from north Queensland and Victoria, irrespective of whether comparisons are made using prey taxa categories based at the class level, prey-size categories based on the size of northern *D. maculatus*, or prey size categories based on the size of southern *D. maculatus* from Victoria (Tables 6.2-6.4). Dietary differences were greater between sites within regions than between the regions themselves (Tables 6.2-6.4).

Table 6.2. Results of a Split-Plot ANOVA testing for differences in Spot-tailed Quoll diet between regions (Nth Qld and Victoria), and sites within regions at the level of prey taxonomic class.

Note that site within region is treated as a random variable. All other variables are treated as fixed variables. The response variable is the proportional occurrence of each prey class in the diet of *D. maculatus.*

Variable	SS	DF	MS	F	P
Region	0.11	1	0.11^1	0.1	0.769
Site within Region	3.2	3	1.07^1	8.35	0.01
Class	7.63	3	2.54^2	19.94	0.001
Class*Region	0.23	3	0.08^1	0.59	0.638
ERROR	0.89	7	0.13		

Note:

1. **tested against ERROR**
2. **tested against Class*Region**

Table 6.3. Results of a Split-Plot ANOVA testing for differences in Spot-tailed Quoll diet between regions (Nth Qld and Victoria), and sites within regions at the level of mammal size class, unstandardised for weight differences between north Queensland and Victorian quolls.

Note that site within region is treated as a random variable. All other variables are treated as fixed variables. The response variable is the proportional occurrence of each prey size in the diet of *D. maculatus.*

Variable	SS	DF	MS	F	P
Region	0.42	1	0.42^1	0.53	0.518
Site within Region	2.37	3	0.79^1	24	0.001
Size	0.93	2	0.47^2	14.11	0.005
Size*Region	0.83	2	0.41^1	12.52	0.007
ERROR	0.2	6	0.03		

Note:

1. **tested against ERROR**
2. **tested against Size*Region**

Table 6.4. Results of a Split-Plot ANOVA testing for differences in Spot-tailed Quoll diet between regions (Nth Qld and Victoria), and sites within regions at the level of mammal size class, standardised for weight differences between north Queensland and Victorian quolls.

Note that site within region is treated as a random variable. All other variables are treated as fixed variables. The response variable is the proportional occurrence of each prey size in the diet of *D. maculatus*.

Variable	SS	DF	MS	F	P
Region	0.04	1	0.04[1]	0.05	0.833
Site within Region	2.49	3	0.83[1]	25.38	0.001
Size	1.77	2	0.88[2]	27.04	0.001
Size*Region	0.15	2	0.8[1]	2.32	0.179
ERROR	0.2	6	0.03		

Note:

1. **tested against ERROR**
2. **tested against Size*Region**

6.3.2. Prey selectivity

I made 77 individual mammal sightings and 419 mammal captures during 40 hours of spotlighting and 1080 trap nights respectively. The relative abundances of the seven prey species that I captured or detected in sufficient numbers for analysis, varied from between 0.04 and 6.4 individuals/ha (Table 6.5).

Table 6.5. Abundance estimates of eight mammal taxa from the Mt Windsor Tableland.

Prey Species[1]	Density (individuals/ ha)	Pi[2]	Ri[3]	No. of sightings/ captures	Method censused
M. cervinipes	6.4	0.53	0.33	170	Live-trapping
Rattus spp	2.9	0.24	0.29	220	Live-trapping
P. breviceps	0.15	0.01	0	2	Spotlighting
D. trivirgata	0.04	0.003	0.01	4	Spotlighting
P. nasuta	0.9	0.075	0.01	7	Spotlighting
Ps. cinereus	1.46	0.12	0.11	25	Spotlighting
P. archeri	0.15	0.003	0.01	3	Spotlighting
T. stigmatica	1.1	0.09	0.06	32	Spotlighting

Note.

1. *R. fuscipes* and *R. leucopus* are combined.
2. Pi refers to the proportional abundance in the wild at the Mt Windsor Tableland.
3. Ri refers to proportional abundance in the diet of *D. maculatus*.

On the Mt Windsor Tableland, *D. maculatus* showed little selectivity or avoidance for any of the eight mammal species which could be censused by me (Figs. 6.6-6.8) suggesting that the species is opportunistic in its dietary habits.

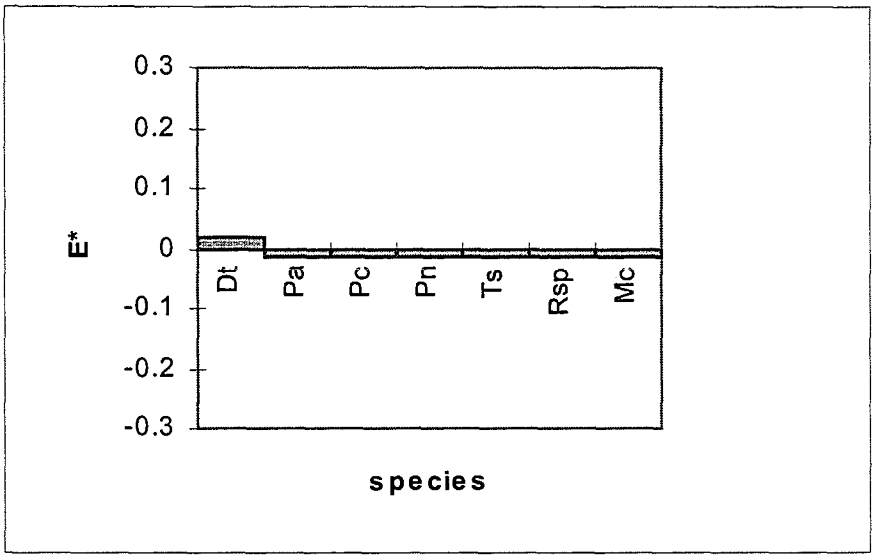


Fig. 6.6. Electivity indices (E*) for eight species of mammalian prey during the Wet season.

Species codes: Dt, *Dactylopsila trivirgata*, Striped Possum; Pa, *Pseudochirops archeri*, Green Ringtail; Pc, *Pseudochirulus cinereus*, Daintree River Ringtail; Pn, *Perameles nasuta*, Long-nosed Bandicoot; Ts, *Thylogale stigmatica*, Red-legged Pademelon; Rsp, *Rattus fuscipes/leucopus*, Bush/Cape York Rat; Mc, *Melomys cervinipes*, Fawn-footed Melomys.

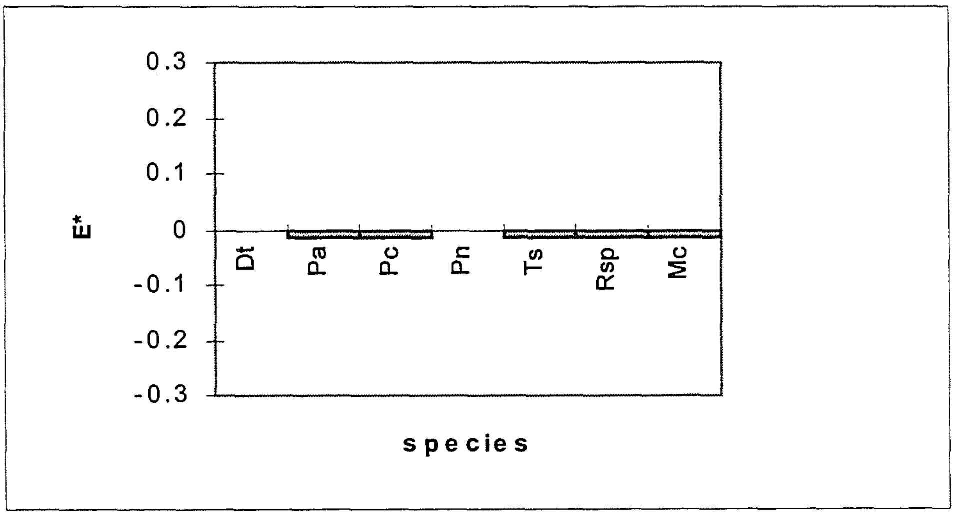


Fig. 6.7. Electivity indices (E*) for eight species of mammalian prey during the dry season.

Species codes: Dt, *Dactylopsila trivirgata*, Striped Possum; Pa, *Pseudochirops archeri*, Green Ringtail; Pc, *Pseudochirulus cinereus*, Daintree River Ringtail; Pn, *Perameles nasuta*, Long-nosed Bandicoot; Ts, *Thylogale stigmatica*, Red-legged Pademelon; Rsp, *Rattus fuscipes/leucopus*, Bush/Cape York Rat; Mc, *Melomys cervinipes*, Fawn-footed Melomys.

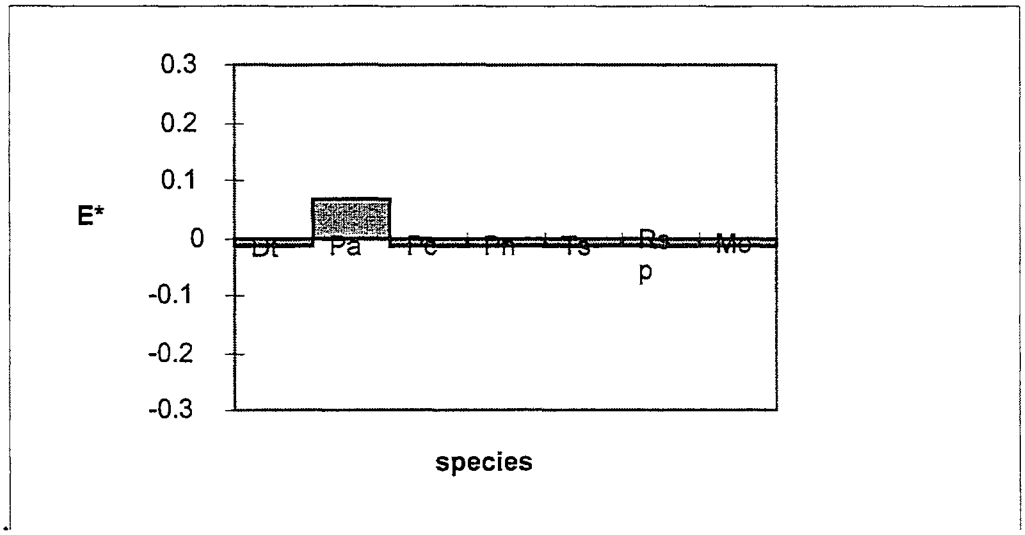


Fig. 6.8. Electivity indices (E*) for eight species of mammalian prey during the storm season.

Species codes: Dt, *Dactylopsila trivirgata*, Striped Possum; Pa, *Pseudochirops archeri*, Green Ringtail; Pc, *Pseudochirulus cinereus*, Daintree River Ringtail; Pn, *Perameles nasuta*, Long-nosed Bandicoot; Ts, *Thylogale stigmatica*, Red-legged Pademelon; Rsp, *Rattus fuscipes/leucopus*, Bush/Cape York Rat; Mc, *Melomys cervinipes*, Fawn-footed Melomys.

6.3.3. Sexual differences in diet

Male and female *D. maculatus* eat significantly different proportions of mammalian and non-mammalian prey ($\chi 2=4.15686$, d.f=1, p=0.041) (Fig 6.9). The major difference as revealed by standardised residual values is that females eat relatively greater proportions of non-mammalian prey, especially reptiles and invertebrates (r.v. 3.1). The differences in dietary habits of males and females are further borne out by the observations that only one of 17 male scats contained only non-mammalian prey (a bird), whilst seven of 22 female scats contained only non-mammalian prey (including birds, reptiles and invertebrates). The diets of male and female Spot-tailed Quolls also differ in the types of mammalian prey eaten. Of those mammalian species represented in the diet of one sex only, those species found only in male scats are large and/or pugnacious species (i.e. *Thylogale*, *Uromys* and *Dactylopsila*) and those species found only in female scats are small arboreal species (i.e. *Petaurus* and *Pogonomys*)(Appendix 6.2).

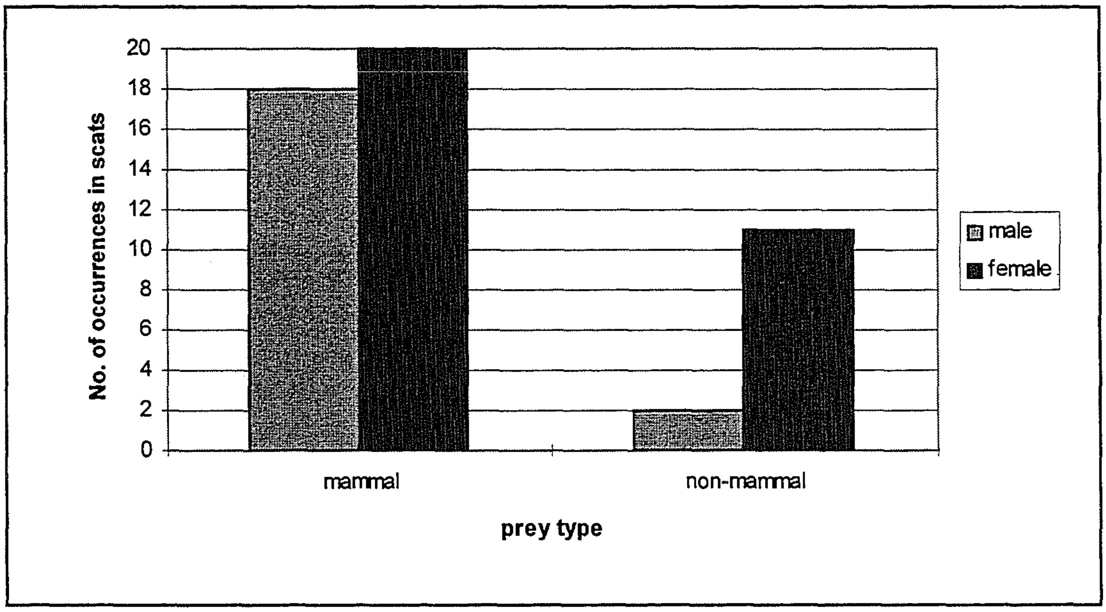


Fig. 6.9. Number of occurrences of mammalian and non-mammalian prey species in 17 scats from male and 18 scats from female, *D. maculatus* from the Mt Windsor Tableland.

6.4. Discussion

6.4.1. General

This study suggests that in the Wet Tropics Area, Spot-tailed quolls are generalist mammal-eaters which select for medium-sized arboreal mammals. Invertebrates, reptiles and birds also comprise a minor proportion of the diet. No plant material was found in the 1310 scats which were analysed, which confirms *D. maculatus* to be Australia's most carnivorous mammal, together with the Tasmanian Devil, *S. harrisii.*

This study agrees with Belcher's (1995) findings on several counts including;

- no evidence of deliberately ingested plant material in the diet of *D. maculatus*,
- importance of mammals, especially medium-sized species in the diet of *D. maculatus*,
- the wide variety of mammals consumed by *D. maculatus*, and,
- the minor occurrence of other vertebrate groups and invertebrates in the diet of *D. maculatus*.

The predominance of mammals in the diet of *D. maculatus* suggests that mammals are especially vulnerable to quoll predation, especially considering that the species consumes all other vertebrates and invertebrates. The Spot-tailed quoll's well developed Jacobsen's organ (Russell 1985) and my observations (also Green and Scarborough 1990), suggest that the species hunts primarily by smell and that its eyesight is poorly developed (unpublished obs.). This may explain its reliance upon mammalian prey which are more odorous than other prey classes.

6.4.2. Spot-tailed quoll diet in the Wet Tropics Area

Although the rainforest mammalian fauna of the Wet Tropics area consists of 29 species (26 of which were recorded in quoll diet), I found that only six occur as greater than 10% occurrence of prey items at any site. Even at sites separated by 170km and differing in altitude by 400m, the same species (or a subset of the same species) predominate in the diet: *Hypsiprymnodon moschatus*, *M. cervinipes*, *P. nasuta*, *P. cinereus/herbertensis*, *R. fuscipes/leucopus*, and *P. archeri*. Percent occurrence data overestimate the number of individual larger mammals eaten compared to individual smaller mammals because one individual of a larger species will appear in more scats than a smaller species. However, such data underestimate the contribution to the diet of larger species (and individuals) because larger mammals have a smaller hair (surface area)/body volume ratio. As such, the importance of medium-sized mammals is probably even greater than indicated by comparative proportions presented here (Fig 6.5; Appendix 6.1). Thus medium-sized mammal species are not only the preferred prey but are also eaten in greater proportions. Even though they are probably underrepresented by scat analyses, the incidence of large mammals in the diet is so low that they still constitute a very small proportion of the total prey consumed. The availability of medium-sized mammals, of which one individual would be expected to provide all of a quoll's energetic requirements for a number of days, may be a critical factor in determining suitable Quoll habitat.

Only three species of wet tropical rainforest mammal were not recorded by me in quoll scats: the Atherton Antechinus, *Antechinus godmani,* the Rusty Antechinus, *A. adustus* and the White-footed Dunnart, *Sminthopsis leucopus*. All of these are small, scansorial/arboreal and/or rare or locally distributed members of the Dasyuridae. Evidence from owl diets shows that these species are available within the study areas, but quolls apparently can not capture these small and very agile scansorial and arboreal species. For example, *A. flavipes* is represented in only 0.01% of quoll scats from the Windsor Tableland, but was represented in 0.1% of live-captures and in 5% of 300 pellets of the Lesser Sooty Owl, *Tyto multipunctata,* collected by me from the same area at the same time. In the Lamb Range, where no *Antechinus* spp or *S. leucopus* were detected in 94 quoll scats, these species were represented in 24.3% and 5% respectively of 599 pellets belonging to *T. multipunctata.* I collected these owl pellets at the same time and in the same area as the Quoll scats. Even though it is a capable climber, *D. maculatus* is evidently unable to capture these nimble scansorial species which are capable of running upside down along branches and of hiding in very small refugia. Interestingly, Belcher (1995) found *Antechinus* spp to represent 7.9% of total prey items in his study of quoll diet. The higher incidence of *Antechinus* in his study can probably be explained by the presence of the relatively large (*Melomys cervinipes*-sized) terrestrial species, the Dusky Antechinus, *A. swainsonii,* at his site. No completely terrestrial *Antechinus* occurs in the Wet Tropics area.

The virtual absence of the Lemuroid Ringtail, *Hemibelideus lemuroides,* in the diet of *D. maculatus* is also notable. This medium-sized arboreal species is at least as abundant as *P. cinereus* and *P. herbertensis* in the Lewis and Lamb Range regions (Winter and Goudberg 1995a & b, Winter and Trenerry 1995, Kanowski *et al.* 2001). I found that *H. lemuroides* represented only 1% of prey items while *Pseudochirulus* represented 24% of prey items in those areas combined. Unlike the *Pseudochirulus* species which are cautious climbers (Winter and Goudberg 1995b, Winter and Trenerry 1995), *H. lemuroides* travels by leaping across gaps in the forest canopy (Winter and Goudberg 1995a). This difference in behaviour probably explains the virtual absence of *H. lemuroides* from the diet of *D. maculatus* where the two co-occur. Additionally, *H. lemuroides* is not solitary (unlike the two *Pseudochirulus* species), and usually occurs in groups of two or three related individuals (Winter and Goudberg 1995a). This group behaviour may confuse a quoll launching an attack, further adding to a low success rate in capturing the species.

Anurans were notably absent from the diet of *D. maculatus* in this study. The implications of the presence/absence of frogs in quoll diet pertain to the potential impact of the highly toxic Cane Toad, *Bufo marinus,* on quoll populations. The absence of the species from the 1310 quoll scats analysed in this study could be an artefact of the presumably low detectability of the group in scats, because they lack resilient outer body coverings, e.g. scales, feathers of fur, and because quolls chew bone so finely that characteristic Anuran bone structures (urostyle) maybe masticated beyond recognition. At this stage, a complete examination of skeletal elements recovered from the quoll scats has not been undertaken. By contrast, in the only analysis made of gut contents of *D. maculatus*, four of the 33 prey records from Tasmanian *D. maculatus*, were of frog remains (Green and Scarborough 1990). If frogs are also consumed in north Queensland, even if only at times of nutritional stress (for example by lactating females or by dispersing animals), *D. maculatus* may be at risk of Cane Toad poisoning over a large part of its range (e.g. Burnett 1997).

Several large species or species with a high defensive capacity which I recorded in quoll diet are probably consumed as carrion. These species include the Echidna *Tachyglossus aculeatus,* the Dingo/Feral Dog, *Canis familiaris,* and the Pig, *Sus scrofa.* The incidence of the Swamp Wallaby, *Wallabia bicolor,* Tree Kangaroos, *Dendrolagus* spp., and the Red-legged Pademelon, *Thylogale stigmatica,* may result from either predation upon juveniles and/or scavenging of carcasses. It is likely that at least some of the records of other prey species recorded during this study are also of scavenged carcasses.

6.4.2. Intra-wet tropical dietary variation

While the data presented here provide an exhaustive prey species list, detailed analyses of inter-site comparisons are hampered by a lack of information concerning prey availability and quoll foraging behaviour.

The most significant difference in the proportions of prey between four wet tropical populations of Spot-tailed quoll are higher than expected medium terrestrial mammals, and concomitantly fewer than expected medium arboreal mammals in scats collected from the highland South Johnstone population compared to the three upland populations in the Lamb Range and Windsor and Carbine Tablelands. This pattern is explicable in light of the altitudinal distribution patterns of rainforest ringtails in which densities are generally much greater above 800 asl than below that level (Kanowski *et al.* 2001). The statistical difference between diets from the four populations is also attributable to the higher than expected number of medium arboreals from the Lamb and Lewis populations, both of which are areas in which possum species richness and density is apparently much higher than in the other upland site, the Mt Windsor Tableland (unpublished data).

6.4.2. Prey preferences

Electivity data from the Windsor Tableland suggest that Spot-tailed Quolls are opportunistic predators, showing no avoidance or selectivity of any of the eight mammal species which I censused at the study site. The broad range of vertebrate and invertebrate prey species consumed also suggests that quolls are opportunistic predators. The opportunistic diet of *D. maculatus* has been noted by many settlers and contemporary rural householders who have suffered the depredations of quolls upon their chicken pens (e.g. Frawley 1987, Green and Scarborough 1990). The apparent susceptibility of quolls to 1080 poison baiting programs (Murray *et al.* 2000), and the ease with which they are captured in baited traps (e.g. Chapter 5), further highlights their opportunistic foraging habits. I do not know whether Quolls strongly avoid or select for any of the other small or medium-sized mammals with which it cohabitats, and for which I was unable to collect data.

6.4.4. Sexual differences in diet

The limited data set presented here suggests that male quolls consume larger and/or more pugnacious prey than do females. This result is not unexpected given that male quolls from this study site weigh on average 45% more than females, and have an equivalently larger head volume measurement (see Chapter 5, Table 5.4). Despite the small sample size and the barely significant result (n=39, p=0.041) these results mirror Jones' (1995a) results from Tasmania (based on an even smaller sample), in which females eat smaller prey, suggesting that the patterns I observed are valid.

6.4.5. Inferences about Quoll foraging behaviour from diet

Several conclusions can be drawn about the foraging ecology of *D. maculatus* based on the relative occurrence of some of the prey species recorded here.

1. Quolls forage in trees and on the ground.

The high proportion of arboreal prey in its diet suggests that the Spot-tailed quoll captures prey in the trees as well as on the ground. The striated interdigital pads on the pes and manus, and the long tail are indicative of arboreal habits. My own observations suggest that while the Spot-tailed Quoll lacks opposable digits or prehensile tail, it is quicker and more agile within the inner branches of trees than the generally cautious rainforest ringtails which are such an important part of its diet in the wet tropics. While ringtails of the genera *Pseudochirulus* and *Pseudochirops* are reluctant to leap between branches, I have observed quolls bounding between the woody branches of rainforest trees, and even cross, albeit hesitatingly, between adjoining rainforest canopies. Possums on the other hand are capable of traversing the lightest of foliage where quolls can not go.

2. Quolls limit arboreal hunting to after dark

The absence of *H. lemuroides* and the high incidence of *P. archeri* in the diet, suggest that quolls catch most of their Pseudocheirid prey during the night when that prey is active. If quolls were capturing much of their possum prey in their daytime retreats, then *H. lemuroides*, the most agile (Winter & Goudberg 1995a) of the Pseudocheirids would be expected to occur in much higher abundances in quoll diet, based upon its density in the field which Kanowski *et al.* (2001), found to be three times that of the Herbert River (*Pseudochirulus herbertensis*) and Green (*Pseudochirops archeri*) Ringtails. Similarly, *P. archeri* which does not utilise daytime retreats, (it sleeps on exposed branches by day; Winter & Goudberg 1995b), would be expected to occur in very low numbers if quolls were predominantly feeding on possums captured by day in their dens. This is not the case, *P. archeri* occur in high proportions of quoll scats in some regions.

6.4.6. A role for the Spot-tailed quoll as a determinant of rainforest community structure?

The role of predators in structuring prey communities has received considerable attention as summarised by Sih *et al.* (1985) and Begon *et al.* (1986). Theory suggests that, when predators select for competitively inferior prey species, community diversity declines, but that when predators select for competitively superior species, community diversity is increased (the keystone predator effect). As most predators positively select for the most abundant prey, the latter is probably more often the case. Additionally, the role of predators in structuring community organisation is expected to be greatest in environmentally more benign habitats (Begon *et al.* 1986), although this may be offset by the negative relationship between effectiveness of predation and habitat complexity (Sih *et al.* 1985) in the case of rainforest communities. Aside from killing their prey directly, predators can also influence prey communities through changes in the anti-predator behaviour of the prey. For example, Lagos *et al.* (1995) showed that experimental exclusion of predators from sites in semi-arid Chile resulted in a decrease in the open-space avoidance behaviour of a rodent species there. Such changes in behaviour may have ramifications with regard to the ecological niche of prey species which together with the keystone predator effect may have ecological repercussions throughout the community in question. This complex issue requires detailed experimental field work which has not been conducted in Australia and thus this discussion is largely conjectural.

Polis (1999) discusses the role of predators in constraining the capacity of herbivores to regulate plant biomass. The most important mammal species in the diet of the Spot-tailed quoll in north Queensland (those species which contribute greater than 10% of prey frequency occurrence), include the ringtails which are folivores, and rodents and musky rat-kangaroos which are important tree seed predators. The loss of Spot-tailed quoll populations from fragmented habitats (Chapter 8) and the decrease in Quoll abundance in edge habitats, has unknown effects upon populations of these species. However, given that quolls are probably the only effective mammalian carnivores within rainforest habitats (this chapter and Chapter 9), the potential for changes to the dynamics of the relationship between these prey populations and rainforest plant populations is likely to be great and is deserving of further investigation. A host of avian and reptilian predators also exist within these habitats, but their diets and foraging behaviour are unknown.

6.5. Summary

- The Spot-tailed Quoll is a top order predator within Australia's wet tropical rainforests.

- Diet analyse show that the species is primarily a mammal-eater, although anything of animal origin is consumed. *Melomys cervinipes*, *Pseudochirulus* ringtails, Long-nosed Bandicoots *Perameles*, and Musky-Rat Kangaroos, *Hypsiprymnodon*, are the primary prey of *D. maculatus* in the Wet Tropics Area.

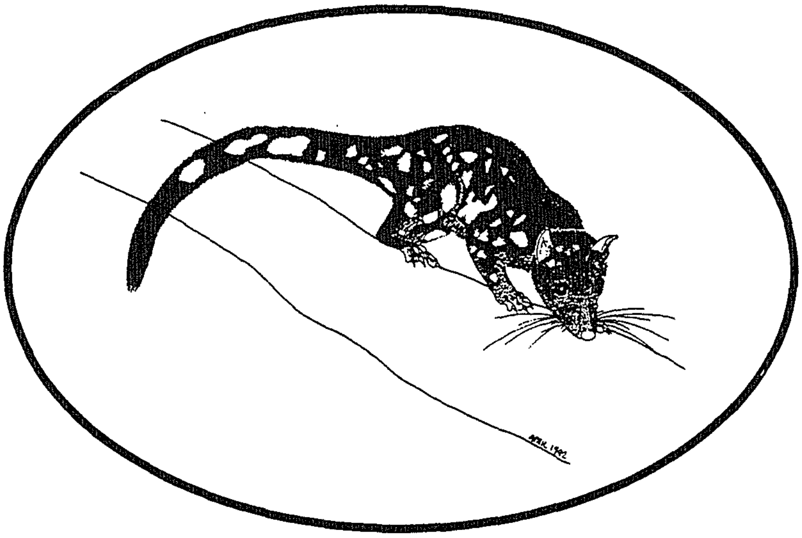
- On the Mt Windsor Tableland, *D. maculatus* showed no strong selection for any species for which field abundance data were available.

- The Spot-tailed Quoll's opportunistic diet, including predation upon birds and a willingness to consume carrion renders the species vulnerable to anthropogenic mortality agents, including: death at chicken pens when harassing poultry, roadkill when scavenging corpses, direct and secondary 1080 and other poisoning when scavenging meat baits and corpses.

- Additionally the species' potential for rapid travel over several kilometres (Chapter 7), increases the likelihood of individuals coming into contact with all of the above, resulting in a higher encounter rate with these threatening scenarios than the low density at which the species occurs (Chapter 5) would suggest.

Chapter 7.

Ranging behaviour and latrine use by the Spot-tailed Quoll



In this chapter, I examine some trends in scat placement and in spatial activity patterns of Spot-tailed Quolls, *Dasyurus maculatus*, in a relatively pristine environment in north Queensland. I found that Spot-tailed Quolls are highly mobile animals and that they occupied large home ranges. While solitary, several individual quolls can share a stationary food resource (in this case a dead cow), by partitioning their time there and avoiding each other. Quolls preferentially deposit their scats on roads, in aggregates (latrines), and always close to the centre of the road. I discuss the implications of these trends with respect to the conservation of quoll populations in the increasingly modified landscapes which they are forced to inhabitat throughout Australia today. Accordingly, the results of this work are applicable throughout the geographic range of the Spot-tailed quoll in Australia.

Chapter 7. Ranging behaviour and latrine use by the Spot-tailed Quoll

7.1. Introduction

The ranging behaviour of the Quolls (*Dasyurus*), including their spatial organisation, home range size and mobility, has received very little attention. Published references to the ranging behaviour of the Spot-tailed Quoll, *Dasyurus maculatus,* are limited to two studies which have described the positioning of latrine sites and speculated on their use in Victoria (Belcher 1995) and in New South Wales (Kruuk and Jarman 1995). Belcher (1995) conducted a study at two latrine sites in east Gippsland. These latrines were sited on rock ledges which were part of larger cliff faces and were eight kilometres apart. A total of 319 scats were collected from these latrines and subsequent camera surveillance of the sites showed that they were being used by several individuals (Belcher 1995). Kruuk and Jarman (1995) described latrine sites in northern New South Wales. These latrines were located on top of flat-topped boulders within a river bed. Fifty-one latrines were found over a distance of 1.5km of riverbed and the number of scats within each varied from 1 to 14. Live trapping of a 500m length of the gorge resulted in the capture of five different quolls, including adult male and female and juveniles.

Latrine use has also been documented in Tasmanian devils (Pemberton and Renouf 1993), and the Western quoll (Serena and Soderquist 1989), and in the Northern quoll (pers. obs.)

In this chapter, I examine some trends in scat placement and in spatial activity patterns of Spot-tailed Quolls, *Dasyurus maculatus*, in a relatively pristine environment in north Queensland. I found that Spot-tailed Quolls are highly mobile animals and that they occupied large home ranges. While solitary, several individual quolls can share a stationary food resource (in this case a dead cow), by partitioning their time there and avoiding each other. Quolls preferentially deposit their scats on roads, in aggregates (latrines), and always close to the centre of the road. I discuss the implications of these trends with respect to the conservation of quoll populations in the increasingly modified landscapes which they are forced to inhabit throughout Australia today. Accordingly, the results of this work are applicable throughout the geographic range of the Spot-tailed quoll in Australia.

7.2. Methods

7.2.1. Study Site

I conducted this study on the Mt Windsor Tableland, north Queensland (see Chapter 4 for details of the study site).

7.2.2. Spatial ranging behaviour

I studied the ranging behaviour of Spot-tailed Quolls by live-trapping as described in Chapter 4, and radio-tracking which I conducted intermittently between November 1992 and March 1994. I radio-tracked nine individual adult Spot-tailed quolls using a 3-volt, 2-stage radio-collar with a whip aerial. Because of the very rugged topography and dense and often very wet nature of the terrain at the study site, it was not possible to locate animals accurately by triangulation; animals had to be located by homing. I achieved this by picking up the focal individual's signal from a high point along a road or a high, bare granite area and homing to approximately 100m of the source of the signal, as estimated based on signal strength. I calculated home range areas using the minimum convex polygon (MCP) method and the 50% kernel (core home range) using both radio-tracking and live-trapping locations for each individual. These home ranges were plotted using the Animal Movement Analyst Extension to ArcView GIS (Hooge *et al.* 1999).

During field trips, I located each quoll at least once per day during daylight hours because of the impracticalities of night navigation at the site. These impracticalities included my inability to travel quietly and to keep track of my location due to the very dense shrub layer throughout much of the site, and the steeply dissected nature of the terrain.

When located during radio tracking, I categorised animals as active or not, and on the ground or above the ground. Retreat sites were described where they could be identified.

I investigated sexual differences in spatial ranging behaviour by t-tests for each of four different linear movement types: distance moved between successive captures (DMSC) between my field trips, DMSC within my field trips, distance between furthest capture points, and linear distance moved in 24 hours. The last measure was made on radio-collared animals only. No data for males could be collected, as no males were relocated once released with radio-collars. In order to avoid the use of repeated measures in these analyses, a single value for each measurement was calculated for each individual using the first relevant capture records only.

7.2.3. Scat placement

I investigated scat placement by examining spatial patterns in the deposition of scats on the Mt Windsor Tableland. I made three measurements, designed to test whether scat placement was random. Non-random deposition of scats was taken to indicate a social function in scat placement. Latrine sites were defined by at least two scats within two metres of each other.

Measurement 1. I counted scats along 15, 300m transects in order to examine whether scat densities on the single maintained road traversing the Mt Windsor Tableland were higher than along overgrown logging tracks or within the adjacent forest. Transects were three metres wide and were searched on foot in June 1993 and again in June 1994. The transects included five, 300 m transects along the Mt. Windsor Road, five, 1km transects along overgrown logging trails feeding into the Mt Windsor Road, and five 300m transects within forest with poorly developed understorey layers. The resultant comparisons between substrate types are so disparate as not to warrant statistical analyses.

Measurement 2. In order to assess whether scats were deposited in any particular position across the road profile I measured their location on the Mt Windsor A-Road.

One hundred and four scats were mapped along a three kilometre transect along the Mt Windsor Road. Each scat was mapped relative to the centre of the road. The entire road width (Y) was divided by two to find the centre point. The distance from the centre point to the road margin (x) was divided by 10 to produce 20 sectors across the road profile; 10 on either side of the centre point (Fig 7.1). The distance of each scat from the centre point was measured and allocated to one of these sectors. This is a relative scheme, as road width varied by between 6.5 to 12 metres along the stretch of road surveyed. Each corresponding tenth unit on each side of the road were pooled for analysis, which consisted of a X^2-homogeneity test which compared observed frequencies of scats with an expected even distribution of scats across the road profile.

Measurement 3. In order to examine whether quolls deposited scats in random positions along the length of the road, I mapped the distribution of scats along 15 km of the Mt Windsor Road. I measured this transect five times between November 1991 and March 1993. The number of scats within each 20m section of the road was recorded and this distribution was compared with a Poisson distribution.

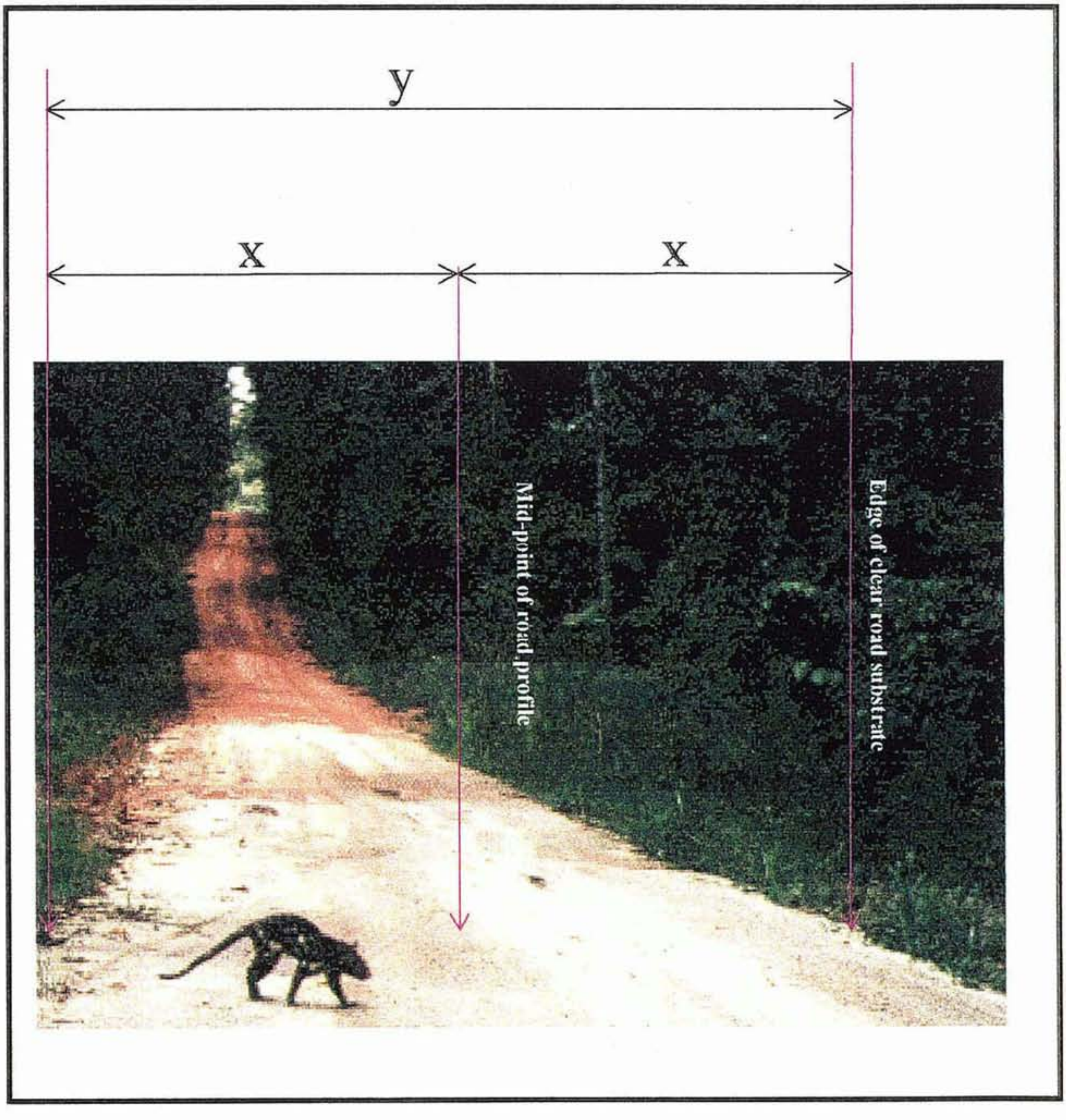


Fig. 7.1. Dimensions used to locate scat positions across the road profile. Note: y, width of clear road substrate; x = y/2.

7.3. Results

7.3.1. Spatial ranging behaviour

Both radio tracking and live trapping indicate that male *D. maculatus* are more mobile than females (Table 7.1). The distance moved between successive captures (DMSC), between my field trips was significantly greater for males (Table 7.1). Although there were no significant statistical differences between the sexes for other indices of mobility, the maximum male values of two of these indices were 155% and 265% greater than the corresponding values for females. Radio tracking also provides an indication of the mobility of the species. Lactating females with young in the den regularly travelled a straight-line distance of 1000m in a 24h period. I recorded movements of 1.5km over less than 2.5 hours for radio-collared females. I have no comparable data for males because I was unable to relocate any radio-collared *D. maculatus* of that sex (see methods).

Table 7.1. Indices of mobility of male and female D. maculatus on the Windsor Tableland, north Queensland.

In all cases where a statistic is provided, the null hypothesis is that there is no difference between male and female ranging distances. DMSC refers to the distance moved between successive captures.

	Sample size		**mean +/- 2. S.E**		**range**		**Statistic**
	m	f	M	f	m	f	
DMSC between trips (m)	36	37	1350+/-530	661+/-188	0-6100	0-2450	t=2.44,df=44, p=0.01
DMSC within trips (m)	23	17	854+/-386	614+/-136	0-4200	100-1150	t=1.16,df=27, p=0.25
Distance between furthest capture points (m)	13	13	1725+/-888	1096+/-448	250-6650	100-2600	t=1.26,df=19, p=0.22
24h movements (m)	No data[1]	29	No data[1]	820+/-160	No data[1]	100-1839	No data[1]

Note.

1. Information on movements over a 24 hour period was obtained from radio-tracking data, none of which is available for male Spot-tailed quolls.

I attached radio-collars to six females and three males between July 1992 and December 1993. Home range data could be obtained for six females only. I calculated home ranges from a total of 98 fixes for these animals (Table 7.2). Using the Minimum Convex Polygon method, the estimated minimum home range size for five of these females ranged from 98 ha to 205 ha (Table 7.2) with a mean of 150 ha (s.e =24.08). The sixth female (female #3) was killed by a Wedge-tailed eagle, *Aquila audax,* 10 days after she was fitted with her collar (see Burnett *et al.* 1996). The three collared males disappeared from reception range and were not detected again, although I subsequently re-trapped two males and removed their radio-collars. Radio-telemetry of males was discontinued after the third male could not be relocated or recaptured. Plots of cumulative home range size vs no. of fixes (Appendix 7.1) suggest that a minimum between 18 and 20 fixes are required to provide a representative home range size.

Table 7.2. Home range data for six female *D. maculatus* on the Mt Windsor Tableland, north Queensland.[1]

Animal No.	No. fixes[2]	No. days[3]	Minimum home range size (ha)
1	20	140	177
2	30	138	205
3	6	10	57
4	15	91	107.5
5	15	74	119.5
6	12	89	98

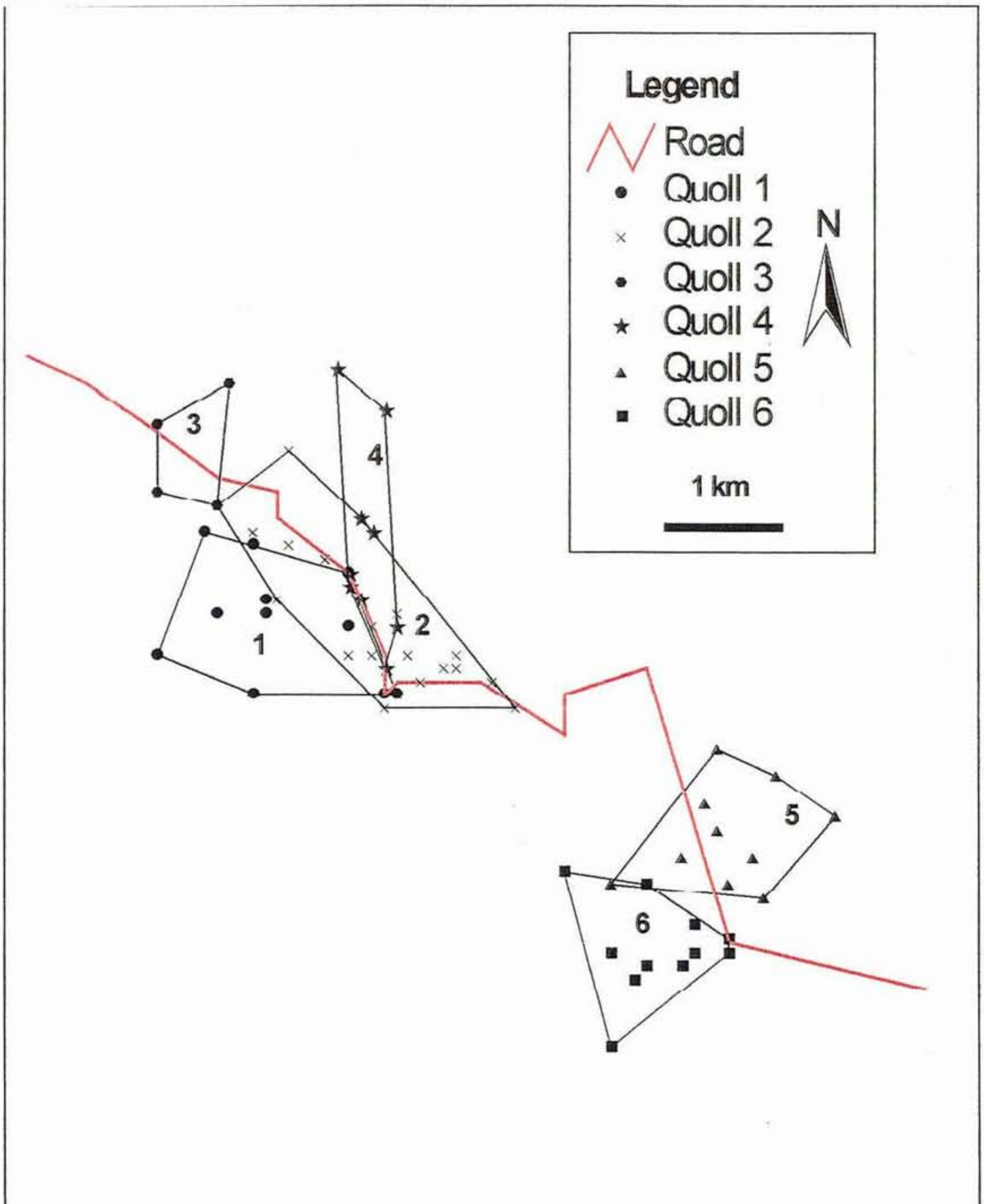
Note.

1. See Maps. 7.1 and 7.2 for a graphical representation of these home ranges
2. Fixes include radio-locations and capture localities.
3. No. days refers to the number of days over which fixes were taken.

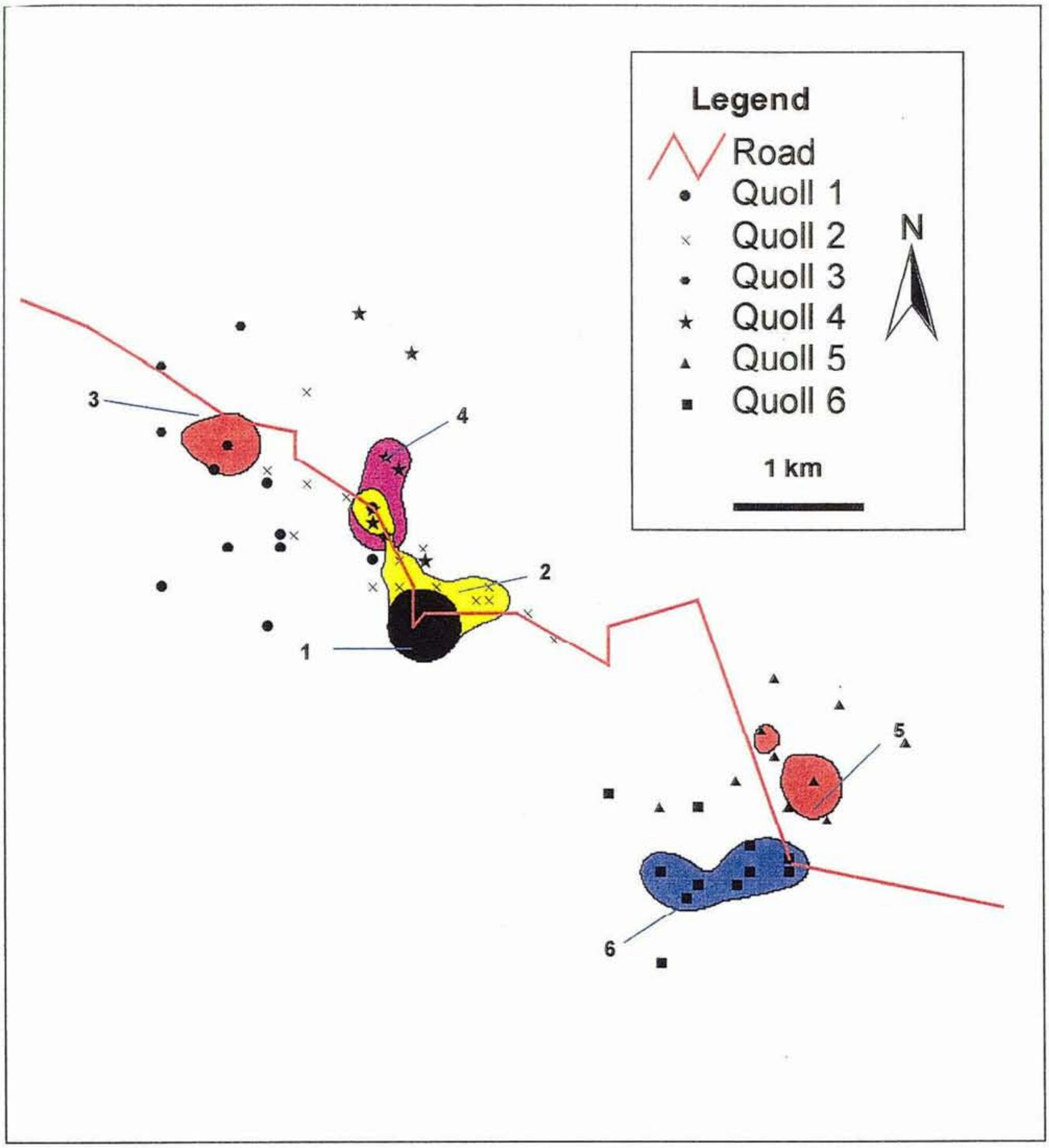
The home ranges of six resident female quolls exhibited little overlap using the MCP technique (Map 7.1). The core areas of these home ranges illustrated even less overlap (Map. 7.2). Interestingly, the only female whose MCP and core kernel home range overlapped with those of other females (female 1), was female 44. She was the only first year female which failed to give birth to a litter during the course of this study. While no male home ranges are known, indications are that they are larger than those of females. In addition, the fact that I caught as many males in the study area as females (Chapter 5), suggests that there must be considerable overlap between the home ranges of males, or that a large proportion of males have a loosely defined or no defined home range.

Radio-tracking information and wild sightings suggest that Spot-tailed quolls are solitary. All but one of my 23 sightings of quolls in the wild were of lone animals. Similarly, of 44 sightings made of live quolls by other people and collated by me (Appendix 8.2), all but one were of single animals.

I radio-located six individual quolls on 70 occasions during daylight. Seventeen percent of these locations were either active or inactive in the canopy and 83% were either active or inactive on the ground.



Map 7.1. Home ranges of six female Spot-tailed Quolls on the Mt Windsor Tableland defined using the Minimum Convex Polygon Method (Burt 1943). Numbers within each polygon refer to individual females as listed in Table 7.2. Note that many fixes fall exactly on the same point and so the number of symbols do not match the number of fixes reported in Table 7.2.



Map 7.2. Home ranges of six female Spot-tailed Quolls on the Mt Windsor Tableland defined using the kernel home range technique (Worton 1989) and displaying the 50% contour or core area of activity.

Numbers refer to the core home ranges of individual females (see Table 7.2).
Note that many fixes fall exactly on the same point and so the number of symbols do not match the number of fixes reported in Table 7.2.

7.3.2. Patterns of scat placement

I found many more scats on the maintained road than on overgrown roads or within the forest (Fig. 7.2). Scats are not randomly placed on the road. Significantly more quoll scats were placed within the centre portion of the road than expected from a uniform distribution across the road (X^2 homogeneity = 33.6, d.f=7, $p<0.0001$) (Fig 7.3). Scats were not randomly distributed along the length of the road either. The distribution of scats did not conform with a random (Poisson) distribution (X^2 = 141.6121, 113.0175, 144.7298; df=6, $p< 0.01^{-10}$ for each time respectively).

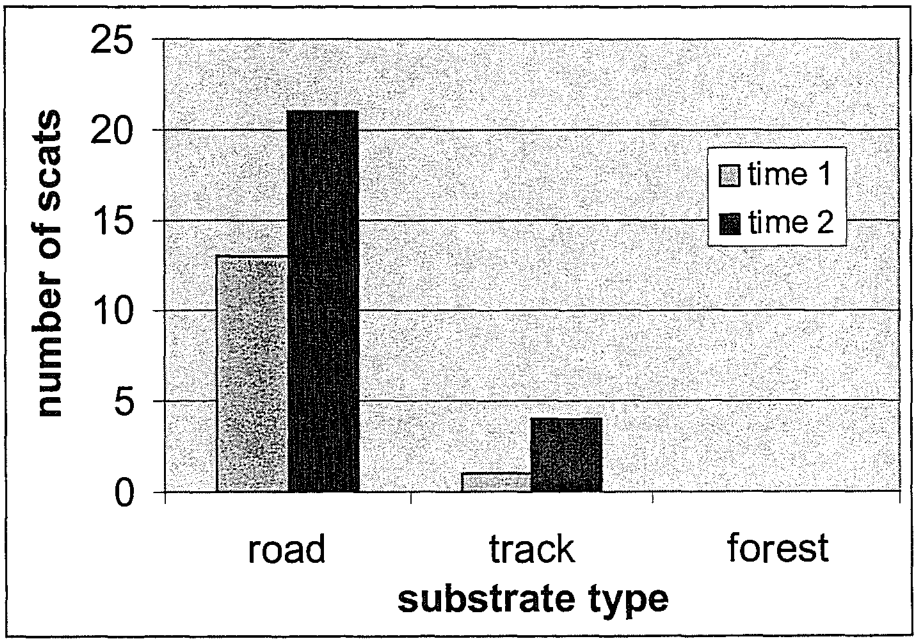


FIG. 7.2. THE NUMBER OF SPOT-TAILED QUOLL SCATS COLLECTED FROM TRANSECTS ON THREE SUBSTRATES.

VALUES ARE SHOWN FOR EACH OF THE TWO TEMPORAL REPLICATES FOR EACH SUBSTRATE TYPE. SEE TEXT FOR FURTHER DETAILS OF TREATMENTS.

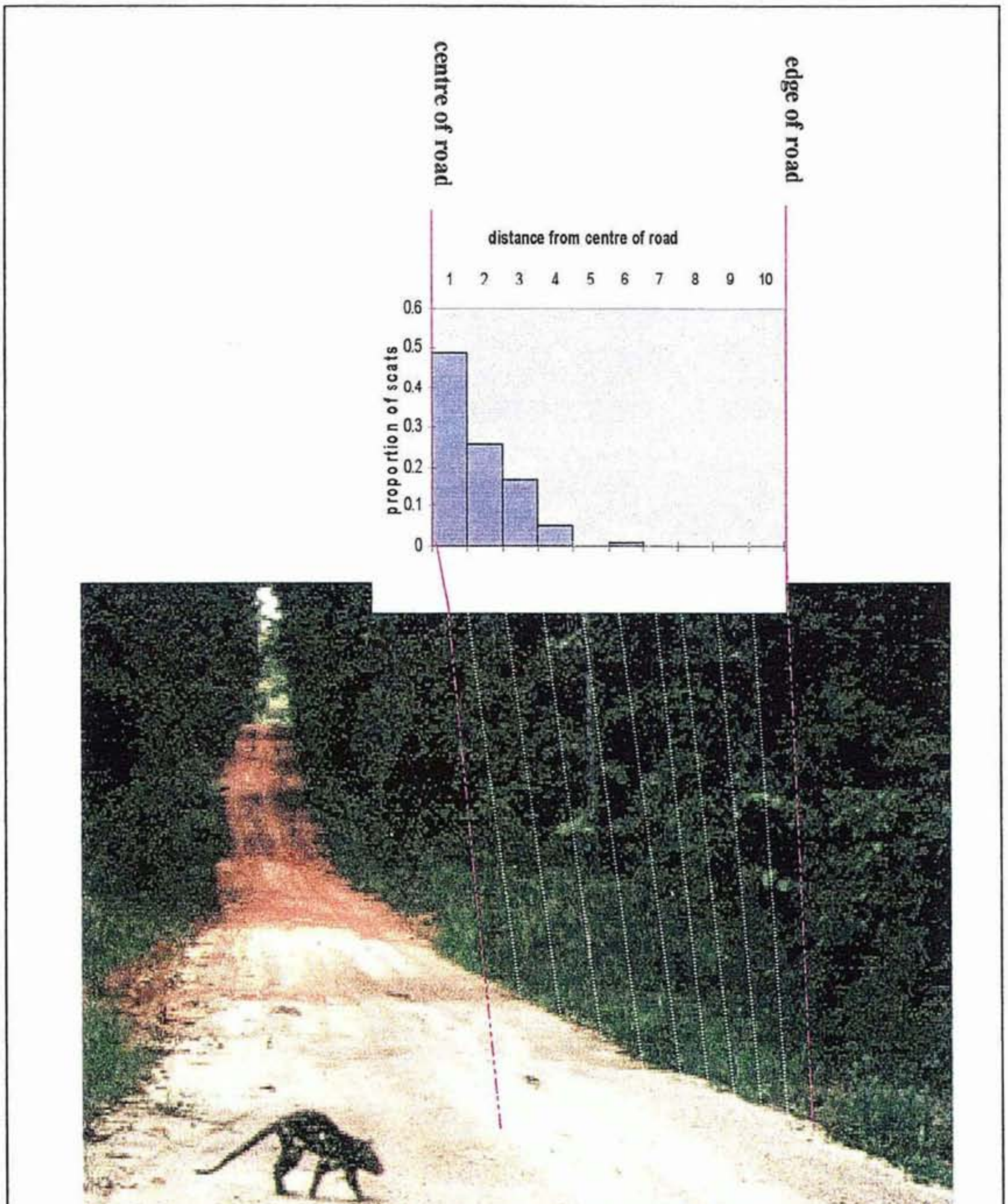


Fig. 7.3. The distribution of 104 Spotted-tailed quoll scats relative to the road cross-section, on the Mt Windsor Forestry Road.
Scats from corresponding positions on either side of the centre of the road are pooled.

7.4. Discussion

7.4.1. Spatial ranging behaviour

Spot-tailed quolls are solitary and, resident females at least, exhibit little overlap of home range as delineated by the MCP technique or of core home ranges delineated by the Kernel technique. It is interesting that the only female Quoll (#44) whose home range overlapped with those of other individuals, was below average weight and failed to produce any young during the 1993 breeding season after which she disappeared from the trapping transect. Male quolls ranged over greater distances than females, as evidenced by the significantly greater distances moved by males between recaptures between trips (Table 7.1), and by the fact that although other measures of mobility were not significantly different, maximum values for males still represent considerably greater values than for females (Table 7.1). This greater mobility of males which are the larger sex (see Chapter 5), is not surprising given that larger animals are typically more mobile than smaller ones (Mace and Harvey 1983). Males are probably also prone to wander over larger areas than females as they are presumably not burdened with parental care, or attached to specific den sites as are females during the litter-rearing season. The larger body size of males has probably been at least secondarily selected for, because of the greater roaming potential, and thus greater mating potential which higher mobility confers on polygynous species such as *D. maculatus*. Analysis of nuclear and microsatellite diversity among a population of *D. maculatus* at Barrington Tops, New South Wales, also indicates that female Spot-tailed Quolls are more sedentary than males (Firestone *et al.* 1999).

The mean female home range size of 150 ha presented here does not include that of female 3, who was killed by a predator only 10 days after radio-tracking commenced. Even excluding this individual and despite the apparent asymptotes evident in the cumulative home range size charts for four of the radio-collared females (Appendix 7.1), it is likely that the home range estimates presented here are underestimates. The small number of locations on which these home ranges are based and the short time span of tracking of some individuals (Table 7.2) makes it impossible to discern whether these apparent asymptotes (Appendix 7.1) really are, or whether there are steps in a climbing cumulative home range total. Additionally, I conducted most radio-telemetry during the period when females had dependent, nest-bound young and the effects that this has on their ranging behaviour is unknown. I suspect that females with dependent young spend less time in investigatory and/or socially oriented wandering, and more time foraging than do males or first year females. Thus it may be that occasional forays outside of their core area, which would represent significant increases in home range size, are less common at this time and so were not detected by me. The differences in area covered during these respective activities have been shown to be significant in some smaller dasyurid species, such as *Antechinus stuartii*, in which social home-range is up to five times the area of the foraging range (Lazenby-Cohen and Cockburn 1991).

I have found no evidence to suggest that *D. maculatus* is other than solitary. Casual observations at feeding stations suggest that Quolls avoid one another and in only one instance did I observe two adults together. This was a hostile interaction in which the female behaved aggressively to the male. None-the-less individual females at least, do seem to share spatial resources such as large persistent carcasses. In one case, a carcass of a cow on the Mt Windsor Tableland was visited by three female Spot-tailed Quolls although never at the same time over about one month of observation. Interestingly, no males were ever observed at the carcass.

I found 17% of radio-located quolls high in the canopy. However, because of Quolls' habit of secreting themselves in standing hollow trees, fallen hollow logs and even within accumulations of leaf litter between buttress roots, when persistently tracked, it was not possible to differentiate between quolls which were denned up in the canopy or those which had been foraging there and had taken temporary refuge upon my arrival. Although I did not observe Quolls to seek refuge in the canopy after release from traps, one was seen to scamper up a tree when chased by a scrub turkey. However, given the high percentage of strictly arboreal species in their diet (e.g. Ringtail possums, Chapter 6), quolls presumably spend considerable time hunting in the canopy.

Although Quolls lack the clenching first toe and prehensile tail of the ringtails (F. Pseudocheiridae) they are accomplished climbers. This is facilitated by their clawless first toe, (which is absent in less arboreal quolls (Strahan 1995)), the striated pads on the soles of their pes and manus, their long, sharp claws, their ability to rotate the pes 180^0 (S. Burnett unpublished data), their grasping manus and long, stiff, rudder-like tail.

7.4.2. Patterns of scat placement

My data on the placement of scats suggest: (i) that they are deposited much more frequently on the maintained road on the Windsor Tableland than upon other substrates which I examined; (ii) that scats are invariably deposited close to the centre of that road (Fig 7.3); and (iii) that the distribution of scats along the road is clumped. These observations meet Kliemans' (1966) criteria for distinguishing scent marking from elimination behaviour: the scats are oriented to a specific landmark (the road), and they were repeatedly deposited at localised sites, or latrines. Similar latrine use along roads or other prominent landscape features (for example cliffs and dry creek beds) has been observed in canids, felids, mustelids, herpestids, and viverrids (Rothman and Mech 1979, MacDonald 1980, Urios and Castroviejo 1994) and in *D. maculatus* by Belcher (1995) and by Kruuk and Jarman (1995). The purpose of this behaviour has variously been ascribed to communicating with conspecifics including: territorial marking, communication of reproductive and/or hierarchical status, communication of presence (not necessarily with territorial overtones); and/or to marking the environment for the purpose of familiarisation or even as a reminder to the individual of where it has travelled or foraged within its range (Gorman 1980). In the vast majority of cases, several of these reasons may operate simultaneously and without further investigation, I can only speculate on the purpose of latrine formation by *D. maculatus*. Given that females, at least, appear to occupy exclusive home ranges, which maybe aligned along one side of the road (e.g. see Maps 7.1 and 7.2), latrine sites may have a territorial function. Additionally, the sparse population density (Chapter 5), apparently solitary life-style, and limited annual breeding opportunity (Chapter 5) available to the Spot-tailed Quoll (Settle 1978), necessitated the reliable communication of reproductive information from females to males. The vomeronasal (Jacobson's) organ which Estes (1972) considers a specialised receptor of sex hormones, is well developed in this species (Russell 1985), supporting this possibility. The role of defecation in communication between individuals of the same sex, or as "trail markers" for individuals can not be discounted. My observations of latrines on carcasses, and observations of a female cloacal dragging at a scavenging site suggest that messages of ownership/territoriality are transmitted via this medium. Scat deposition patterns suggest that roads play an important role in the social life of quolls whose home ranges include such features. Well-formed and maintained roads constitute a very distinct environmental discontinuity and as such represent a desirable scent station locality.

On the Mt Windsor Tableland as well as at other sites in the Wet Tropics Area, I occasionally found Quoll scats in association with landscape features less extensive than roads including: expanses of bare granite in the forest, on logs bridging creeks, and on or near carcasses. Where I have observed Quolls defecate, (on carcasses, on the road, and on concrete slabs), it has been accompanied by urination and cloacal dragging, suggestive of scent-marking behaviour as observed in other dasyurids (Croft 1982).

Roads may also be attractive as convenient places to search for prey trails or carrion. I suggest that roads probably represent a regularly visited feature within any individual Quoll's range and have a considerable influence on Quoll social biology. This represents a significant mortality risk in some cases. The scent marking behaviour described above also provides an opportunity for the rapid assessment of quoll distribution in north Queensland by scat surveys.

7.5. Summary

- Female Spot-tailed Quolls on the Mt Windsor Tableland occupied exclusive home ranges of at least 200ha. No data on male home range size were able to be collected.

- Indices of mobility suggest that male Quolls move greater distances than females. The maximum straight line distances recorded for male and female Spot-tailed Quolls in this study were: males 6650m and females 2600m.

- Spot-tailed Quolls in north Queensland rainforests show a tendency to utilise roads as scent marking substrates.

- Aspects of the ranging behaviour of Spot-tailed quolls increase the probability of anthropogenic mortality. These factors include: the very high mobility of individuals, and a tendency to return time and again to food sources. The tendency for quolls to use roads as scent marking substrates also places individuals at risk from roadkills, and perhaps increases the chances of individual quolls being poisoned by Cane Toads, which anecdotal evidence suggests are much more common on roads than in adjacent rainforest (unpublished observations). The very high mobility of Spot-tailed Quolls means that the circle of influence of any mortality agent extends beyond its local neighborhood. My data on the maximum distances between the furthest capture points for male and female Quolls (Table 7.1), suggest that a poultry yard for example, can potentially be visited by male quolls from a circular area of 139 km^2 and females from an area of 21.2 km^2.

- I have shown above that Spot-tailed Quolls use roads for scent marking, and that individual Quolls have wide ranging capabilities. Each of these factors increase the chances of an individual quoll encountering anthropogenic mortality such as vehicles, feral animals and humans and thus increase the probability of extinction of local populations.

Chapter 8.

Distribution, Abundance and Conservation Status of The Spot-Tailed Quoll In North Queensland

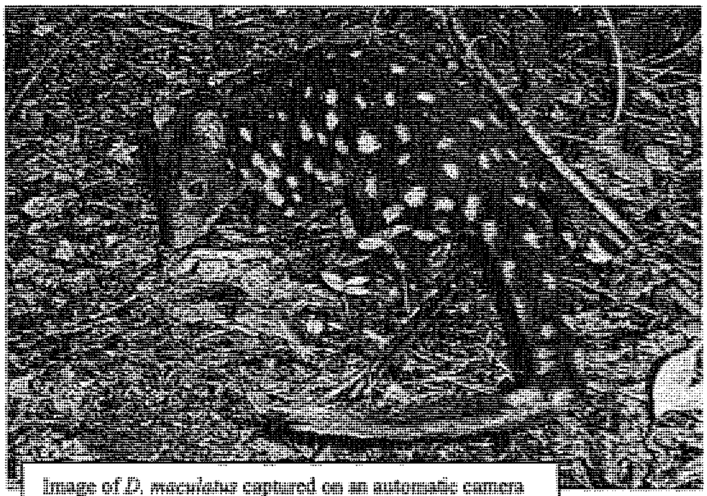


Image of *D. maculatus* captured on an automatic camera 26/7/2001. Lamb Range, Atherton Tablelands. QPWS, Atherton.

In this chapter, I collate records of *Dasyurus maculatus* in north Queensland. Patterns which have emerged from these data were then used to stratify field surveys along road-based transects. In this way, I have clarified the relationships between the distribution of *D. m. gracilis* and broad scale vegetation types and altitudinal zones. I have found that *D. maculatus* is distributed throughout the northern Wet Tropics area and is restricted to rainforest habitats above 900m. Trends in overall distribution in north Queensland and estimations of the number of quolls within the wet tropics area suggest that the species should be regarded as endangered.

Chapter 8. Distribution, Abundance and Conservation Status of The Spot-Tailed Quoll In North Queensland.

8.1. Introduction

In the mid-1880's, Norwegian naturalist Karl Lumholtz spent time with the Aboriginal people of the Abergowrie area, near Ingham, north Queensland. During this time he collected the first specimen of *Dasyurus maculatus* from the disjunct north Queensland population (Lumholtz 1888). His Aboriginal informants suggested that in order to procure 'Yarri', (the Abergowrie Aboriginal word for *D. maculatus)*, they would have to travel to the mountaintops of the eastern escarpment. It was at such high altitudes, in the hills behind Abergowrie that Lumholtz eventually procured a specimen (Lumholtz 1888). More recently but still based on a small number of sightings, Winter *et al.* (1984) suggested that in north Queensland *D. maculatus* was restricted to rainforest and its margins and that it is found throughout the altitudinal range of the Wet Tropics Area.

In southeastern Australia, *Dasyurus maculatus* occurs in a range of forest types including, woodland, sclerophyll forest, tall open forest, and rainforest (Mansergh 1984). It also occurs at all altitudes from sea-level, to above the snowline, in the Snowy Mountains. In Tasmania, most records of the species are from the wettest, most productive environments on the north and eastern coasts of that state (Jones and Rose 1996). Mansergh (1984) makes passing reference to the north Queensland population giving it the label of uncommon along with the south-east Queensland population. *Dasyurus maculatus* has declined in southern and eastern Australia (Mansergh 1984, Lunney and Leary 1988, Watt 1993). Mansergh (1984) suggests that the species range has declined by 50% in that area.

In this chapter, I collate records of the species in north Queensland. Patterns which have emerged from these data were then used to stratify field surveys along road-based transects. In this way, I have clarified the relationships between the distribution of *D. maculatus* in north Queensland and broad scale vegetation types and altitudinal zones. I have found that *D. maculatus* is distributed throughout the northern Wet Tropics area and is restricted to rainforest habitats above 900m. Trends in overall distribution in north Queensland and estimations of the number of quolls within the wet tropics area suggest that the species should be regarded as endangered.

8.2. Methods

8.2.1. Distribution

I obtained baseline data on the distribution of *D. maculatus* in North Queensland by collating locality records from sources including: national and international museum records, historical literature, questionnaires distributed to Forestry workers through the district offices in Atherton and Ingham, and personal communications and observations including an appeal for information from the public in the "Cairns Post" newspaper. I also obtained records from naturalists with considerable experience in the Wet Tropics Area, in particular, from the records of Dr. John Winter, Mr. Rupert Russell and Mr. Mike Trenerry. Early analysis of the distribution of sighting records suggested that quolls occurred in higher densities in higher altitudes. Therefore I stratified my field sampling to maximise the sampling of high altitude areas, especially those stretches of the road cutting most deeply into the relevant rainforest units. This design also enabled me to test the effects of altitude and habitat type on quoll distribution.

I examined the patterns of distribution with regard to geographic and anthropogenic features of each biogeographic unit by correlation analyses. The densities of quoll sightings and of scats within each upland unit were tested against each other and against the following variables:

- rainforest area,
- rainforest area above 900 m asl,
- density of roads (km/1000 ha),
- number of kilometres of road,
- density of roads above 900 m (km/1000 ha),
- kilometre of roads above 900 m,
- indices of land use, and,
- cane toad distribution.

I scored land use indices on an ordinal scale of one to five as follows:

- 1: wilderness, that is, no disturbance greater than a walking track,
- 2: unimpacted apart from logging on a relatively localised scale,
- 3: logged throughout, no settlement within but extensive roads,
- 4: logged and some permanent human settlement within, and,
- 5: extensively cleared, including logging, and containing permanent human settlement.

The distribution of the Cane Toad *Bufo marinus*, was scored on a four point scale as follows:

- 1: toads absent,
- 2: toads present along roads which provide access to a small proportion of total area,
- 3: toads present along roads which provide access throughout the bioregional unit, and,
- 4: toads distributed throughout bioregional unit.

I used Spearman Rank Correlations to examine the relationship between ranked quoll density (sighting and scat), and these indices of land use and cane toad distribution. Road statistics were obtained from a database compiled and supplied by the Wet Tropics Management Authority.

My co-ordinates for Quoll localities in the Wet Tropics Area were modelled using the DOMAIN program (Carpenter *et al.* 1993); using the full dataset, and using a subset of that data from post 1945. These two sets of Quoll locational data were compared to examine any changes in Quoll habitat since 1945, as modelled by DOMAIN. 1945 was chosen because it marks: (1) the last known sighting of the Spot-tailed Quoll in the Spec Uplands, and, (2) the beginning of intensification of human landuse in the Wet Tropics Area following the cessation of World War II. These maps were generated by GIS staff at the CSIRO Sustainable Ecosystems Tropical Forest Research Centre, in Atherton.

8.2.2. Abundance

I calculated the relative density of Spot-tailed quolls within each unit using both sighting and scat densities. I calculated sighting densities by dividing the number of sightings by the number of years since the first sighting was recorded in each unit. I exclude my own sightings from these data because they are heavily biased towards the Windsor Tableland and because of the specialised methods that I used to locate Quolls. I calculated scat densities as the number of scats divided by the length of road searched in each biogeographic unit.

I obtained a crude estimate of the absolute abundance of each sub-population of *D. maculatus* by multiplying the area of available habitat (rainforest) above and below 900 m asl within each bioregional unit, by the density of quolls within that habitat. In estimating the abundance of quolls above 900m asl, I used quoll density values of 0.31 individuals of each sex per km^2, as determined for the Mt Windsor Tableland population (see Chapter 5 for methods and assumptions). In estimating quoll abundance below the 900m asl mark, I multiplied the area of rainforest by 0.031 quolls of each sex. This figure is based on my observation that quoll scat and sighting densities are about an order of magnitude lower below 900m asl, than above it. This estimate is likely to be a maximum value, as discussed later.

8.2.3. Habitat preferences

I described the habitat preferences of Spot-tailed quolls in terms of their altitudinal distribution and the broad vegetation associations of sightings from the north Queensland population. I surveyed eight transects for Quolls scats in November 1994, in order to test hypotheses relevant to the altitudinal and habitat trends of Spot-tailed quolls as discerned from second-hand locality data collated by me. In particular, I tested the hypotheses that: (a) Spot-tailed quolls occur at significantly higher densities above about 900m asl than below that level, and (b) that Spot-tailed quolls occurred at significantly higher densities in closed forest habitats than in adjacent open forest or pastureland habitats.

Transects which examined altitudinal trends included all roads which passed through known quoll habitats, and which spanned a suitable altitudinal range (that is either side of the 900m asl contour). I only used transects which met the above criteria and in which habitat along the transect remained rainforested. Transects testing the altitudinal hypothesis included:

- one altitudinal transect spanning rainforest from 500 m asl to 1300 m asl on the Carbine Tableland and measuring 40km in length,
- two altitudinal transects ranging from 700 m asl up to 1200 m asl and measuring 7.5 and 8 km in length respectively on the Lamb Range and,
- one transect ranging from 70m asl to 700m asl in the South Johnstone unit.

Transects which examined habitat trends included all roads which traversed sections of rainforest known to be inhabited by quolls and other vegetation types along their length. These roads were only used if they remained at a constant altitude (Lamb Range), or if non-rainforest habitats were at higher altitudes than rainforest habitat (Atherton). All else being equal, sections of the road at higher altitudes should pass through higher density populations of quolls (based on the trends observed from sighting records). Transects testing the habitat preference hypothesis included:

- one transect surveyed on the Windsor Uplands in October 1992, October 1993, and November 1994, and which included 5km of rainforest and 5km each of Wet Sclerophyll and dry woodland forests respectively,
- one transect in the Lamb Uplands which was surveyed in November 1994 and which included 3 km of rainforest and 3 km of adjacent sclerophyll habitats, and,
- one transect in the Atherton Uplands which was surveyed in November 1994 and which included 15km of continuous rainforest and 15 km of pasture and rainforest isolates.

8.2.4. Conservation Status

The north Queensland population of *D. maculatus* (conventionally regarded as *D. m. gracilis* but see Chapter 1), was listed as Endangered by the Commonwealth and Queensland Governments in *Environment Protection and Biodiversity Conservation Act (1999)* and *Nature Conservation (Wildlife) Regulation (1994)*, respectively. That assessment was based primarily on the results of this thesis which were summarised in the 1996 Marsupial Action Plan (Maxwell *et al.* 1996). In this Chapter I have re-evaluated the conservation status of the disjunct north Queensland population of *D. maculatus* using RAMAS Red List (Akçakaya and Ferson 1999). This Windows-based software package uses the IUCN Red List Criteria (IUCN 2000)(Appendix 8.1), to assess conservation status incorporating uncertainty into the input data. In this case, I allowed for a five-fold increase in the density of *D. maculatus* in the Wet Tropics compared to that which I measured and estimated in this study, and utilised this range of values for all related data used in the computation of conservation status. The input data utilised in this assessment were conservative, and where there was doubt, I used the most conservative option or range of input values.

8.3. Results

Excluding my own observations, I recorded a total of 152 separate sightings of live and/or dead Spot-tailed quolls from north Queensland (Map 8.1)(Appendix 8.2). Sighting records span the period from 1888 to 2001. Of these sightings 150 originated in the Wet Tropics Area, the remaining two originated in the Eungella region (one confirmed sighting) and the Basalt Wall Area (one sighting). Except where specifically stated, I only discuss those sightings from the Wet Tropics Area for the rest of this Chapter.

The number of records from each of the sources used in this study are:

Source	No. of records
Lay public	40
Museum specimens	33

Naturalists and biologists	73
Published records	6
TOTAL	**152**

Eighty-six of these sightings are accompanied by data relevant to the setting in which the sighting was made. Most of those 86 sightings were made on roads (52%), followed by around camps or dwellings (19%), on foot in the forest or during scrub clearing operations (12%), and live-trapped during field studies, excluding my own (3%)(Fig 8.1). These figures illustrate one of the biases inherent in the use of opportunistic sightings records; proportionally more records come from areas with high indices of human activity or presence than from more isolated or inaccessible areas.

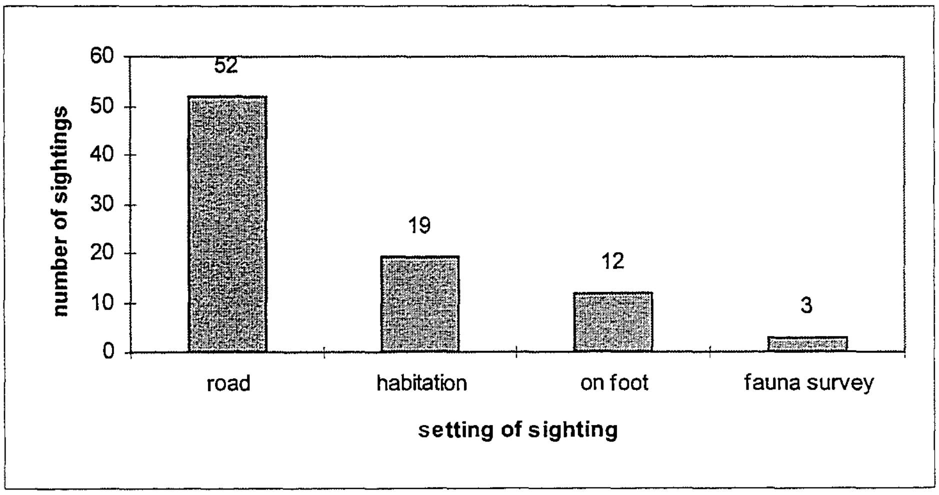
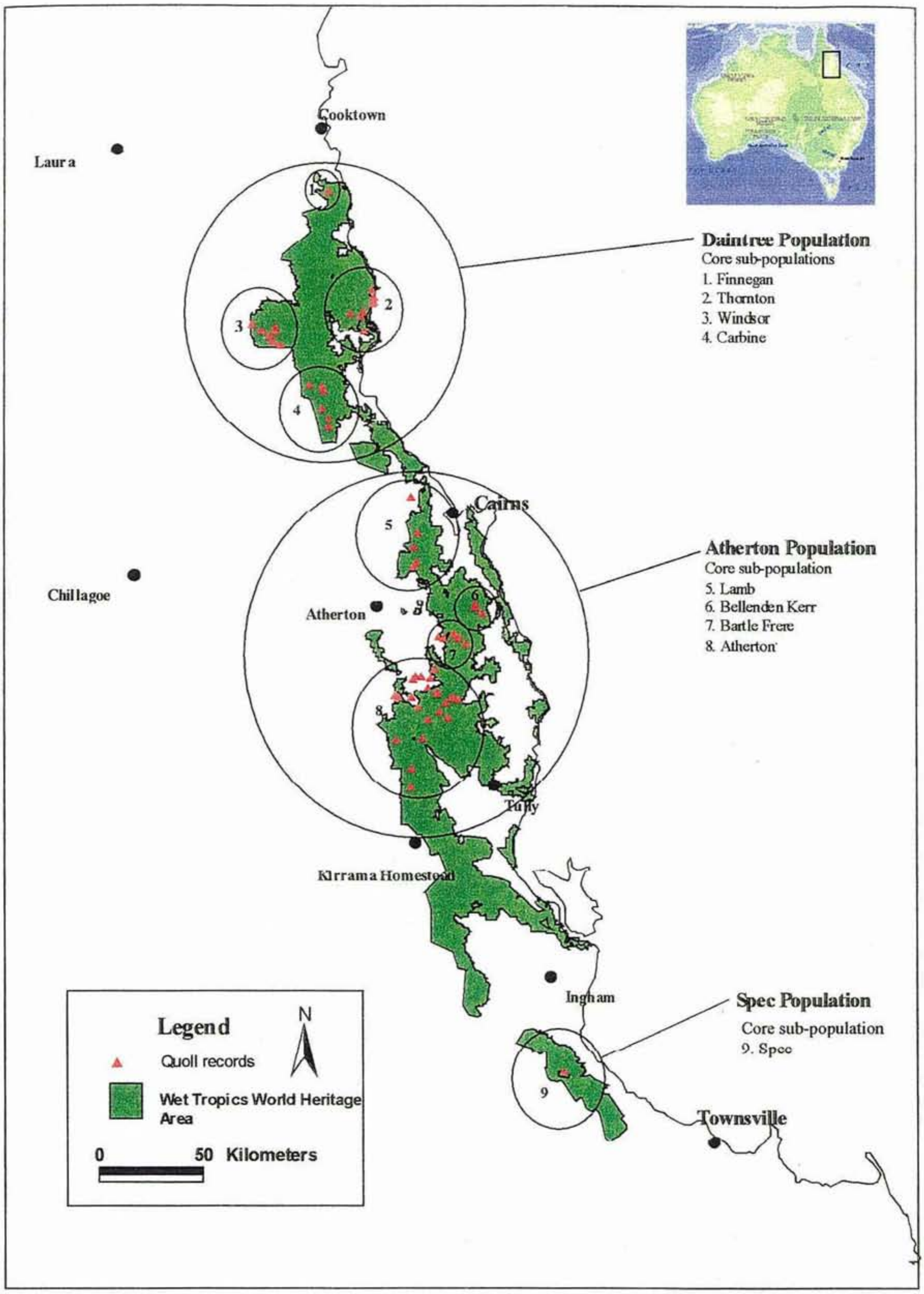


FIG. 8.1. THE NUMBER OF SIGHTINGS OF THE SPOT-TAILED QUOLL FROM NORTH QUEENSLAND MADE IN EACH OF FOUR SETTINGS.



Map 8.1. Populations and core sub-populations of *D. maculatus* in the Wet Tropics Area, based on 152 historical and contemporary sighting records. Numbers within each circle relate to the numbered sub-populations on the map. See Appendix 8.2 for details of these sightings.

More than half (59%) of my records of Spot-tailed quolls in north Queensland come from the 1980s and 1990s (Fig 8.2).

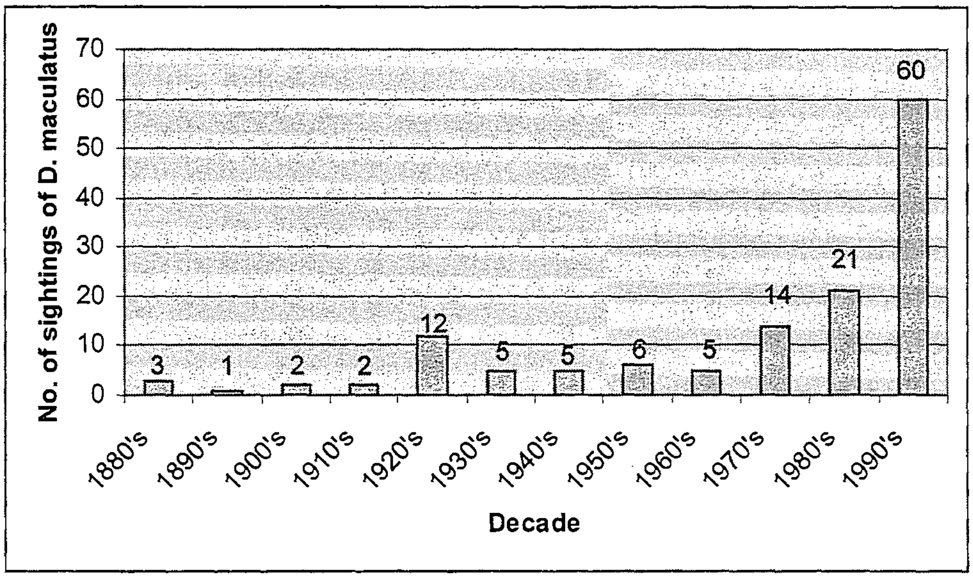


FIG. 8.2. THE DISTRIBUTION OF SIGHTINGS OF D. MACULATUS IN NORTH QUEENSLAND, BY DECADE BASED ON 136 RECORDS WITH ACCURATE DATE DATA.
Note that the current decade is not included in this figure as it has only begun.

Peaks in the monthly distribution of sightings of *D. maculatus* correspond with stages in the life-history of the species in north Queensland namely the mating season and the peak in independent juveniles leaving their mothers (Fig. 8.3)(see Chapter 5). The last half of the year is also a time when females are most nutritionally stressed and probably more likely to take risks (for example, increase in daytime activity and scavenging around human habitations)(c.f. findings of Green and Eberhard (1983) for Eastern Quoll *Dasyurus viverrinus*), and thus be seen by humans.

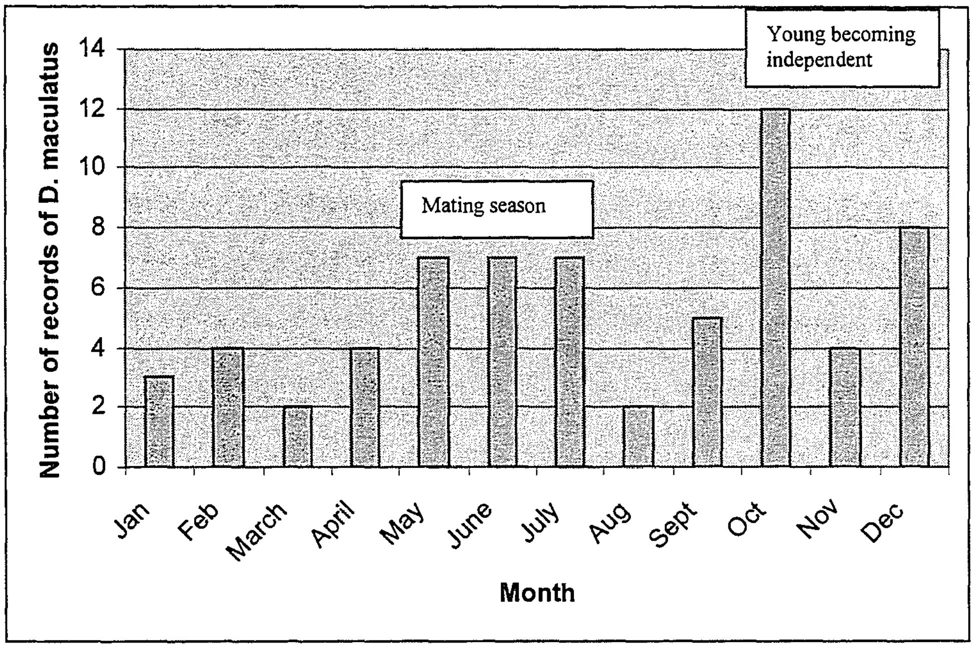


FIG 8.3. THE MONTHLY DISTRIBUTION OF SIGHTINGS OF D. MACULATUS IN NORTH QUEENSLAND BASED ON 63 RECORDS SUPPLIED WITH RELEVANT DATA.

Note that peaks in the number of sightings correspond with two events in the annual life-history of D. maculatus, the winter mating period, and the Spring and early summer independence of juveniles (see Chapter 5).

Scat density

I found a total of 863 Spot-tailed quoll scats during my surveys. Average scat density from 12 transects spanning a total of 230 km in the Wet Tropics Area was 3.75 scats per kilometre. The density from transect to transect ranged from 0 to 34 scats per km (Appendix 8.3).

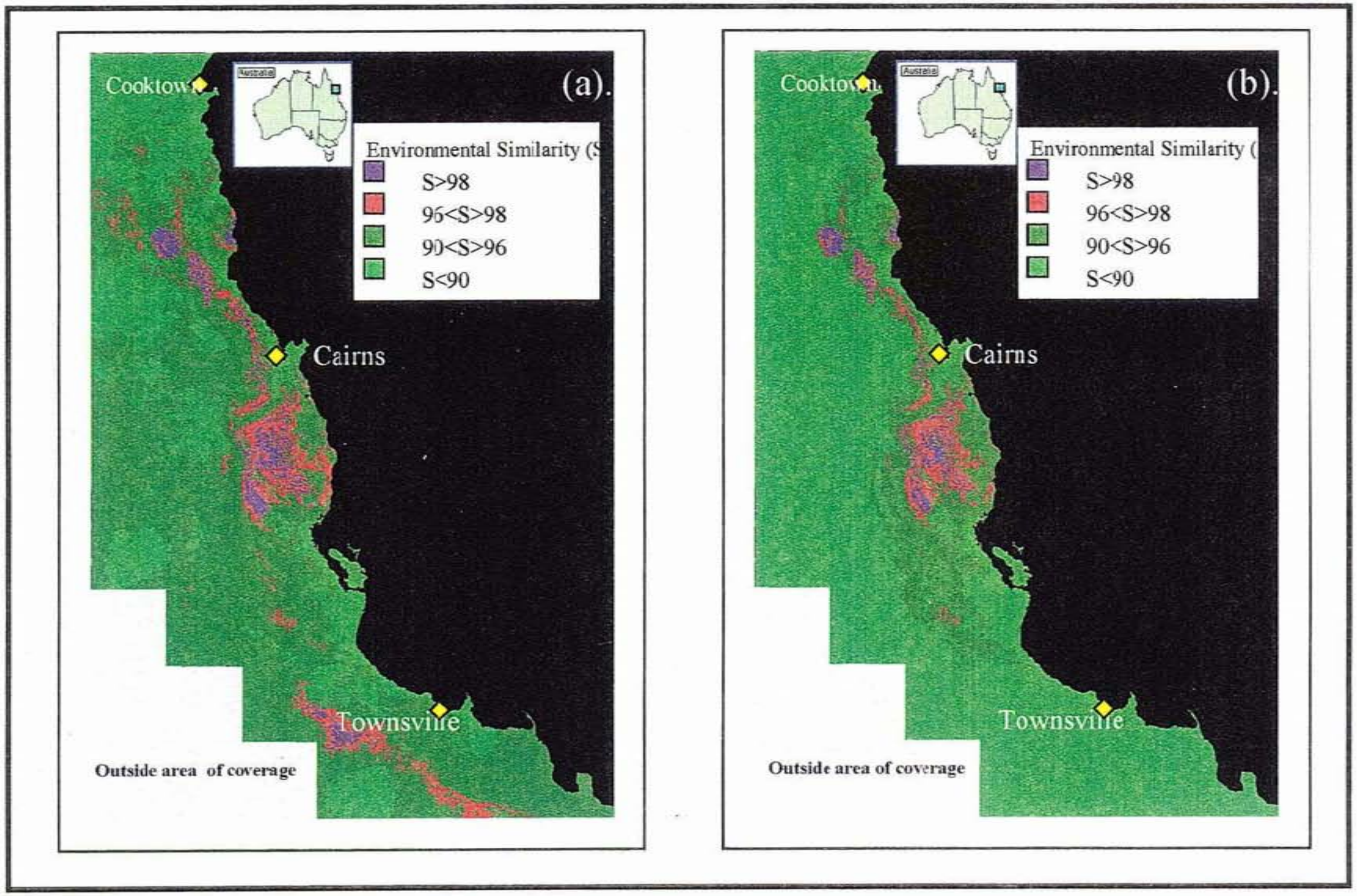
8.3.1. Distribution and Abundance

8.3.1.1. Current distribution in north Queensland

Sighting data and scat surveys suggest that there are eight core Spot-tailed quoll populations in the Wet Tropics Area (Map 8.1). These populations occur in 13 of the 27 bioregional units of the Wet Tropics World Heritage Area. These 13 units span nearly the entire latitudinal range and the entire altitudinal range of the Wet Tropics Area. A further two populations within the Eungella Range and the Great Basalt Wall region respectively, are also noted. The eight populations within the Wet Tropics Area occur within two geographically distinct areas. One consists of four presumably separate populations north of the Black Mountain Corridor and centred on the watersheds of the Daintree, Mitchell and Bloomfield Rivers. The other, south of that corridor, consists of four populations centred on the watersheds of the Barron, Russell, Mulgrave, Tully, and North and South Johnstone Rivers. My scat surveys failed to detect quolls within any bioregional units from which no historical or contemporary sighting records had been obtained.

Predictive modelling based on 84 historical and recent Spot-tailed Quoll sighting locations (Map 8.2), suggests that, in addition to the eight core populations identified from scat and sighting surveys, quoll populations could, historically at least, be expected in the primarily rainforested Mission Beach area, the Black Mountain Corridor, the Halifax Uplands, the Mt Lee Uplands and in sclerophyll forested uplands immediately to the west and south of the Wet Tropics Area.

The **extent of occurrence** is the area of a convex polygon which joins the outer geographical limits of the recorded distribution of a species, and the **area of occupancy** is the area covered by tracing the outline of the species' distribution (IUCN 2000). For Spot-tailed quolls in the Wet Tropics Area, these parameters measure approximately 7129km^2 and 2877km^2 respectively. As is the case with several other members of the Wet Tropics vertebrate biota (Nix and Switzer 1991), the distribution of *D. maculatus* is apparently broken into two meta-populations, separated by the Black Mountain Corridor. The extent of occurrence and the area of occupancy of the northern and southern metapopulations are 3211km^2 and 1641km^2, and 3943km^2 and 1236km^2 respectively.



Map 8.2. The predicted distribution of the northern Spot-tailed Quoll *Dasyurus maculatus* in north Queensland as modelled by DOMAIN (Carpenter *et. al.* 1993): (a) using all records since 1888 and (b), using records since 1950 only.
S refers to the environmental similarity to point locations from which Quolls are recorded.

8.3.1.2 Historical changes in distribution

Historically, the Spot-tailed quoll has been recorded in 13 of the 27 biogeographic units of the Wet Tropics Area (as defined in Chapter 4, Map 4.1), from the Spec Uplands in the south to the Finnegan Uplands in the north. However, my sightings and scat survey data suggest that the distribution of the Spot-tailed quoll has contracted since the 1940s and that it has disappeared from the Spec Uplands and from cleared portions of the Atherton Uplands, and may have disappeared from the Kirrama Uplands. Comparative mapping of predicted Spot-tailed Quoll habitat modelled with DOMAIN from 81 locations since 1945, suggests a major contraction in predicted distribution (Map 8.2). This contraction includes loss of Quolls from the Spec and Halifax Uplands and the ranges to the south and west of Townsville, and from the Lee Uplands. It also suggests the loss of a great amount of marginal habitat from which no Spot-tailed quolls have been recorded, to the west of the Wet Tropics area and in the Townsville Lowlands.

8.3.1.3. Abundance

Scat and sighting densities are highly correlated ($r = .947$, $p < 0.001$), and both suggest that Spot-tailed quoll populations reach their highest densities on the Windsor Uplands, followed in descending order by the Carbine Uplands, the Lamb Uplands, the South Johnstone Uplands and the Koombooloomba Uplands. Populations in all other areas are too sparse to be able to determine an order of abundance.

Based on estimated densities of Quolls of 0.31 individuals of each sex per km^2 in rainforest above 900m asl, and 0.031 individuals of each sex per km^2 in rainforest below 900m asl, I estimate that the approximate numerical size of the Spot-tailed quoll population within the Wet Tropics Area is in the order of a maximum of about 540 individuals (Table 8.1). Based on areas of suitable habitat within each of the three populations; Daintree, Atherton and Mt Spec, the estimated abundance of quolls within each population varies between 19 and 280 individuals (Table 8.1).

Table 8.1. The estimated abundance of Spot-tailed Quolls in each of the three populations and nine core sub-populations from which they are known in the Wet Tropics Area.

Population[1]	Core sub-populations[2]	Rainforest > 900m asl (km^2)	N[2] > 900m asl	Rainforest <900m asl (km^2)	N[3] < 900m asl	Total N
Daintree						
	Mt. Finnegan	2	2	279	17	19
	Thornton	12	7	226	14	21
	Windsor	132	82	124	8	90
	Carbine	224	139	170	11	150
	Total Daintree Population	**370**	**230**	**799**	**50**	**280**
Atherton						
	Lamb[5]	20	12			
	Bellenden Ker	8	5	177	11	16
	Bartle Frere	5	3	103	6	9
	Atherton	90	56	2541	158	214
	Total Atherton population	**123**	**76**	**2821**	**175**	**239**
Mt Spec						
	Spec	**15**	**10**	**152**	**9**	**19**
Total		**508**	**316**	**3772**	**234**	**538**

Note.

1. Quolls occur in three populations, the Daintree, the Atherton and the Spec.
2. These populations consist of several core populations in upland bioregions. Abundance data are presented for each of these.
3. N >900m asl calculated using a density of 0.62 (0.31 each sex)*D. maculatus*/km^2 of rainforest (see text for justification)..

4 N <900m asl calculated using a density of 0.062 *D. maculatus*/km^2 of rainforest (see text for justification).

5 Data on the area of rainforest below 900m asl for the Lamb Range were not available and the Lamb data were pooled with those of the Atherton core sub-population.

8.3.1.4. Correlates of distribution and abundance

Quoll sighting densities and scat densities are highly correlated. Each of these indices of quoll abundance is highly correlated with area of rainforest above 900m asl and the length of rainforest road above 900m asl within each biogeographic area (Table 8.2). Both scat and sighting densities are negatively correlated with extent of forest disturbance as reflected by different human land use histories (Table 8.3). All other correlations are non-significant (Table 8.2).

	Total area of rainforest	**Area rainforest > 900m asl**	**Road density**	**Length of road**	**Road density > 900m asl**	**Length road > 900m asl**	**Quoll sighting density**	**Quoll scat density**
Total area of rainforest		R= 0.457 P= 0.056 N= 18	R= 0.342 P= 0.212 N= 15	R= 0.296 P= 0.284 N= 15	R= 0.15 P= 0.565 N= 17	R= 0.44 P= 0.077 N= 18	R= 246 P= 0.325 N= 18	R= 0.307 P= 0.307 N= 13
Area rainforest > 900m asl			R= 0.229 P= 0.412 N= 15	R= 0.076 P= 0.787 N= 15	R= 0.325 P= 0.0203 N= 17	R= 0.955 P= 0.000 N= 17	R= 0.711 P= 0.001** N= 18	R= 0.768 P= 0.002** N= 13
Road density				R= 0.711 P= 0.003 N= 15	R= 0.035 P= 0.902 N= 15	R= 0.168 P= 0.549 N= 15	R= 0.112 P= 0.69 N= 15	R= 0.235 P= 0.487 N= 11
Length of road					R= 0.201 P= 0.473 N= 15	R= 0.132 P= 0.64 N= 15	R= 0.109 P= 0.7 N= 15	R= 0.078 P= 0.82 N= 11
Road density > 900m asl						R= 0.529 P= 0.029 N= 17	R= 0.256 P= 0.32 N= 17	R= 0.224 P= 0.484 N= 12
Length road > 900m asl							R= 0.74 P= 0.001** N= 17	R= 0.855 P= 0.0001** N= 12
Quoll sighting density								R= 0.947 P= 0.0001** N= 13
Quoll scat density								

Table 8.2. Correlates of Spot-tailed Quoll density within each bioregional unit of the Wet Tropics World Heritage Area. Significant correlations flagged with **.

Table 8.3. Spearman Rank Correlations of indices of quoll density and of landuse patterns and disturbance, in each of the biogeographic areas of the Wet Tropics World Heritage Area.

Significant correlations are highlighted.

	Toad infiltration	Landuse	Quoll density (ranked)	Scat density (ranked)
Toad infiltration		**R=.558** **P=.020** **N=17**	**R=-.504** **P=.039** **N=17**	**R=-.861** **P=.000** **N=13**
Landuse			R=-.268 P=.282 N=18	**R=-.571** **P=.042** **N=13**
Quoll density (ranked)				**R=.843** **P=.000** **N=13**
Scat density (ranked)				

8.3.2. Habitat Preferences

8.3.2.1. Altitude

Ninety-five of the 152 sighting records compiled by me from within the Wet Tropics Area were accompanied by data precise enough to allow their broad habitat type to be determined. Sighting records have come from altitudes ranging from sea-level in the Thornton Lowlands to 1600m asl on the summit of Mt. Bartle Frere. However sightings and specimens are significantly skewed towards higher altitudinal zones. Fifty-five (55%) of these records came from altitudes greater than 900m asl (Table 8.4). The number of Spot-tailed quoll sightings from each altitudinal band is significantly different (X^2=37.56, d.f=5, p<0.0001) (Table 8.4). Standardised Residual values from this analysis show this difference to result from fewer than expected Quoll records from the lowlands, and more than expected from the uplands. The distribution of scats along altitudinal transects corroborates this trend of increasing quoll abundance at increasing altitude. Significantly higher numbers of scats occur above 900m asl than below that altitude for all transects where that altitudinal range was traversed (Table 8.5). Both sighting and scat densities suggested that quoll densities were an order of magnitude lower below approximately 700-900 m asl, depending on the latitude of the transect, and that if present as resident populations below 300m asl, the species was extremely localised (Table 8.4). Two of the ten identified populations of *D. maculatus* occur in detectable numbers at much lower altitudes (and lower densities) than elsewhere where populations are known, these being in the Thornton Lowlands and the South Johnstone Uplands (Table 8.4, Map 8.1).

Table 8.4. Spot-tailed quoll sighting and scat densities and proportion of total rainforest area in the three conventional altitudinal zones of Winter *et al.* 1984.

	Altitudinal zone		
	0-299m asl	**300-899m asl**	**900 +m asl**
% rainforest area	**32**	**58**	**10**
% of quoll records	**10.5**	**34.7**	**54.7**
area of rainforest (ha)	**288 492**	**514 724**	**90 532**
number of quoll sightings	**7**	**43**	**55**

Table 8.5. Density of scats/km collected from above and below 900m asl on altitudinal transects conducted during this study.

	Transect	
Altitudinal Zone	Lewis	Lamb
901+ m asl	12.9	18.4
301 - 900m asl	0.01	0.5
< 300m asl	n/a	n/a

8.3.2.2. Vegetation

Ninety percent of the eighty-six records of *D. maculatus* which I could assign to general habitats were from unfragmented rainforest. The remainder came from wet sclerophyll forest (5 records), fragmented forest surrounded by pastures and from pastures themselves (2 records). The distribution of scats from habitat transects support the hypothesis that quolls are most abundant in large tracts of closed forest (Table 8.6).

Table 8.6. Results of scat transects within rainforest and adjacent sclerophyll and pasture habitats.

Half of each transect lies within rainforest (rf) and half lies within the adjacent sclerophyll/pasture (scl/pasture) habitat.

Bioregional unit	**Transect length(km)**	**No scats**	
		Rainforest	Sclerophyll forest/pasture
Lamb Upland	6	21	0
South Johnstone	30	55	0
Windsor Upland	10	32	0
Total	**46**	**108**	**0**

8.3.3. Conservation Status

RAMAS Red List confirmed the conservation status of the north Queensland population of *D. maculatus* as Endangered based on IUCN Red List Criterion C:

- "population estimated to number less than 2500 mature individuals, and; a continuing decline projected in numbers of mature individuals and population structure because populations are severely fragmented (i.e. no subpopulation estimated to contain more than 250 mature individuals). " (IUCN 2000).

8.4. Discussion

Three regions within north Queensland historically supported populations of the Spot-tailed quoll. These included; the Wet Tropics Area, the Eungella rainforests and the Great Basalt Wall area. The Wet Tropics Area contains the greatest extent of habitat and accordingly, the highest numbers of Spot-tailed quolls. It is uncertain whether the Quoll populations of Eungella and the Great Basalt Wall are extant because of a lack of research on these populations. Except where explicitly stated the following discussion refers to the Wet Tropics Area only.

When considering the distributional data presented here, it is necessary to bear in mind the limitations of the survey methods, including variable human accessibility of different bioregional units, differences in suitability of units to scat surveys and probable under-representation of low density populations of quolls. Thus, although general trends such as relative densities between bioregional units, broad vegetation types and altitudinal zones reflect real patterns, failure to locate populations in any area may reflect very low population densities rather than the absence of the species from that particular bioregional unit. Because of the capacity of individual Spot-tailed Quoll's to range widely (Chapter 7), it is difficult to define the habitat relationships of the species any more explicitly than I have below.

8.4.1. Distribution

I found that two extant populations of Spot-tailed quolls occur within the Wet Tropics Area and consist of four and five core sub-populations each. These two populations occur on either side of the Black Mountain Corridor (Map 8.1). In the southern, Atherton population, core sub-populations occur in a linear north-south strip along the watershed of the eastern escarpment. As such, I predict that the survival rate of dispersing animals in this area is relatively low compared to dispersers within the more circularly distributed Daintree population, which as a consequence, have a greater chance of dispersing into friendly habitat.

I have failed to find any Quoll records from some units of the Wet Tropics Area. It is possible that this is an artefact of the relative inaccessibility of some of these areas. Thus Quolls may exist in: the Halifax Uplands, Mt Lee Uplands and Kirrama Uplands. I consider that Quolls are unlikely to occur in other units from which no records have been forthcoming. These units are either regularly visited by land managers and biologists or are surrounded by areas of high human activity. These units include: the Malbon Thompson Uplands, Cairns Lowlands, Cooktown Lowlands and the Bloomfield Lowlands.

8.4.1.2 Historical changes in distribution and abundance

The recent historical pattern of distribution of Spot-tailed quolls places them at the northern and southernmost units of the Wet Tropics Area (Map 8.1), however intervening units and habitats appear to lack any Quoll populations today. This suggests that the species has undergone some habitat contraction. Whether this occurred as a result of climate change over the past several thousand or hundred years (e.g. see Nix and Switzer 1991), or following European colonisation of the Wet Tropics Area in the mid-late 1800s is unknown.

It is not inconceivable that Spot-tailed Quolls ranged throughout the altitudinal and habitat range of the Wet Tropics region at the time of European settlement, especially given recent records from the Thornton Lowlands and Basalt Wall, and the opportunistic feeding (Chapter 6) and high mobility (Chapter 7) which characterises the species. All else being equal, hypothetical populations in lower altitude rainforests and open forests would be relatively more prone to extinction by human influences. The greater extinction probability of these populations would be a natural result of: (i) their presumably smaller population size as a result of lower density and perhaps more localised distribution in these more marginal and heterogeneous habitats (Caughley and Gunn 1996), and, (ii) because lower altitude and/or open habitats are generally closer to humans and their secondary mortality agents, including habitat clearance, logging, cane toads, grazing, introduced Carnivores, human settlement and infrastructure. Apart from the effects of small population size, these populations would also be more susceptible to extinction from environmental causes because of greater climatic seasonality of lower altitude and western open forests. It is possible that there has been a historical contraction of quoll populations out of these habitats, presumably sometime in the late 1800s or early 1900s, without their ever having been recorded there.

8.4.1.2.1 Declines

My distributional data suggest that the Spot-tailed Quoll has disappeared from some areas in which it formerly occurred in the Wet Tropics Area, namely the Mt Spec area and the 25% of the Atherton Uplands which have been cleared (Winter *et al.* 1984). The status of the species on the Finnegan and Kirrama Uplands is unknown with the last specimen being recorded in the 1960s and 1880's respectively. No records of any type have been collected of the species from the following units: Mt Elliot Uplands, Mt Halifax Uplands, Mt Lee Uplands, Malbon Thompson Uplands or the Black Mountain Corridor, nor from any of the lowland units apart from the Thornton Lowlands (Map 8.1). Because of the incomplete nature of the historical biological record of north Queensland, it is impossible to say whether the Spot-tailed Quoll ever occurred in these bioregions, or whether it has become extinct there without being recorded.

Spec Uplands

Despite a history of permanent human settlement, a permanent Parks and Wildlife Service office, high tourist activity and high visitation by biologists from James Cook

University, I was unable to collect any records of the Spot-tailed Quoll since the 1940s. The last Spot-tailed quoll record from the Spec Uplands was of an animal which visited a road workers' camp near the vicinity of the present Paluma Dam in 1945. Two other records from before that time are of Spot-tailed Quolls which were killed at poultry yards; one in the township of Paluma itself (see Title page of Chapter 10 for a photograph of this animal), and the other close to the intersection of the Taravale and Hidden Valley Roads (Lat Long). I failed to gather any contemporary signs of the species from my two scat transects or from my canvassing of locals or forestry workers in the area. It thus seems fairly certain that the species is extinct in the Spec Uplands. Extrapolation of density data from the Windsor Tableland suggests that the population in the Spec Uplands would not have numbered more that about 16 individuals of each sex. Thus, despite that fact that little rainforest clearing has been conducted there, the mortality caused by irate chicken owners, the construction of a dam in the 1950's, and the occasional road, dog or cane toad kill, was apparently enough to cause the extinction of this population.

Atherton Tablelands

Short (1988) and museum records suggest that the Spot-tailed quoll existed throughout the rainforests of the Atherton and Evelyn Tablelands before they were cleared around the late 1800s and early 1900s. Apart from occasional sightings close to tracts of rainforest, I have not found any contemporary sightings of Spot-tailed quolls from the cleared portions of the Atherton Tableland. Thus it is likely that the species has become extinct over most of that area. Forestry employees who worked in the Maalan district when it was first opened up to large scale logging and settlement in the 1950s, state that Spot-tailed quolls were quite common in the area at that time (pers. comm. Gordon Baker 1992, pers. comm. Barry Thurling 17/7/01). Likewise, one of Frawley's (1987) interviewees, who had moved to the Maalan area in the 1950s when it was first opened up to settlement, states that initially the "...place was infested with those Spotted native cats...(P. 14)". Today quolls are rare in this area, (as exemplified by Laurance's (1989)) failure to locate the species despite over 2000 trapnights of live-trapping targeting this species in the late 1980s). Similarly, my surveys of 15 km of road in that area failed to locate any sign of the species although scats were found along 15 km of road in adjacent forested areas in the South Johnstone Uplands which is of lower altitude. Occasional records of individuals in the rainforest edge habitats of the southern and eastern Atherton Uplands represent transient animals from deep within the remaining forested areas on the slopes of the Tablelands.

Cardwell Lowlands/Kirrama Uplands

A similar syndrome of very low population size and high sensitivity to increased mortality may have occurred in the Kirrama uplands/Cardwell lowlands regions where *D. maculatus* has not been detected since the 1800s. Much of the Cardwell Range is inaccessible and so the species may continue to exist there. James Cook University Wildlife Ecology field trips have been conducted to Kirrama State Forest every year since the late 1960s. The area has also been the site of intensive, if localised, collecting by the Queensland Museum and the Queensland Parks and Wildlife Service, suggesting that if populations do still occur there, they are very localised and sparse.

Decline from non-rainforest habitats throughout north-eastern Queensland?

Predictive habitat modelling using DOMAIN (Carpenter *et al.* 1993), suggests that the decline in Spot-tailed Quoll distribution in north Queensland may be much more severe than that suggested by superficial consideration of sighting localities and dates. I produced two DOMAIN generated maps of Spot-tailed Quoll distribution, one using all records (Map 8.2a) and another using only those records collected since the 1950 (Map 8.2b), when the species apparently declined in the Spec Uplands and human land use within the Wet Tropics intensified (e.g. Frawley 1987, Winter *et al.* 1984). These images suggest that, as well as a decline from some rainforest areas, a significant contraction of distribution may also have occurred eastward out of more open habitats to the west of the Wet Tropics World Heritage Area (WTWHA). The extent of occupation by *D. maculatus* of these sclerophyll habitats to the west of the WTWHA is unknown. Both Spot-tailed and Northern Quolls occupied the wet sclerophyll forest to the west of Paluma in the 1930s, although both species appear to be extinct there now (based on this study and discussions with long-time local residents). It is therefore likely that the species once inhabited or at least ranged through habitats other than rainforest in the wet tropics. Another indication that the species recently inhabited the high altitude dry vegetation communities west of the Wet Tropics, is the recent and perhaps continuing presence of the species in the Great Basalt Wall area as noted above. This vine thicket outlier is separated by over 100km from the rest of the known distribution of *D. maculatus* in north Queensland. Given the extinction proneness of populations of *D. maculatus* (Chapter 5), it seems likely that this population was established or has been maintained through a connection with the Wet Tropics populations within the very recent past. If this is the case, then the decline in the species' distribution is much more extensive than merely a contraction within the Wet Tropics Area, instead it represents the disappearance of the species from the high altitude open forests of north Queensland.

8.4.1.2.2. Increases in distribution and/or abundance

Based on the skewness of the distribution of sighting records towards the later decades of the twentieth century (Fig. 8.2), it is tempting to suggest that quolls have become more common over the past two decades and especially within the 1990s. An hypothetical tendency for interviewees to remember more recent encounters and forget older encounters may also explain this temporal pattern as would the fact that knowledge invariably gets lost as people with relevant information die or move from an area. Because of the inaccessibility of so much potential Spot-tailed quoll habitat, and because there has been no systematic survey of the species in north Queensland, no comment can be made as to population fluctuations in areas remote from human disturbance.

8.4.2. Abundance

As discussed above, quoll density is higher above about 900m asl than below that altitude. Abundance also varies between units, as measured by scat and sighting densities, which provide consistent information on the patterns of density of Spot-tailed quoll populations within the Wet Tropics Area. The species is more abundant north of the Black Mountain Corridor (the Windsor, Carbine and possibly the Thornton uplands) than in the bioregional units south of that corridor. The spate of records in the Thornton Lowlands in 1992, also suggest that quoll populations may occur in lowland habitat there, albeit at low densities. I attribute the trend to higher density and abundance of quolls north of the Black Mountain Corridor to two factors. Firstly, the Windsor and Carbine units at least, contain close to twice the area of highland (>900m asl) forest than any unit south of the Black Mountain Corridor (see Table 8.1). Secondly, the northern area has been relatively remote from human activities compared to the area of the southern meta-population (for example see Winter *et al.* 1984). Although the status of the Basalt Wall and the Mackay area populations is uncertain, Spot-tailed Quolls must be at best, very sparsely distributed in these regions.

In calculating the absolute abundances of Spot-tailed quolls within the Wet Tropics Area, I made the following assumptions: (1) that there is no overlap between home ranges within sexes (a conservative assumption see Chapter 7), (2) that all rainforest habitat within appropriate altitudinal zones is utilised, (3) that the density of quolls above 900m asl is as high elsewhere as it is on the Mt Windsor Tableland, and, (4) that below 900 asl altitude, quolls occur at densities an order of magnitude lower than above that altitude. Radio-tracking of a small sample of four female Quolls with adjacent home ranges demonstrated that in accordance with assumption (1), there was relatively little overlap in home range between individuals (Chapter 7). Such data are not available for males. It is unlikely that all rainforest within each altitudinal zone is used by Quolls. It is clear from the data presented in this Chapter, that Spot-tailed Quolls are absent from much of the Wet Tropics Area, including most of the Atherton Tableland. Given the lack of records of Spot-tailed Quolls, it also seems unlikely that they occur in several of the bioregions of the Wet Tropics Area, although whether this is due to historical or ecological causes is unknown. Data from scat and sighting records (Appendix 8.3) indicate that the Windsor Tableland supports a higher density of Spot-tailed Quolls than any other of the Wet Tropical bioregions. This is likely to result in exaggerated estimates of Quoll numbers in the Wet Tropics. Scat and sighting data also concur that Spot-tailed Quoll density is an order of magnitude lower below approximately 900m asl than above that level (Tables 8.4 and 8.5). As such my absolute abundance estimates of approximately 540 individual Spot-tailed Quolls in the Wet Tropics probably represent maximum values. Despite the approximate nature of these figures, they demonstrate that the Spot-tailed Quoll occurs in relatively very low numbers in the Wet Tropics.

8.4.3. Patterns of distribution and abundance

The positive relationships between both quoll sighting and scat density (Table 8.2), and area of rainforest above 900m asl within each bioregional unit (Table 8.2), further illustrate the relationship between this species and highland rainforest habitats. This relationship may be so strong as to explain the absence of quolls from bioregional units which lack substantial areas above 900m asl. Whether this distribution reflects pre-European distribution patterns, or whether it is an artefact of the presumed greater resilience of upland populations is unknown.

Both indices of quoll density (sightings and scats) correlate negatively with two related factors: the distribution of cane toads and human land use within each unit. Correlation cannot prove causation, however, Quolls are clearly less often encountered in more greatly modified environments. As quolls have been shown to disappear from intensively modified areas in southern Australia in which toads are not present (Lunney and Leary 1988, Bennett 1990) and are suspected of being susceptible to cane toad poisoning (Burnett 1997), arguments exist for the negative impact of both effects. Quolls have apparently disappeared from areas of the Atherton and Evelyn Tablelands from which they were known, prior to the invasion of those areas by cane toads, but after agricultural development and human settlement. Toads have been shown to be toxic to Western quolls (Covacevich and Archer 1975). Northern quoll populations have been shown to have declined in areas of north Queensland immediately following the invasion of those areas by cane toads (Burnett 1997), and amphibians have been found in the stomach contents of Spot-tailed quolls in Tasmania (Green and Scarborough 1990). I suggest that both the presence of Cane Toads and habitat loss through human activities express a negative relationship with quoll distribution and place further limitations upon what constitutes suitable habitat for the species within the already stringent habitat requirements imposed by its life-history strategy (Chapter 5).

8.4.4. Habitat preferences

Sighting and scat distributions suggest that in the Wet Tropics Area of north Queensland, the preferred habitat of the Spot-tailed quoll is upland rainforest above 900 m asl. The only area in which a regularly locatable population exists below this altitude is the South Johnstone area, which is unique in several ways, as discussed below. Occasional sighting records suggest that populations occur at very low densities at mid-and low-altitudes at other sites. However, these populations are so sparse as to be undetectable by scat analyses and are rarely encountered by either the wider community or biologists.

This distribution pattern of Spot-tailed quolls may be exaggerated by the presumed greater extinction rates of low altitude populations, (because of greater human accessibility and lower prey diversity in low altitudes). None-the-less the stronghold of the species in north Queensland appears always to have been the high mountaintops. This view is supported by the experiences of Lumholtz (1888) and Ramsay (1888), both of whom secured their single specimens from mountaintops in the area, despite considerable time spent in lower altitudes. A spate of sightings from the Thornton lowlands in 1992, which are described below, constitute the only confirmed records of Spot-tailed Quolls in the lowlands.

The altitudinal distribution pattern observed in the Spot-tailed quoll in north Queensland is similar to that observed in some other species with disjunct distributions extending into tropical Australia from temperate and subtropical regions. In these species, their northern populations are more restricted altitudinally than their southern congeners. Examples include the White-footed dunnart, *Sminthopsis leucopus* (Van Dyck 1984), and the Rough-scaled snake, *Tropidechis carinatus* (Queensland Museum unpublished data). All these species are much more common in, if not restricted to altitudes greater than 800m asl in north Queensland, but occur from sea level to the mountaintops in southern Australia. Similarly, these species and the Spot-tailed quoll show similar patterns of habitat specialisation in the Wet Tropics Area compared to subtropical and temperate parts of their ranges. In southern Australia for example, all these species are found in a wide range of habitats including rainforest, open forest types and heath (see these species accounts in Cogger 2000, Wilson and Knowles 1988, and Strahan 1995). In contrast, in the Wet Tropics Area they are restricted to rainforest and its immediate environs. Similar distribution patterns, in which species which are widespread at high latitudes occur only as high altitude relict populations in lower latitudes, are also known from Australian butterflies, amphibians and birds, and in ecosystems in North America (Graham and Graham 1994) and in Europe (Cox and Moore 1985).

Van Dyck (1984) has attributed this pattern of altitudinal and habitat restriction of dasyurids in north Queensland to the low winter rainfall and high evaporation rates in this region. He contends that this creates a bottleneck in resources during the Winter months. Nix and Switzer (1991), show that higher altitudes in the Wet Tropics experience wetter and cooler climates throughout the year than do lower altitude areas and so probably experience less of an annual bottleneck in resources.

Given that the Queensland National Parks and Wildlife Service kept two Spot-tailed Quolls successfully in natural temperature conditions for over 12 months in Townsville (a lowland city at the southern end of the Wet Tropics Area), in 1991, it seems unlikely that environmental factors such as temperature limit the distribution of the Spot-tailed Quoll directly. Rather, it is probably the effect of climate on prey species abundance and diversity that limits Quoll distribution. For example, Kanowski *et al.* (2001) found that the abundance and diversity of rainforest possums, which are very important prey of the Spot-tailed Quoll (Chapter 6), is an order of magnitude higher above approximately 800m asl than below that level.

The altitudinal restriction of the Spot-tailed Quoll may also be exaggerated by the presumably higher extinction probability of lower altitude populations, which because of lower prey density, would be expected to occur at lower densities than high altitude populations. In Chapter 5, I have shown that because of its life history strategy, *D. maculatus* is particularly susceptible to population extinction through negative recruitment over as few as three years. Populations, which occur at lower densities also, have to contend with higher chances of extinction via stochastic demographic and environmental factors. The hostility of low altitudes may also be exacerbated by the presence of Cane Toads and presumably higher anthropogenic impacts.

The one area at which I was able to detect a lower altitude population of the Spot-tailed Quoll is the South Johnstone unit which occurs on the south-eastern ramparts of the Atherton Uplands bioregion. This population occurs on basaltic soils at altitudes of between 800 and 500 m asl. This area receives relatively high rainfall both annual and in the mean driest quarter (Nix and Switzer 1991). The high amounts of solar radiation per unit area, due to its tableland like landscape also probably increase the productivity of this area compared to the steeper slopes which characterize most of the remaining eastern fall of the Wet Tropics highlands. As a result, this area maybe more productive than other areas of similar altitude in the Wet Tropics Area which typically exhibit one or more of the following limiting factors: very steep grades, granitic soils and/or lower annual and mean driest quarter rainfall.

The restriction of the Spot-tailed Quoll to rainforest habitats was pronounced in all three of my habitat transects. All sightings that I collated from non-rainforest habitats were within 1.5km of the rainforest edge and were apparently one-off sightings of large male Quolls, ranging outside of their normal areas. This apparent restriction of quolls to rainforest is probably tied to the fact that this habitat covers most of the high altitude (and thus climatically equable) areas of the Wet Tropics, and contains the greatest abundance and diversity of mammalian prey. High altitude open forests are fairly scarce and so may be unrepresented in terms of quoll sightings. Open forest may also represent suboptimal habitat in which carrying capacity is low because of relatively low prey densities, low prey catchability (quolls are not particularly adept at climbing smooth-barked Eucalypts (pers. obs.), and perhaps because of higher Quoll mortalities in this habitat, including increased risk of predation and increased encounters with poisonous Cane Toads. I consider that Quoll populations are unlikely to become established in pasture habitats within their climatic range because of the low carrying capacity of that habitat, and perhaps more importantly, because of the high mortality rates including, predation by raptors and dogs, roadkills and conflict with landowners over poultry. It is feasible that some of the sightings of quolls from within non-rainforest habitats are representatives of resident populations. However, it seems less likely that sightings in agricultural landscapes are of residents given the paucity of records from this habitat of high human activity.

8.5. Summary

- The Spot-tailed Quoll is historically recorded from throughout the latitudinal and altitudinal range of the Wet Tropics World Heritage Area although it is by far most abundant in high altitude rainforests above 900m asl.

- The species demographic requirement for low extrinsic mortality (Chapter 5) and its dietary need for abundant small and medium terrestrial and arboreal mammals (Chapter 6) probably influence its restriction to upland rainforests which meet these requirements.

- The naturally limited distribution of upland rainforest, and the Quoll's low population density (Chapter 8), indicate that it occurs in low numbers and as such meets the IUCN Red List Criteria for Endangered status.

- Within north Queensland, Spot-tailed Quolls occur within three populations; (1) the Wet Tropics population; (2) the Great Basalt Wall population, and; (3) the Eungella population. The latter two populations are known from a single record each and their conservation status is unknown.

- Within the Wet Tropics area, Spot-tailed Quolls historically occurred as three sub-populations centred respectively on; (1) the Daintree Uplands; (2) the Atherton Uplands, and; (3) the Spec Uplands.

- A lack of recent records suggests that Spot-tailed Quolls are extinct in the Mt Spec Uplands (Paluma area), and from the 80 000 ha of the Atherton Tablelands in which it once occurred.

- Two records of Spot-tailed Quolls from outside of the rainforested Wet Tropics: one from the Eungella area and another from the Great Basalt Wall are also associated with vine-forests, and require further investigation.

Chapter 9.

An Exploration of the Potential Immediate and Long-term Impacts of Eutherian Carnivores on the Spot-tailed Quoll

In this Chapter I investigate the relative, potential impacts of direct predation and competition by Eutherian carnivores upon the conservation status of the Spot-tailed quoll, *D. maculatus*. I compare aspects of the ecology, diet and habitat preferences of the three Australian Eutherian predators with that of *D. maculatus* using a rank scoring approach.

I also use population viability analysis to compare the persistence of populations of *D. maculatus* and each of the Eutherian carnivores under conditions of increased mortality. I suggest that the Eutherian carnivores do exert a predatory and a competitive impact on *D. maculatus*, and that wild marsupial carnivore populations in non-rainforest habitats are likely to be replaced by the Eutherian carnivores.

Chapter 9. An Exploration of the Potential Immediate and Long-term Impacts of Eutherian Carnivores on the Spot-tailed Quoll

9.1. Introduction

Predation by eutherian carnivores has been implicated in the decline of some Australian mammals. For example, cats and foxes have been implicated in the decline of at least nine now extinct and several endangered members of the Macropodidae, Peramelidae and Muridae (Kinnear *et al.* 1988, Burbidge 1995, Mackenzie *et al.* 1995, also see Table 3.4 in Caughley and Gunn 1996). However, predator-prey theory (e.g, Caughley and Sinclair 1994) suggests that predators are rarely solely to blame for the demise of species. Their influence is usually only of serious concern when prey populations are already under stress or at low numbers because of other factors such as habitat loss or degradation (Newsome *et al.* 1989, Newsome 1990). Populations of the Spot-tailed quoll, *Dasyurus maculatus* are at critically low numbers (Chapter 8), and are particularly susceptible to extinction through elevated extrinsic mortality rates (Chapter 5). Predation and competition by eutherian carnivores may be a significant contributing factor to this extrinsic mortality.

All three Eutherian carnivores (cats *Felis catus*, foxes *Vulpes vulpes*, and dogs *Canis familiaris*/*C. lupus dingo*), prey predominantly upon mammals although they also consume various amounts of plant, invertebrate, reptile and bird material (see Corbett 1995, Saunders *et al.* 1995, Dickman 1996). They are therefore potentially capable of preying upon *D. maculatus*.

As well as preying directly upon *D. maculatus*, these Eutherian carnivores may also exert a competitive effect on this species. Competition with Dingoes has been identified as a possible cause of: (1) the extinction of the Thylacine *Thylacinus cynocephalus* on mainland Australia (e.g. Archer 1974a, Guiler 1985, Dixon 1989), and (2) the decline of *D. maculatus* in the southern mainland (e.g. Mansergh 1984, Menkhorst 1995).

The Families Canidae and Felidae occur naturally on every continent except Australia and Antarctica. Members of both families, including Dingoes/Domestic Dogs, Red Foxes, and Domestic Cats were introduced to Australia where they have established feral populations (see Chapter 2 for more detail).

No study has explicitly examined the Australia-wide patterns of distribution of the eutherian carnivores listed above, however general syntheses are provided in Strahan (1995) and by other authors (Potter 1991, Wilson *et al.* 1992, Corbett 1995, Saunders *et al.* 1995). These studies indicate that Dogs and Cats are distributed throughout the entire Australian continent (although Dingoes are absent from Tasmania), and Red Foxes are distributed throughout the mainland with the exception of the far northern areas. Although feral domestic and free-roaming dogs are probably widely distributed throughout the continent, patterns in the distribution of Dingoes-Domestic Dog hybrids suggest that feral dogs occur in higher abundances in more densely settled regions than in the more remote parts of the continent (Corbett 1995).

Catling and Burt (1995) documented the pattern of Red Fox abundance in eastern New South Wales and found that in dense forest/agricultural landscape mosaics, foxes occur in highest abundances in agricultural landscapes and they rarely penetrate beyond 1km into forest from open habitats. Catling *et al.* (2000) modelled the distribution of the Dingo, Fox and feral Cat in the forests of north-eastern New South Wales and found the following patterns: Dingoes showed a preference for drier forests with some shrub cover but little ground cover; Foxes showed a preference for structurally simple drier forests; Cats showed a preference for moist habitats with high structural complexity, especially of the shrub layer.

The only published synthesis of Feral Cat distribution and habitat preferences in Queensland (Gordon 1991), concluded that they appeared to be absent from large tracts of closed forest, although they were present in smaller tracts. In a targeted hair-tubing study along a powerline easement through eucalypt forest in New South Wales, Goldingay and Whelan (1997) found no evidence of Feral Cats beyond 200m into the forest from the powerline easement. If cats do occur in extensive tracts of closed forest in north Queensland, they may be extremely difficult to detect because of their relatively small size and secretive habits.

The fossil record of South America and Australia, and recent historical patterns of species extinctions and decline in Australia, suggest that marsupial carnivore faunas are inherently prone to replacement by Eutherian carnivore faunas (Chapter 3). In this Chapter I examine the mechanisms by which this replacement might occur: through predation pressure, competitive pressures, and through differential population extinction probabilities under conditions of elevated mortality, such as might result from environmental stochasticity, or the actions of humans.

This investigation examines the relative potential impacts of direct predation and competition by eutherian carnivores upon the conservation status of the Spot-tailed quoll, *D. maculatus* by comparing aspects of the ecology, diet and habitat preferences of the three eutherian predators with that of *D. maculatus* using a rank scoring approach. Here I show that Dingoes and feral Cats are widely distributed throughout Spot-tailed quoll habitat within the Wet Tropics Area, however the Red Fox is absent from rainforest areas of the Wet Tropics. While *D. maculatus* is occasionally preyed on by Dingoes in the Wet Tropics Area (this chapter), and in southern Australia (Brown and Triggs 1990, Wallis and Brunner 1984), the introduced predators probably do not pose a significant threat to populations of *D. maculatus* in intact rainforest. They probably play an important role by contributing to mortality of *D. maculatus* in sclerophyll forest and in the cleared areas of the Atherton Tableland in the Wet Tropics Area. Furthermore, a comparison of the diet and hunting behaviour of all four species of carnivore suggest that while all species prey predominantly upon mammals, there are important differences in their diets at the level of prey size between the two canid species and *D. maculatus* and at the level of prey size and prey ecomorphic group between *D. maculatus* and Cats. The combined influence of the Dingo and the Feral Cat on *D. maculatus* in the Wet Tropics Area is potentially much more important than either species alone and the combined influence of all three predator species is even greater.

9.2. Methods

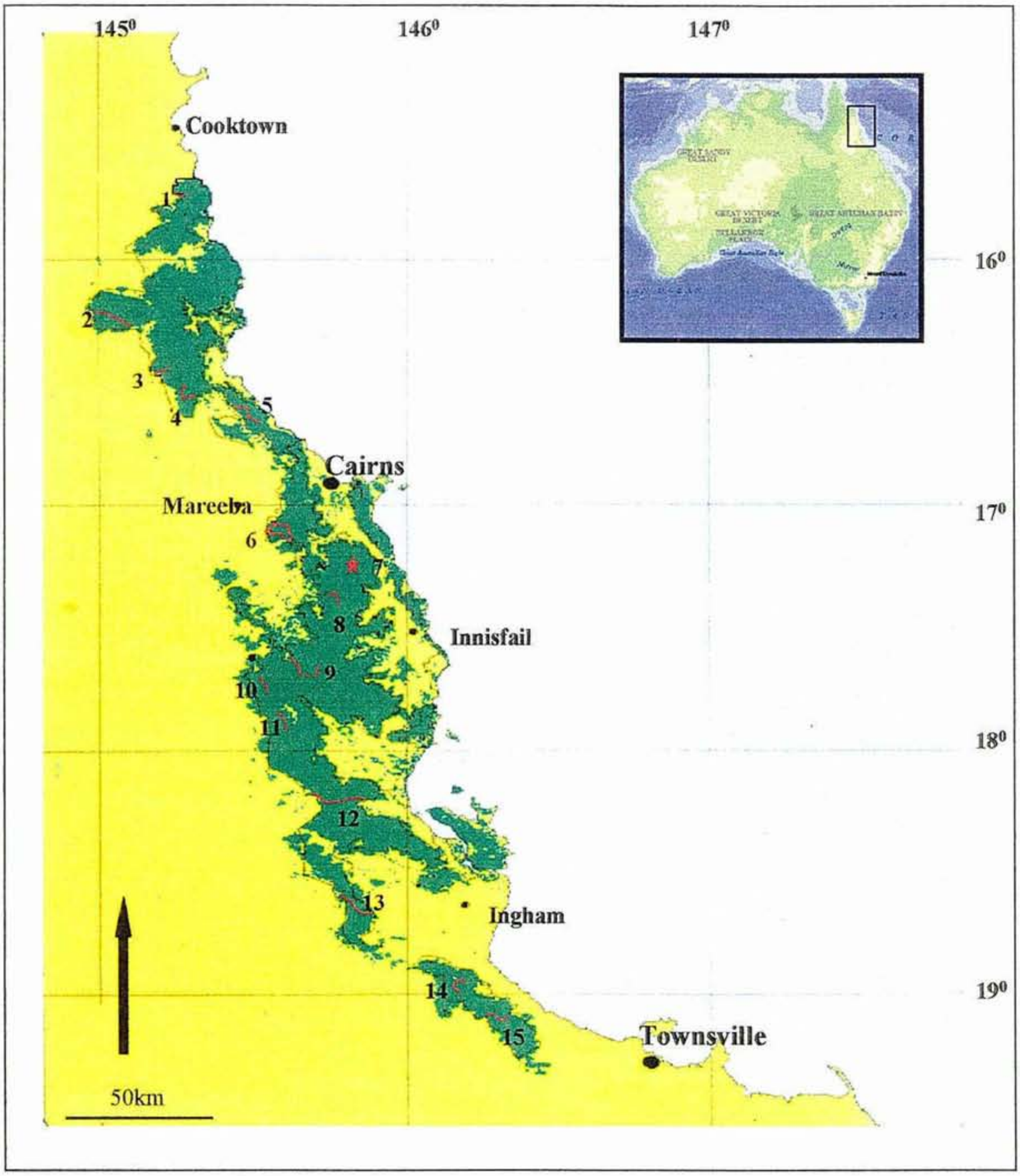
Because of the difficulties in distinguishing between them, and because of their probably similar feeding ecologies and competitive impacts upon marsupial carnivores, Feral dogs *Canis familiaris,* and Dingoes *Canis lupus dingo,* will be referred to as Dingoes throughout the rest of this chapter. Feral cats *Felis catus,* are hereafter referred to as Cats and Red Foxes *Vulpes vulpes,* as Foxes. The term canid refers to Dingos *senso lato* and Foxes.

9.2.1. Distributions of Eutherian Carnivores

The aim of this section is to examine the extent of distributional overlap of the Dog/Dingo, Red Fox and Feral Domestic Cat with the rainforest restricted *D. maculatus* (see Chapter 8). As such, the data presented below are not meant to be representative of eutherian distribution across the whole of north Queensland, merely to illustrate the extent of overlap with *D. maculatus.*

Distribution records for eutherian carnivores were sourced using the following methods: (1) identification of scats collected during scat transects between 1993 and 1995 (Map 9.1), (2) opportunistic scat collection during other aspects of this study (1991- 1995), (3) conversations with land-holders, forest managers, and biologists, (4) my own opportunistically collected data, and (5) Mason's (1995) list of fox sightings from the Wet Tropics Area and environs.

The allocation of scats to one of the four mammalian carnivore species within the study area was facilitated by: (1) microscopic identification of accidentally ingested grooming hairs (see Chapter 4); (2) comparison of scat size; and (3) comparison of the general appearance of the scat. Dingo scats are much larger than the scats of either *D. maculatus* or *F. catus*, measuring greater than 2.5cm in diameter. Spot-tailed quoll scats can be distinguished from those of Cats on the basis of their twisted, ropey look and oily, pungent smell (Triggs 1996). Fox scats are intermediate in size between Dingo and Cat/Quoll. Because no Fox grooming hairs were found in any of the approximately 1700 scats analysed, I ascribed no scats to Foxes.



Map 9.1. Numbered scat survey transects used in this study. Transects marked by thin red lines. Dark shading represents the Wet Tropics World Heritage Area and approximate distribution of Wet Tropics rainforest.

Note: Numeric code: 1, Mungumby track (Finnegan Uplands); 2, Mt Windsor Forestry Rd (Windsor Uplands); 3, Spurgeon transect (Carbine Uplands); 4,, Lewis transect (Carbine Uplands); 5, Black Mountain Forestry Rd (Black Mountain Corridor;6, Mt Edith and Mt Haig Rds (Lamb Uplands); 7, Point location, Bellenden Kerr summit area (Bellenden Ker Uplands); 8, Bartle Frere walking trail (Atherton Uplands); 9, South Johnstone Forestry Rd (Atherton Uplands); 10, Tully Falls Rd (Atherton Uplands); 11, Koombooloomba Road (Atherton Uplands); 12, Kirrama Forestry Rd (Kirrama Uplands); 13, Wallaman Falls Rd (Lee Uplands); 14, Paluma Dam Rd (Spec Uplands); 15, Bluewater Forestry Rd (Halifax Uplands).

9.2.2. Diets of the Eutherian carnivores

Dingo prey species were identified from 282 scats collected during this study. Prey species were identified as described in Chapter 6. In all subsequent analyses, records of *Pseudochirulus cinereus* and *P. herbertensis* are grouped, as are those of *Dendrolagus bennettianus* and *D. lumholtzi*, as each pair represents sister species which replace each other north and south of the Black Mountain Corridor (Nix and Switzer 1991).

Because no fox scats were encountered during this study, I have relied on published studies of fox diet from temperate forested areas of New South Wales and Victoria (Table 9.1). As discussed in Chapters 4 and 8, the uplands of the Wet Tropics Area are mostly rainforested, justifying my choice of comparative studies from rainforest/closed sclerophyll forests in southern Australia.

Cat prey species were identified from 123 Cat scats: 120 of which were collected from a 3km transect on the summit area of Mt Bartle Frere; two from the South Johnstone subunit of the Atherton bioregion; and one from the Halifax Uplands. Prey species were identified as per Chapter 6. Data for cat diet in the Wet Tropics Area are pseudoreplicated as most scats are from a single site in the Mt Bartle Frere summit area.

Table 9.1. Sources used in compiling carnivore dietary data for this study.

Species	**Sources**	
	Wet Tropics	**Other Temperate Forest Habitats**[1]
Fox	N/A	Brunner *et al.* 1975, Triggs *et al.* 1984, Lunney *et al.* 1990
Cat	This Chapter	
Dingo	This Chapter	
Spot-tailed quoll	Chapter 6	

Note

1. One other study on Fox diet in temperate forested regions (Brown & Triggs 1990) does not present data on non-mammalian prey and so was not used in this study.

9.2.3. Potential impacts of Eutherian carnivores on the conservation of D. maculatus

The significance of the three Eutherian predators to the conservation of the Spot-tailed quoll, *D. maculatus,* was inferred with respect to the potential predatory and competitive interactions between them. Relevant attributes that might indicate a predatory or competitive impact by each Eutherian carnivore on *D. maculatus* were assigned classes and scores (Table 9.2). I tallied these scores to rank each Eutherian species with respect to its potential impact on the conservation of *D. maculatus*. This study does not involve any experimental analysis of the competitive effects of the Eutherian carnivores on *D. maculatus*, and as such is entirely inferential.

Table 9.2. Scoring system used to infer predatory and competitive impacts of three Eutherian Carnivore species on the Spot-tailed Quoll, *D. maculatus*.

Criterion	**Score**
1. Predation (records of *D. maculatus* in diet)	
Not known to consume *D. maculatus*	0
Known to consume *D. maculatus*	1
2. Predation[1] (Prevalence of large-sized mammals in diet)	
Incidental prey	0.25 (for each large ecomorphic category)
Secondary prey	0.5 (ditto)
Primary prey	1 (ditto)
3. Competition (Mammalian Prey[2])	
No shared ecomorphic prey types as primary prey	0
One shared ecomorphic prey types as primary prey	1
Two shared ecomorphic prey types as primary prey	2
Three shared ecomorphic prey types as primary prey	3

Note

1. Primary prey is that which occurs as greater than 10% of all prey records, secondary prey is that which occurs as 5-10% of all prey items and occasional prey is that which occurs as less than 5% of all prey records.
2. Ecomorphic prey types defined in Chapter 6.
3. P (persistence modelled using VORTEX population viability analysis software).

9.2.3.1. Potential Predatory Effects of Eutherian carnivores on the Spot-tailed Quoll

Actual and potential predatory effects were gauged in three ways: (1) from the incidence of *D. maculatus* in Dingo and Cat scats collected from areas of sympatry with *D. maculatus* in the Wet Tropics Area (this study), (2) from the incidence of *D. maculatus* in carnivore scats from southern Australia (sources as per Table 9.1), and (3) by assessing the prevalence of large-sized terrestrial, scansorial and arboreal mammalian prey in the diets of each Eutherian species (see Chapter 6 for a full description of these prey ecomorphic categories). The mass of an average-sized Spot-tailed quoll places it at the extreme upper boundary of medium-sized mammals in the study area, and this in combination with its capacity to inflict damage on its attackers, suggests that only carnivores which consume large-sized prey are likely to be able to prey upon healthy, adult *D. maculatus*.

9.2.3.2. Potential Competitive Effects of Eutherian carnivores on the Spot-tailed Quoll

In lieu of any experimental studies, the potential effects of competition by the Eutherian carnivores on *D. maculatus* were inferred by comparison of the relative proportions of different mammalian ecomorphic prey types in the diets of each Eutherian carnivore and *D. maculatus*.

9.2.4. Modelling population persistence of D. maculatus, the Dingo, Fox and Feral Cat.

I examined differences in the innate persistence of populations of all four carnivore species when affected by different schedules of mortality and recruitment. Population persistence was modelled using VORTEX population viability analysis software Version 8.41 (Lacy 1993). The sources for life-history data were:

Spot-tailed Quoll	This study
Dingo	Jones and Stevens 1988, Corbett 1995
Red Fox	Lloyd 1980, Sheldon 1992
Feral Cat	Jones & Coman 1982

Published data for the relevant life-history parameters for the three eutherian carnivores is scant and so I used VORTEX default values for some parameters, and values from *D. maculatus* for others (annual mortality) (see Appendices 9.1 & 9.2). In particular, default values were used for all four carnivores for the Allee parameter, Exponential steepness and the standard deviation for intrinsic mortality values. Other parameters used, and the scenarios modelled are given in Appendices 9.1 and 9.2. I recognise that population viability analysis approach that I have used here provides only an approximate indication of the true response of each of the eutherian carnivores because of the paucity of relevant data for those species.

I modelled the responses of populations of all four carnivores to several scenarios of extrinsic adult mortality and failed recruitment as follows:

Change in Recruitment

Scenario 1: No change in annual adult mortality, but one year in every 10 years, recruitment is zero.

Scenario 2: No change in annual adult mortality, but one year in every 20 years, recruitment is zero.

Scenarios 1 and 2 might approximate a mild drought cycle, in which adult mortality is not affected, but no reproduction occurs.

Changes in Mortality

Scenario 3: An annual harvest of 10% of the population, but no change to the fecundity schedules of surviving adults.

Scenario 4: An annual harvest of 30% of the population, but no change to the fecundity schedules of surviving adults.

Scenario 5: An annual harvest of 50% of the population, but no change to the fecundity schedules of surviving adults.

Scenario 6: An annual harvest of 70% of the population, but no change to the fecundity schedules of surviving adults.

These four mortality schedules approximate conditions that might apply during poison baiting, or trapping campaigns in which survivors breed at the normal rate.

Changes in recruitment and elevated extrinsic mortality

Scenario 7: Recruitment is zero, and extrinsic mortality increases by 25%, once every 10 years. This condition might represent a slightly more severe drought in which some adults die.

The rationale behind using population persistence to examine potential impacts of Eutherian carnivores on *D. maculatus* is that I anticipate that a competitive advantage is conferred to species that have a greater capacity to persist through times of increased extrinsic mortality or reduced fecundity. Such scenarios might include drought, fire or other environmental catastrophe, or human land-use impacts such as habitat loss and wide spread poison-baiting campaigns.

9.3. RESULTS

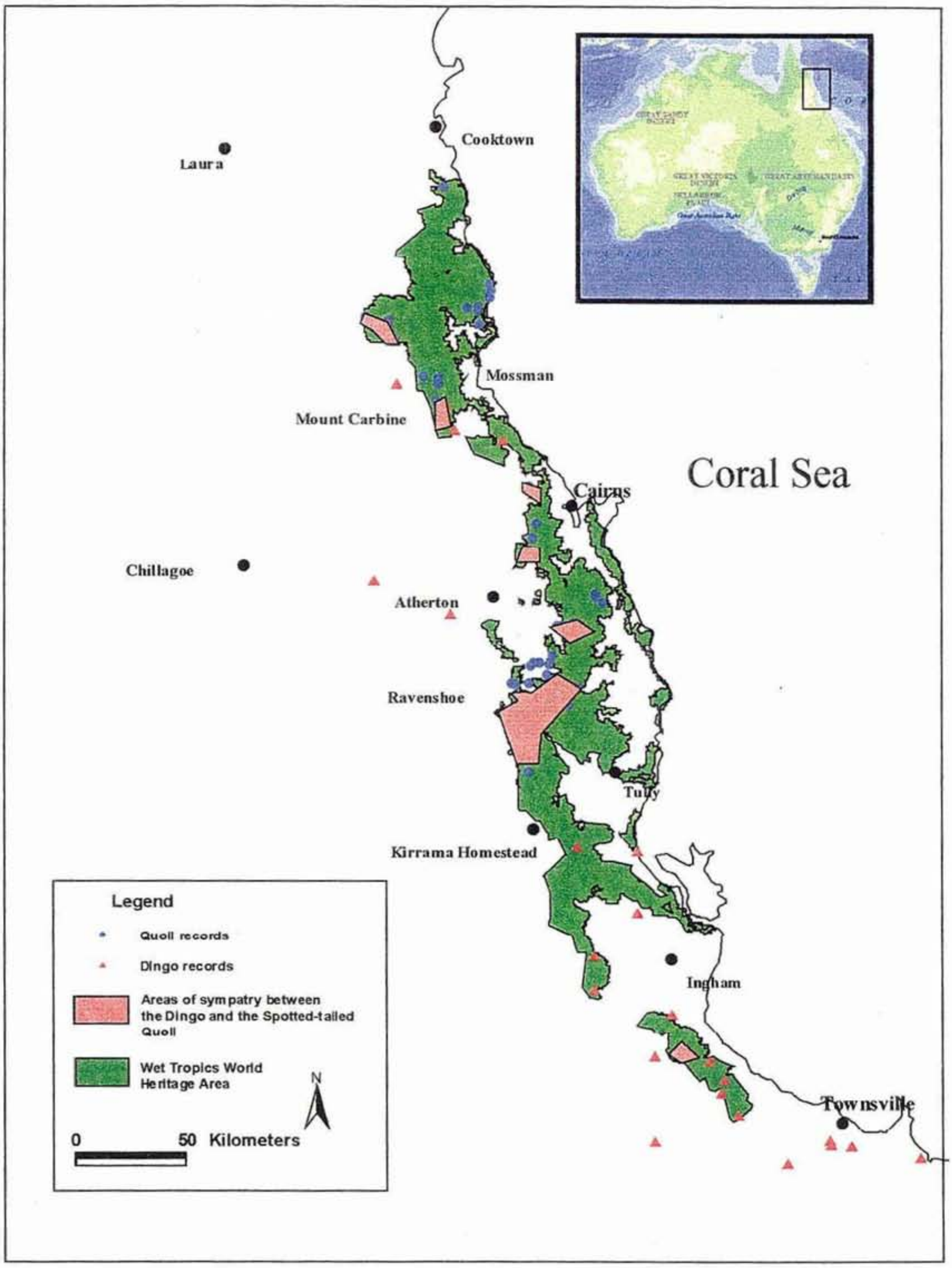
9.3.1. Distribution

I traversed a cumulative total of 350 km of transect within the uplands of the Wet Tropics World Heritage Area searching for signs of eutherian carnivores. I searched 120 km of transect in 1993 and 230km in 1994. I collected a total of 1038 mammalian predator scats (including 123 Cat scats and 173 Dingo scats) from those transects. I sighted Dingoes on two occasions and cats on three occasions. I collected an additional 109 dingo scats from the Mt Windsor Tableland, between September 1991 and December 1994. I attributed the remainder of the carnivore scats (n=733) encountered during this study to *D. maculatus*.

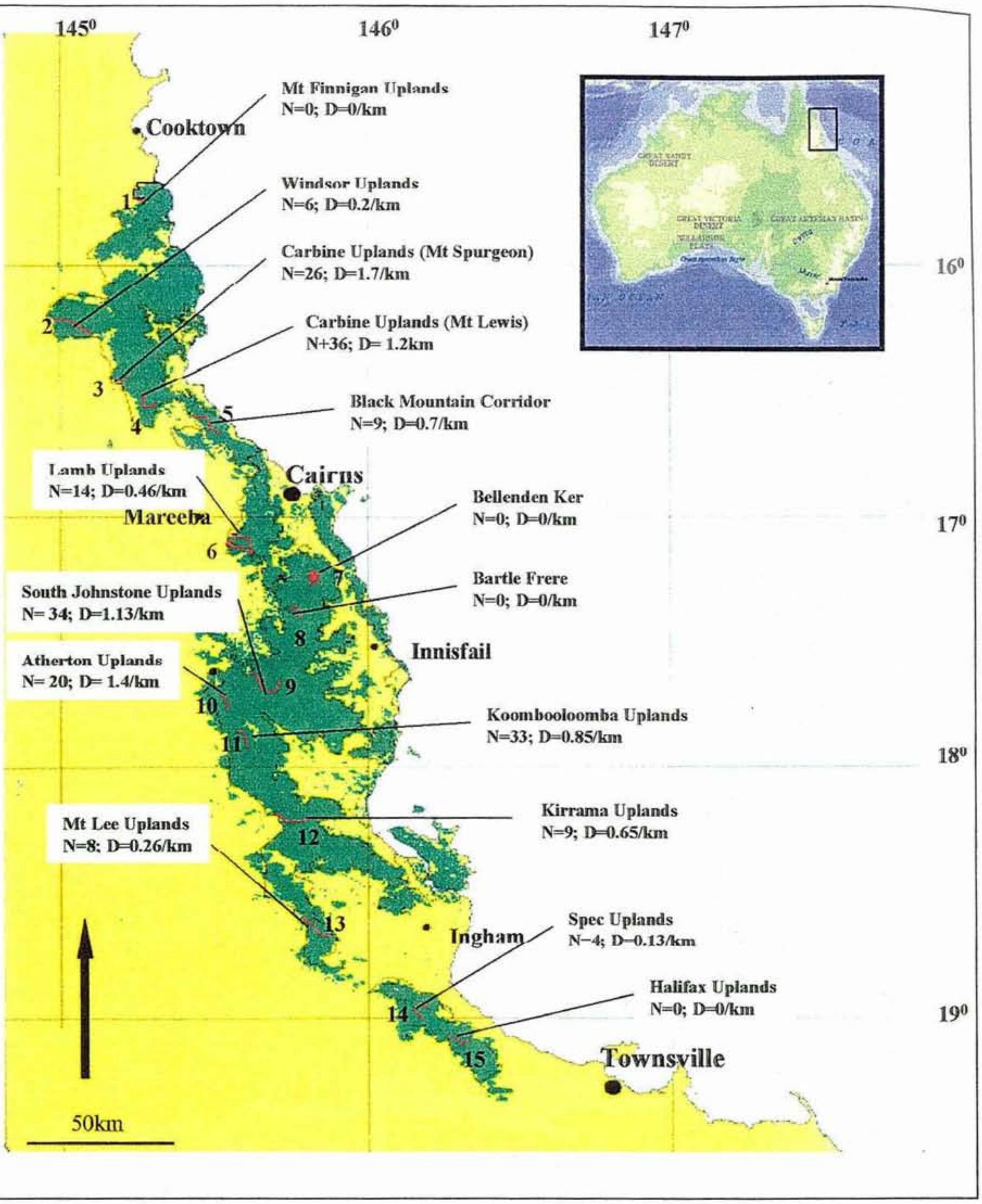
9.3.1.1. Dingo

Opportunistic records show that Dingoes are widespread throughout the rainforests and sclerophyll forests of the Wet Tropics Area and are sympatric with all but one of the nine core sub-populations of *D. maculatus* (Map 9.2)(Appendix 9.3). I found signs or made sightings of Dingoes on all but two of the 17 transects every time that I surveyed them (Appendix 9.4). The exceptions were the Bellenden Ker transect on which no signs of Dingoes were ever noted and the Bartle Frere transect on which scats were recorded once out of the two times that it was surveyed. The overall density of Dingo scats was 0.5/km of transect and varied from between zero scats/km (Mt Spec transect: 1993) to 1.7 scats/km (Mt Spurgeon transect: 1994)(Map 9.3).

With two exceptions, all Dingo records which I collected from within rainforest were found along either maintained or disused vehicular tracks. The exceptions are a scat from the summit area of Mt Halifax (Halifax Uplands), in 1990 and two scats from the summit area of Mt Bartle Frere in 1997. The Mt Halifax record was found approximately 7km from the nearest road or track. The Mt Bartle Frere records were found on a non-graded bushwalking trail, 7km from the car park where the track originated.



Map 9.2. Approximate areas of known sympatry between the Dingo and the Spot-tailed Quoll, recorded during this study.



Map 9.3. The numbers and density of Dingo scats collected over two years of survey. N refers to the total number of scats collected from each survey, and D refers to the mean density of scats from both years of survey. Details on locations and methodology of scat transects are provided in Chapter 4. Base map modified from Nix and Switzer 1991.

9.3.1.2. Fox

I found no signs of Foxes during this study. However I collated 30 published and first hand accounts of Red Fox sightings in the environs of the Wet Tropics Area (Map 9.4)(Appendix 9.5). Foxes and Quolls are marginally sympatric in two areas both within the Atherton population of *D. maculatus*: the southern Atherton Tablelands and west of Kuranda (Map 9.4).

Only one record of a Red Fox was from rainforest habitat and that was from a road that traversed a thin wedge of rainforest sandwiched between agricultural and sclerophyll country in the Kuranda area. Of the remaining nine Fox records for which habitat type can be inferred; seven are from open forest and the remaining two are from agricultural lands (Appendix 9.5).

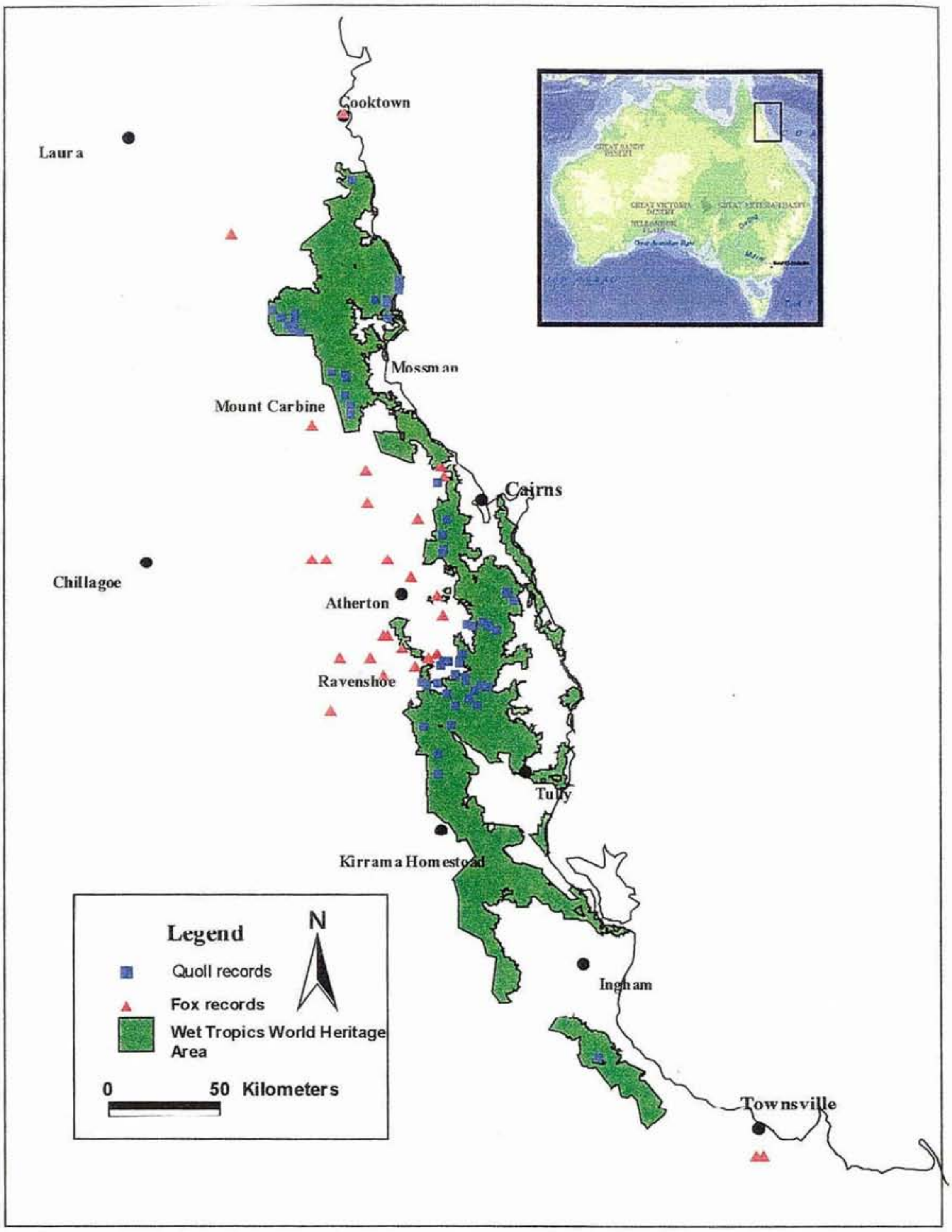
9.3.1.3. Cat

I recorded a total of 149 cat sightings and signs in eight of the upland bioregions surveyed (Map 9.5. & Appendix 9.6). Cat populations occur in sympatry with six of the nine known core sub-populations of *D. maculatus:* Atherton, Bartle Frere, Bellenden Ker, Lamb, Carbine, and Windsor sub-populations (Map 9.5).

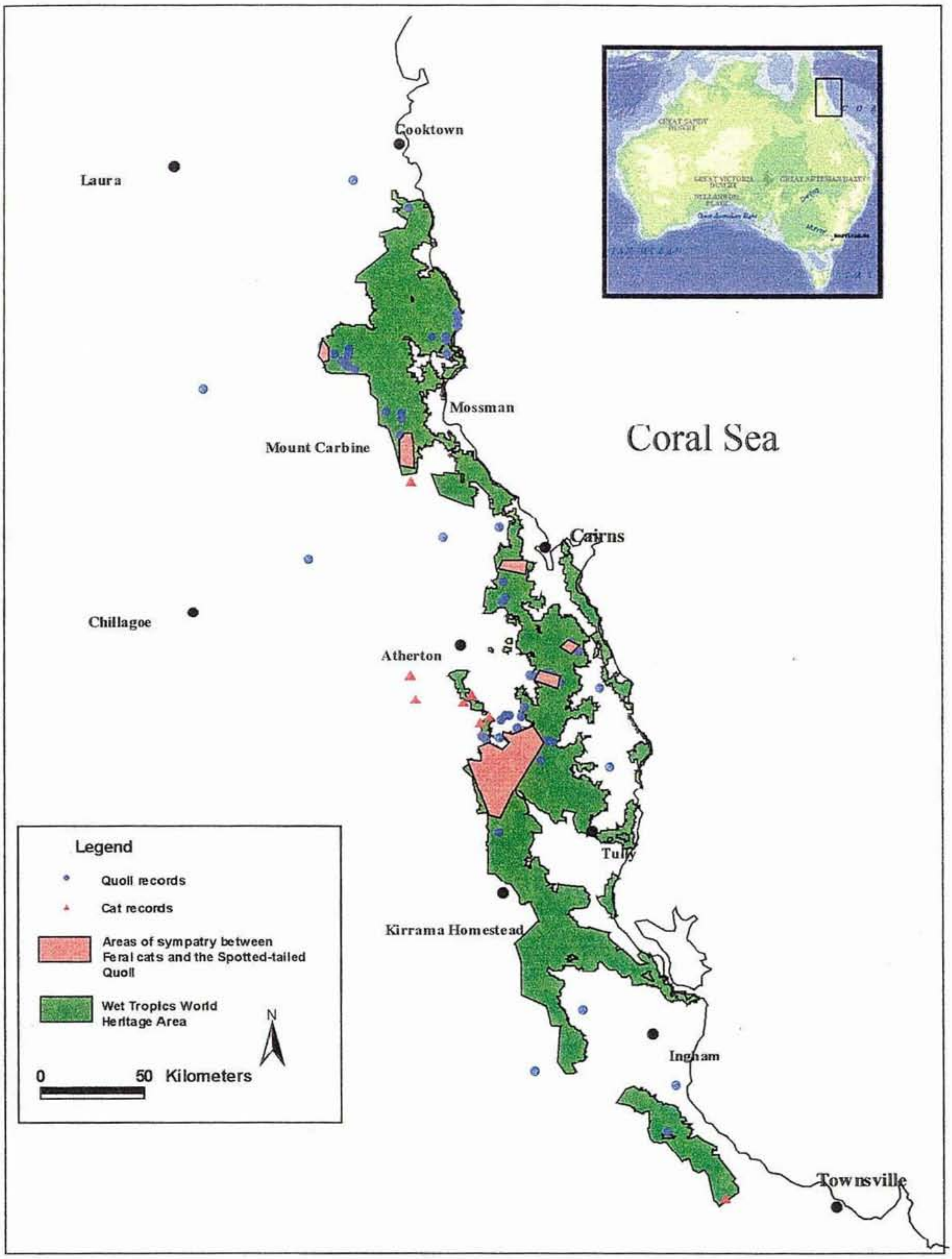
Records of Cats come from all landscapes including the highest altitude closed and open forests (the summit of Mt Bellenden Ker and Mt Windsor Uplands respectively), along roads in lower altitude closed and open forests, and in fragmented forest and pasturelands.

The 149 cat records include 123 scats which I collected from the scat transects during this study: one in the South Johnstone Uplands, one in the Mt Halifax Uplands, one on the summit area of Mt Bellenden Ker, and 120 in the summit area of Mt Bartle Frere. The density of cat scats ranged from 0 (all transects except Bartle Frere, Bellenden Ker, South Johnstone and Halifax) to 11 scats/km of transect (Bartle Frere) (Map 9.6, Appendix 9.7).

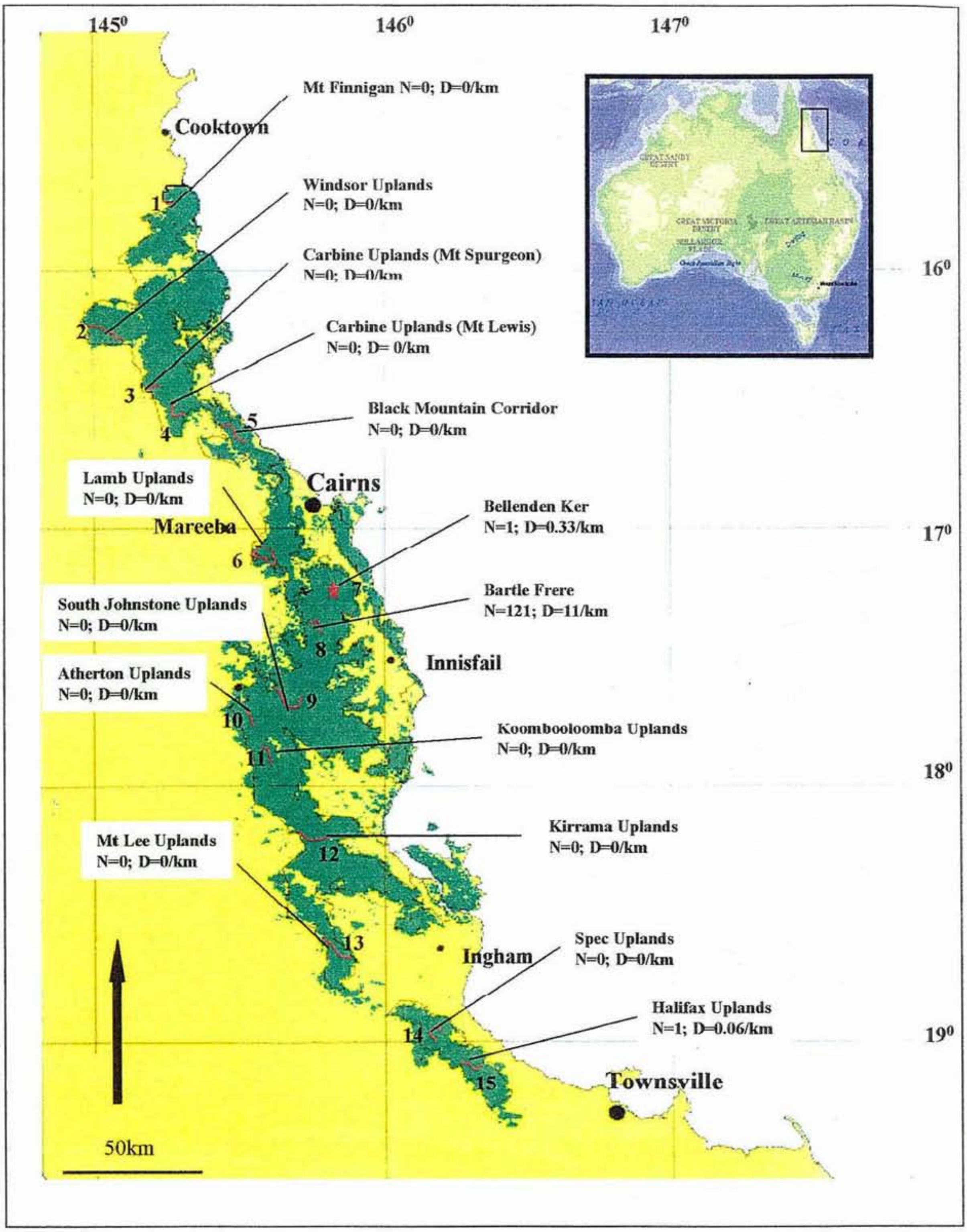
All signs and sightings of cats from rainforest were either from maintained roads (Halifax, South Johnstone, Carbine Uplands) or from along the Mt Bartle Frere bushwalking trail.



Map 9.4. Records collated during this study of Red Foxes and Spot-tailed Quolls from the Wet Tropics Area and environs. Note that the rainforest boundary approximates that of the Wet Tropics World Heritage Area.



Map 9.5. Approximate areas of known sympatry recorded during this study, between the Spot-tailed Quoll and the Feral Cat. Note that the distribution of rainforest approximates the Wet Tropics World Heritage Area boundary.



Map 9.6. The numbers and density of Cat scats collected over two years of survey.

N refers to the total number of scats collected from each survey, and D refers to the mean density of scats from both years of survey. Details on locations and methodology of scat transects are provided in Chapter 4. Base map modified from Nixand Switzer 1991.

9.3.2. Diet

Vertebrates, especially mammals, are the predominant prey of all three Eutherian carnivores and of the Spot-tailed Quoll (Fig. 9.1,Appendix 9.8)

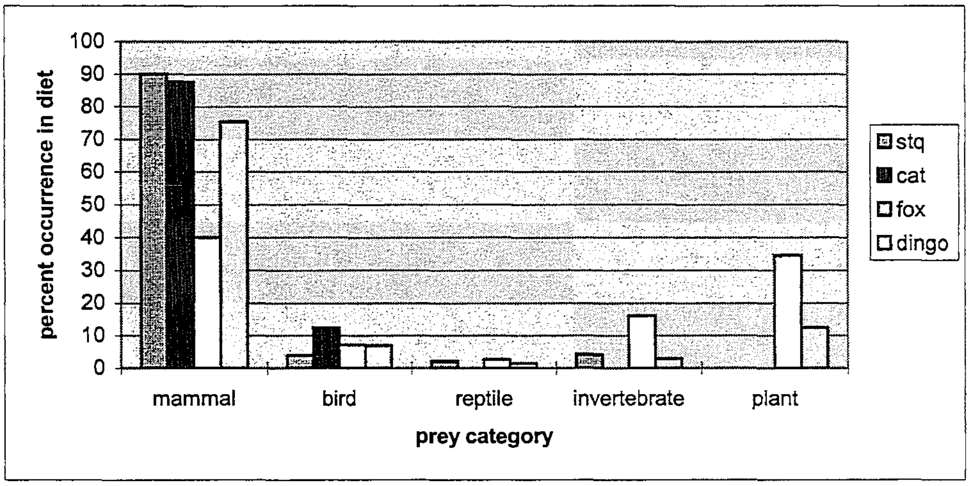


FIG. 9.1. THE PROPORTIONAL OCCURRENCE OF FIVE "CLASSES" OF PREY IN THE DIETS OF ONE MARSUPIAL AND THREE EUTHERIAN MAMMALIAN CARNIVORES IN MESIC FOREST HABITATS IN AUSTRALIA. STQ in the legend refers to the Spot-tailed quoll. All dietary data except for Red fox collected from the Wet Tropics Area.

9.3.2.1. Dingo

Mammals are the most important prey group of Dingoes in the Wet Tropics Area, followed by plant material, birds, invertebrates and reptiles (Fig. 9.1). Twenty-two species of mammals, and unassigned species of bird, reptile, invertebrates, and plants, were recorded in the 282 Dingo scats analysed in this study (Fig. 9.2, Appendix 9.9). Within the mammals, the most important prey in decreasing order of percent occurrence, were: the Red-legged Pademelon, *Thylogale stigmatica* (15.4%), the Long-nosed bandicoot, *Perameles nasuta* (10.1%), the Ringtails, *Pseudochirulus herbertensis/cinereus* (7.2%), the Pig, *Sus scrofa* (7%), and Tree Kangaroos, *Dendrolagus* species (5.3%). Plant material (12.5%) and Birds (7%) were also important components of the diet of Dingoes. None of the remaining 17 mammal species or reptiles or invertebrates recorded from Dingo scats in this study occurred in greater than 5% of prey items (Fig. 9.2).

Large and medium terrestrial mammals and plant material were the only primary food types of Dingoes in the WTWHA (Appendix 9.9). Medium arboreal and large scansorial mammals and birds were the only secondary prey. Despite their generally high abundance (see Chapter 6), small mammals were consumed only occasionally (Table 9.3). I recorded Spot-tailed Quolls from two Dingo scats: one from the Windsor Uplands, and one from the Koombooloomba sub-region of the Atherton Uplands. Spot-tailed Quolls have also been recorded in the diet of Dingoes from one study in East Gippsland (Wallis and Brunner 1984) and from two unidentified canid scats (Dingo/Dog or Fox) from the same area during a later study (Brown and Triggs 1990).

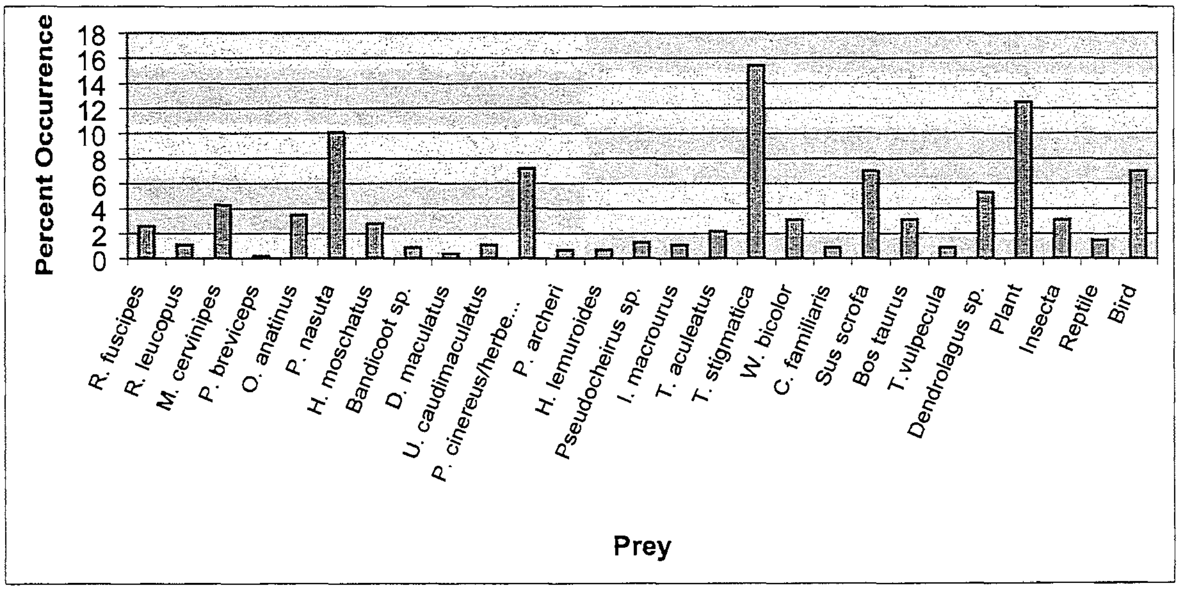


FIG. 9.2. THE FREQUENCY OF EACH PREY SPECIES IN 282 DINGO SCATS COLLECTED FROM WITHIN THE WET TROPICS AREA.

9.3.2.2. Fox

Extrapolation of pooled dietary data from Fox scats from southern Australia indicates that mammals are the most important component of the diet of Foxes. After mammals, plants, birds, invertebrates and reptiles comprise a decreasing proportion of all prey items recorded (Fig 9.1). Foxes differ from the other two eutherian carnivores and *D. maculatus* in that plant material is almost as important in the diet as mammals (Fig 9.1).

Spot-tailed Quolls have never been recorded in Fox scats however two indeterminate Canid scats (Dog or Fox) collected during the 1980's from east Gippsland contained the remains of *D. maculatus*.

9.3.2.3. Cat

Mammals are the most important prey group for cats in the Wet Tropics Area (Fig. 9.1)(Appendix 9.8). Twelve mammal species were recorded from 123 cat scats collected during this study (Fig 9.3, Appendix 9.10). Small terrestrial and scansorial mammals and birds are the primary prey of Cats in the uplands of the WTWHA (Table 9.3). Secondary prey included medium scansorial and terrestrial mammals, while large terrestrial and medium scansorial mammals were rarely eaten. (Table 9.3). Within the mammals, the most important prey in decreasing order of abundance were: the Bush Rat, *Rattus fuscipes* (31%), Marsupial Mice, *Antechinus godmani and adustus* (23.3%), birds (12.5%), the Fawn-footed Melomys, *Melomys cervinipes* (8.5%) and the Giant White-tailed Rat, *Uromys caudimaculatus* (6.2%). The remaining eight mammal species were consumed as occasional prey only (i.e. <5% of occurrences)(Fig. 9.3).

Spot-tailed Quolls have not been recorded in the diet of Feral Cats. However the Museum of Victoria has a record of a juvenile *D. maculatus* which was retrieved from a domestic house cat. One cat scat from the Bartle Frere sub-region of the Atherton Uplands contained the remains of the Northern Quoll, *D. hallucatus,* which is much smaller than *D. maculatus*.

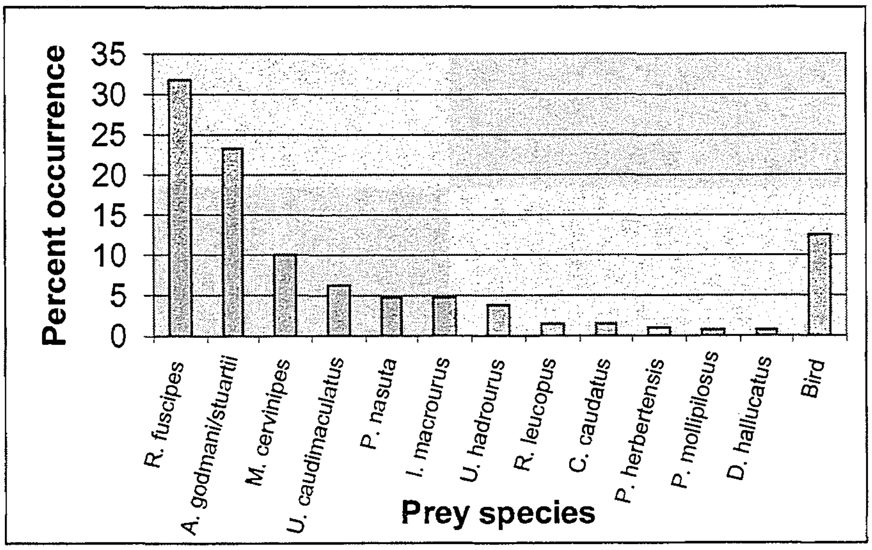


FIG. 9.3 PERCENT OCCURRENCE OF PREY RECORDED FROM 123 CAT SCATS COLLECTED FROM WITHIN RAINFORESTS OF THE WET TROPICS WORLD HERITAGE AREA.

Note 120 cat scats recorded from a single transect (Bartle Frere transect).

Table 9.3. The relative importance[1] of mammalian ecomorphic and other prey categories in the diets of *D. maculatus* and the three eutherian carnivores.

Spot-tailed Quoll	Cat	Fox	Dingo
Primary prey[2]			
Medium terrestrial mammal	Small scansorial mammal	Plant	Large terrestrial mammal
Small scansorial mammal	Small terrestrial mammal	Invertebrate	Medium terrestrial mammal
Medium arboreal mammal	Birds	Small terrestrial mammal	Plant
Small terrestrial mammal			
Secondary prey[3]			
Invertebrates	Medium scansorial mammal	Medium terrestrial mammal	Medium arboreal mammal
Birds	Medium terrestrial mammal	Large terrestrial mammal	Birds
Reptiles		Birds	Large scansorial mammal
		Small scansorial mammal	
Occasional prey[4]			
Large terrestrial mammal	Large terrestrial mammal	Medium arboreal mammal	Small scansorial mammal
Medium scansorial mammal	Medium arboreal mammal	Reptiles	Small terrestrial mammal
Small scansorial mammal		Large scansorial mammal	Invertebrates
Large scansorial mammal		Small arboreal mammal	Medium scansorial mammal
			Reptiles
			Small arboreal mammal

Note

1. Prey ecomorphs listed in descending order of percent occurrence.
2. Primary prey is that which occurred as > 10% of all prey records.
3. Secondary prey is that which occurred as 5-10% of all prey records.
4. Occasional prey is that which occurred as < 5% of all prey records.

9.3.3. Comparative responses of Eutherian and Spot-tailed Quoll populations to increases in mortality and decreases in recruitment

9.3.3.1. Responses to a decrease in recruitment

VORTEX modelling suggest that populations of *D. maculatus* are much more likely to go extinct than are populations of either of the three Eutherian carnivores when there is either a ten or 20 yearly cycle of zero recruitment, but no adult mortality (Figs 9.4 & 9.5).

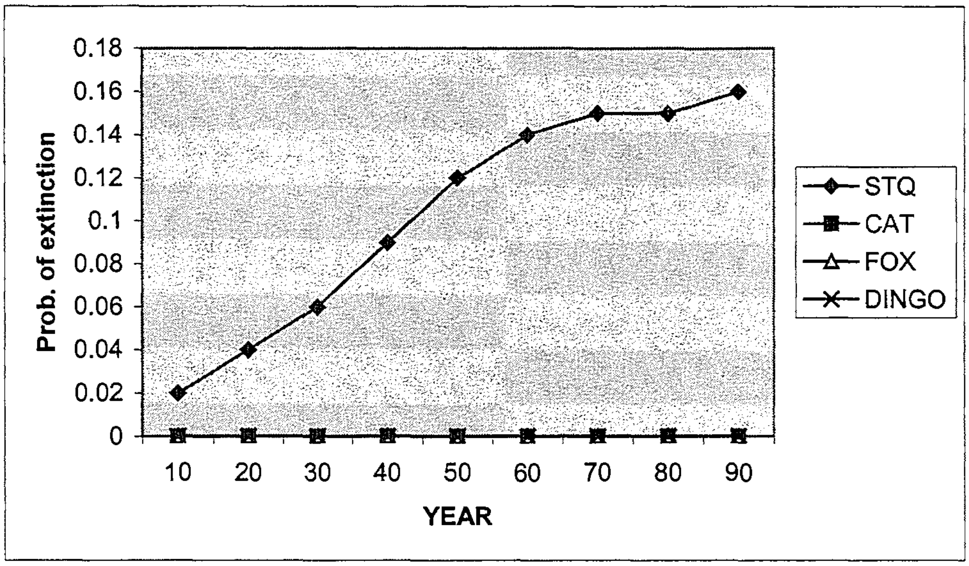


FIG. 9.4. THE PROBABILITY OF EXTINCTION (MODELLED BY VORTEX) OF POPULATIONS OF THE SPOT-TAILED QUOLL AND THE THREE EUTHERIAN CARNIVORES UNDER CONDITIONS OF ZERO RECRUITMENT EVERY ONE YEAR IN 10 (SCENARIO 1).

Initial population size 150 individuals. See Appendix 9.1 for life-history parameters used for each species and the sources of those data.

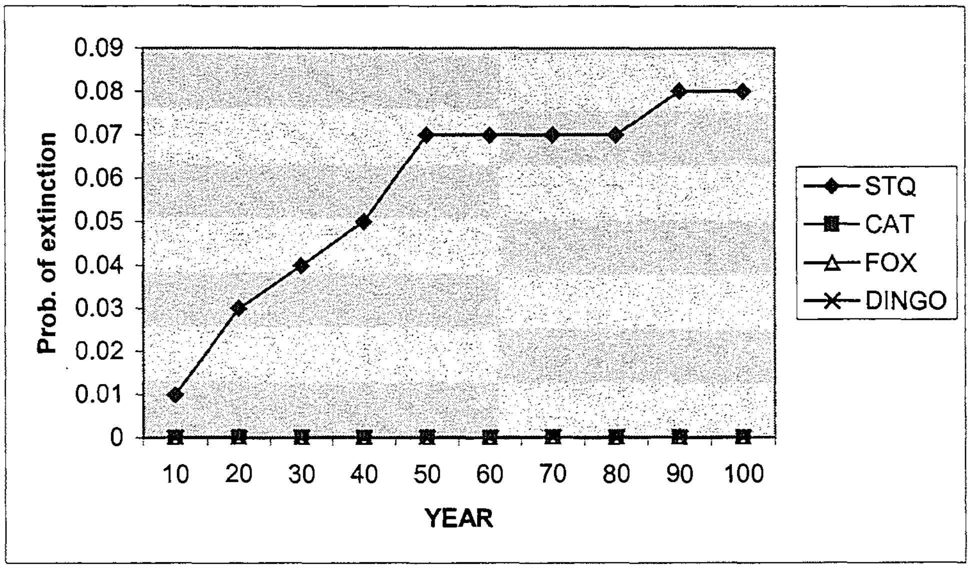


FIG. 9.5. THE PROBABILITY OF EXTINCTION (MODELLED BY VORTEX) OF POPULATIONS OF THE SPOT-TAILED QUOLL AND THE THREE EUTHERIAN CARNIVORES UNDER CONDITIONS OF ZERO RECRUITMENT EVERY ONE YEAR IN 20 (SCENARIO 2).

Initial population size 150 individuals. See Appendix 9.1 for life-history parameters used for each species and the sources of those data.

9.3.3.2. Responses to increases in extrinsic mortality

VORTEX analyses suggest that at low levels of extrinsic mortality, populations of *D. maculatus* are much more prone to extinction than are equal-sized populations of the three eutherian carnivores under conditions of increased extrinsic mortality where survivors breed successfully (Fig. 9.6).

At higher levels of extrinsic mortality, populations of *D. maculatus* and the Red Fox exhibit similar levels of extinction proneness, while populations of the Feral Cat and Dingo remain relatively unaffected (Figs 9.7-9.9).

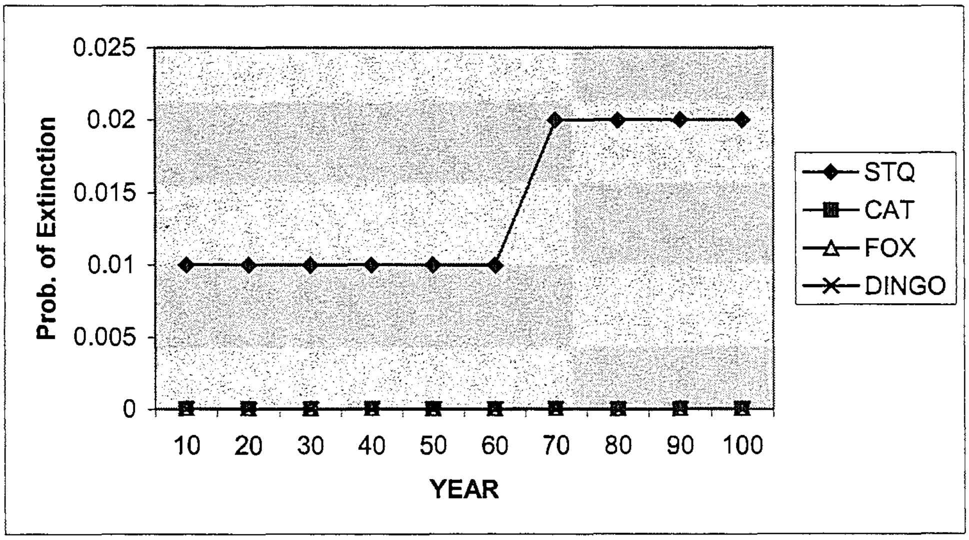


FIG. 9.6. THE PROBABILITY OF EXTINCTION (MODELLED BY VORTEX), OF POPULATIONS OF *D. MACULATUS* AND THE THREE EUTHERIAN CARNIVORES UNDER CONDITIONS OF 10% ANNUAL ADULT MORTALITY EACH YEAR FOR 100 YEARS (SCENARIO 3).

Initial population size 150 individuals. See Appendix 9.2 for life-history parameters used for each species and the sources of those data.

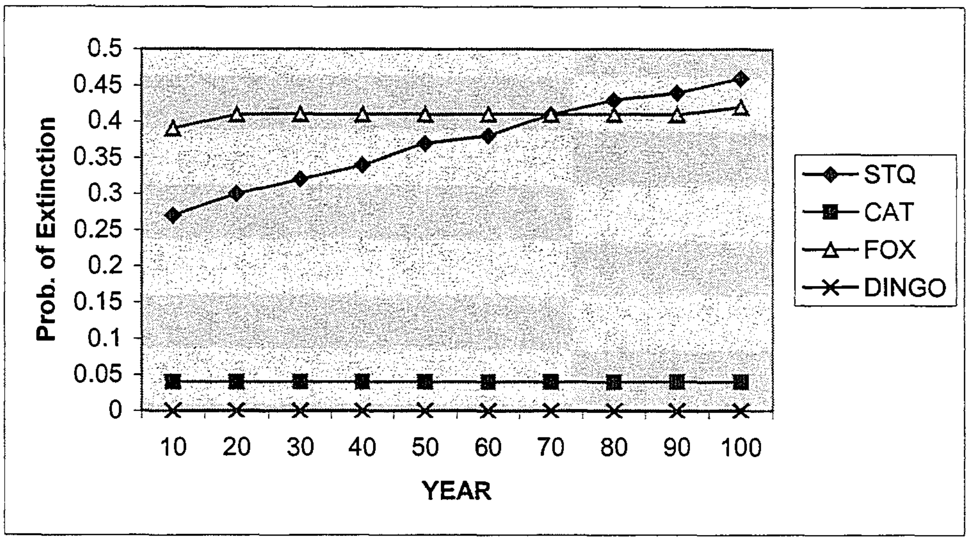


FIG. 9.7. THE PROBABILITY OF EXTINCTION (MODELLED BY VORTEX), OF POPULATIONS OF *D. MACULATUS* AND THE THREE EUTHERIAN CARNIVORES UNDER CONDITIONS OF 30% ANNUAL ADULT MORTALITY EACH YEAR FOR 100 YEARS (SCENARIO 4).
Initial population size 150 individuals. See Appendix 9.2 for life-history parameters used for each species and the sources of those data.

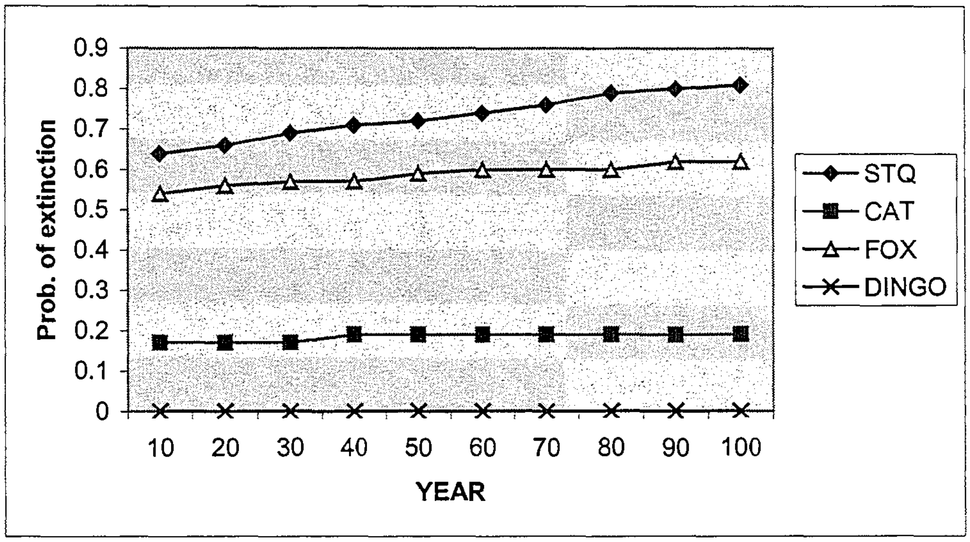


FIG. 9.8. THE PROBABILITY OF EXTINCTION (MODELLED BY VORTEX), OF POPULATIONS OF *D. MACULATUS* AND THE THREE EUTHERIAN CARNIVORES UNDER CONDITIONS OF 50% ANNUAL ADULT MORTALITY EACH YEAR FOR 100 YEARS (SCENARIO 5).
Initial population size 150 individuals. See Appendix 9.2 for life-history parameters used for each species and the sources of those data.

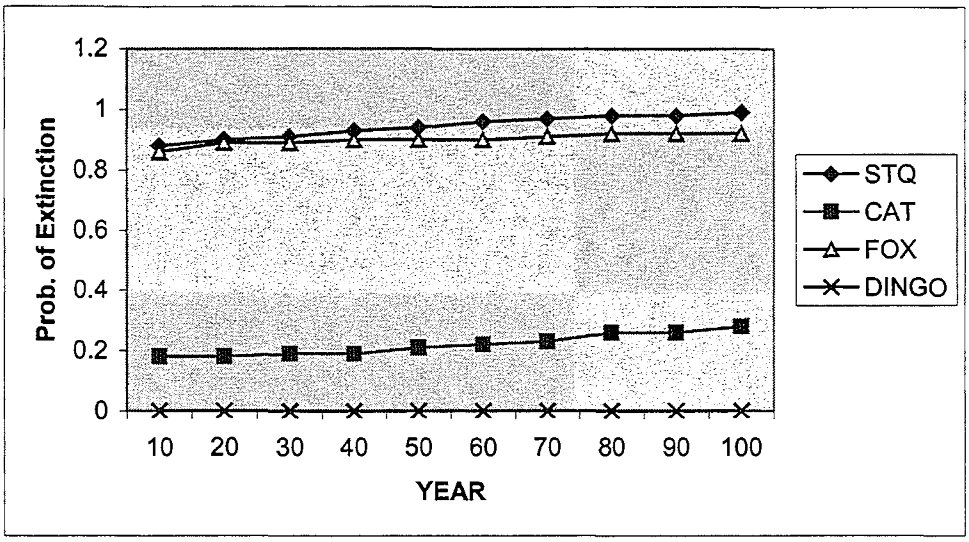


FIG. 9.9. THE PROBABILITY OF EXTINCTION (MODELLED BY VORTEX), OF POPULATIONS OF *D. MACULATUS* AND THE THREE EUTHERIAN CARNIVORES UNDER CONDITIONS OF 70% ANNUAL ADULT MORTALITY EACH YEAR FOR 100 YEARS (SCENARIO 6).

Initial population size 150 individuals. See Appendix 9.2 for life-history parameters used for each species and the sources of those data.

9.3.3.3. Responses to an increase in mortality and a decrease in recruitment

VORTEX analysis suggests that populations of *D. maculatus* are much more prone to extinction than those of the three Eutherian carnivores when one in ten year cycles of zero recruitment are accompanied by an increase in adult mortality of 25% (Fig 9.10).

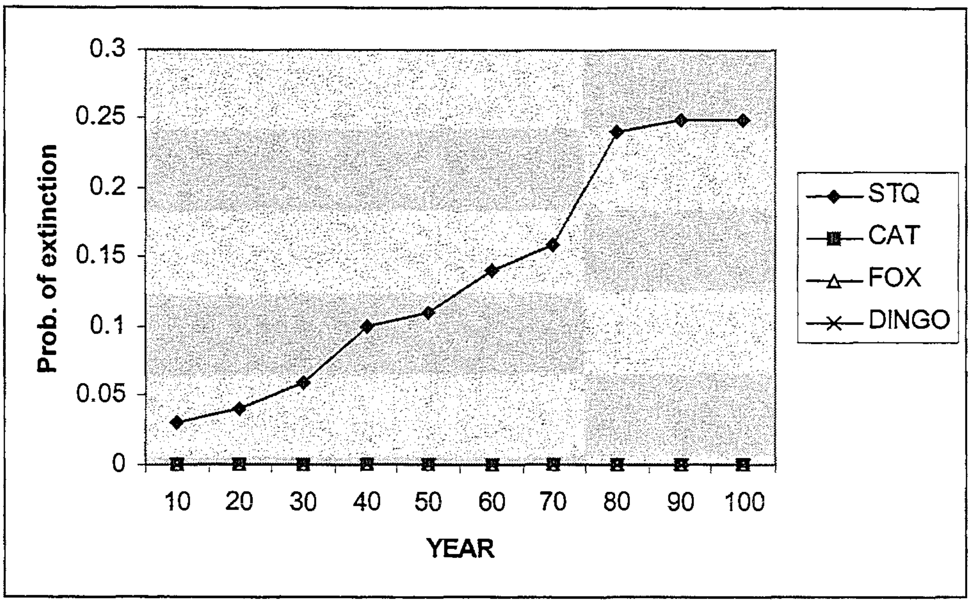


FIG. 9.10. RESULTS OF VORTEX ANALYSES OF THE POPULATION PERSISTENCE OF *D. MACULATUS* AND THE THREE EUTHERIAN CARNIVORES UNDER CONDITIONS OF 25% ADULT MORTALITY AND ZERO RECRUITMENT FOR ONE YEAR IN 10 OVER 100 YEARS (SCENARIO 7).
Initial population size 150 individuals. See Appendix 9.2 for life-history parameters used for each species and the sources of those data.

9.3.4. Rank-scores of the predatory and competitive impacts of Eutherian carnivores on the Spot-tailed Quoll.

The rank scoring approach suggests that the Dingo has the greatest potential predatory effect and greatest overall effect on populations of *D. maculatus* of any of the Eutherian carnivores (Table 9.4). It also suggests that:

- The Red Fox has considerable potential predatory effect but has the overall lowest potential competitive effect based on diet.
- The feral Domestic Cat has the lowest potential predatory effect, but has the highest potential competitive effect based on diet.
- All combinations of Eutherian carnivores have a greater overall potential effect on *D. maculatus* than do any species alone. All three Eutherian carnivore species together have the greatest potential impact on *D. maculatus*.

Table 9.4. Potential significance of Australia's three Eutherian carnivores to the conservation of *D. maculatus*.

See Table 9.2 for details of Rank scores used.

Species	*D. maculatus* recorded as prey?	Large mammals as prey	**Total for potential predatory effects**	No. shared primary prey types	**Total Score**
Dingo	1	1.5	2.5	1	3.5
Cat	0.5	0.25	0.75	2	2.75
Fox	0	0.75	0.75	1	1.75
Dingo & Cat combined	1.5	1.5	3	3	6
Dingo & Fox	1	2.25	3.25	2	5.25
Fox & Cat	0.5	1	1.5	2	3.5
Dingo, Fox & Cat	1.5	2.5	4	3	7

9.3.5. *Role of Eutherian carnivores as disease vectors*

The three eutherian predators all have the potential to be vectors of diseases which affect *D. maculatus*. Dickman (1996) reviewed the issue of disease transmission by Cats to native fauna and his findings apply equally to the Canids. He postulated that the two most important pathogens with the potential to infect wildlife are the tapeworm *Spirometra erinacei,* and the protozoan parasite *Toxoplasma gondii*. Both parasites have been recorded in feral cats (Coman *et al.* 1981, Speare 1985), Dingoes (Coman 1973, Corbett 1995), and dasyurid marsupials (Attwood *et al.* 1975, Munday 1988 in Dickman 1996). *Spirometra* has been recorded in Foxes (Coman 1973) and it is highly probable that Foxes are also host to *Toxoplasma*. Dickman (1996) notes that although there has been much speculation on the potential impacts of these parasites (*T. gondii* in particular) on native fauna, there is no unambiguous evidence of their impact on populations of native species. The only study to have tested for *T. gondii* in a wild population of *Dasyurus*, found that a sample of 20 Northern Quolls in the Northern Territory showed no signs of present Toxoplasmosis infection or of antibodies indicative of past infection (Oakwood and Pritchard 1999). Although potentially very important, this issue of disease transmission is largely hypothetical and I can not add to Dickman's (1996) evaluation.

9.4. Discussion

The rank-scoring approach used here suggests that Dingoes are the most likely of the three Eutherians to prey upon *D. maculatus*, followed by the Fox and the Cat. This approach also suggests that competitive impacts on *D. maculatus* are greatest from Cats, followed in descending order by the Dingo and the Fox. The combined effect of the Cat and the Fox is equivalent to that of the Dingo alone, the effect of all other combinations of these Eutherians is much greater than that of either species alone. It is important to note that this approach to assessing the conservation significance of the Eutherian carnivores is inferential, relying as it does upon indices of competition and predation, rather than experimental observation. It also uses only select aspects of the potential predatory and competitive impacts that Eutherians may have on *D. maculatus* however this reflects the poor state of knowledge about the resource use and behaviour of all four species. None-the-less, the results presented here provide a first indication of the relative impacts of each eutherian carnivore on the conservation of the Spot-tailed Quoll, and show that both the Dingo and the Feral Cat have a potentially much more significant impact on *D. maculatus* than does the Red Fox. This study also demonstrates that both the Dingo and the Cat occur in sympatry with *D. maculatus* in the WTWHA, while the Fox is allopatric.

A fundamental assumption of the rank scoring approach is that each attribute included in the scoring system is of equal importance with regard to impacts on *D. maculatus*. This is not the case. For example, sympatry with Quolls is a prerequisite for any direct ecological impact on them. The importance of any other of the scored attributes is thus made redundant if species are allopatric (i.e. Foxes and Quolls appear allopatric in the Wet Tropics).

9.4.1. Predatory effects of eutherian carnivores upon D. maculatus

Dingoes are known to consume Spot-tailed Quolls (this study, Wallis and Brunner 1984). Although not recorded in the published literature, it is extremely likely that Foxes do prey upon *D. maculatus* when given the opportunity given the incidence of medium and large mammalian prey types in Fox diet (Table 9.3). The low incidence of *D. maculatus* in Dingo scats and its apparent absence from the diet of the Fox suggest that predation on Spot-tailed Quolls is negligible over most of the latter's range. However, predation from these canids may play a role in limiting the Quoll's occupancy of fragmented habitats as discussed below. Data presented here suggest that Cats and Quolls are sympatric in localised areas, allowing for limited predation. However, Cat predation upon *D. maculatus* is expected to be negligible because of their similarity in size, and the difficulty a cat would be expected to have in subduing an adult Spot-tailed Quoll.

The predatory impacts of the Eutherian carnivores on Quolls may be greater in sclerophyll and fragmented forest than in unfragmented rainforest, because of their greater access to quolls in these habitats because of fewer arboreal escape routes available to Quolls and the greater ease of movement by the Canids through more open habitats. Additionally, Quoll populations tend to be sparse and/or transient in these latter habitats (Chapter 8) and thus particularly susceptible to any form of extrinsic mortality (e.g. Chapter 5). Even occasional predation upon *D. maculatus* by eutherian (or any other) carnivores is a potentially important factor in *D. maculatus*' population dynamics in these marginal habitats. In Chapter 8, I presented evidence to suggest that the distribution of the Spot-tailed quoll in north Queensland has contracted from more open habitats during this century. The role of all three introduced predators in this contraction and in restricting subsequent recolonisation of these habitats may be considerable, through the demographic effects of increased extrinsic mortality as well as competition for resources.

9.4.2. Competitive effects of eutherian carnivores on Spot-tailed Quolls

Mammals are the most important prey of all four carnivore species, and thus, where the distribution of the Spot-tailed Quoll overlaps with that of any of the Eutherian carnivores, competition may exist. When mammalian prey are broken down into ecomorphic categories, the combined competitive effect of the eutherian carnivores is greater than any one in isolation. Although none of the eutherian carnivores shares all of the same primary mammalian ecomorph prey of *D. maculatus*, the competitive impacts of the Eutherian carnivores are cumulative, where the Dingo and Cat co-occur with *D. maculatus*, they exert a combined competitive impact which is much greater than either species in isolation. Such as is the case in six of the core sub-populations of *D. maculatus* in north Queensland. Table 9.4 also indicates that where the three Eutherians occur in sympatry, they exert an even greater competitive force on *D. maculatus*.

The Spot-tailed quoll is the most arboreal of the four mainland Australian carnivorous mammals, and is probably the only species which actually forages arboreally. It remains to be seen if any of the eutherian carnivores forages throughout rainforest. I have suggested that the foraging behaviour of Cats and Dingoes may be largely confined to roads (e.g. Mahon *et al.* 1998) and other edges of closed forests, whereas that of Spot-tailed quolls certainly includes areas throughout the forest (Chapter 8).

I have been unable to define the degree of competition on a seasonal basis, and as such, it is possible that competition may be more intense under particular environmental or life-history scenarios, than the broad temporal framework used here indicates. The degree of competition can change over time with changing environmental conditions and can also vary depending upon whether a species is established or recolonising an area.

9.4.3. Differential population persistence and competitive advantage to Eutherian carnivores

The results of Population Viability Analyses conducted above suggest that populations of the Spot-tailed Quoll are more prone to extinction than are those of Australia's three Eutherian carnivores under a range of conditions that might result in increases in extrinsic mortality or decreases in recruitment. Interestingly, the Red Fox showed a level of extinction proneness similar to that of the Spot-tailed Quoll under some conditions of elevated extrinsic mortality (Figs 9.7-9.9). The use of Quoll mortality schedules for the analysis of Fox populations may explain this. On the other hand, perhaps Fox populations are prone to extinction from increases in extrinsic mortality, and the broad diet of the Fox which includes large quantities of plant material is an adaptation by the species to circumvent this state (see Table 9.3).

While the constraints imposed upon the VORTEX analyses presented above (see methods), suggest that they provide only an approximate guide to the relative responses of populations of the four carnivore species, the disparity in responses of populations of the four species in most treatments suggests that there is indeed a real difference in population persistence, especially between *D. maculatus* and the three Eutherian species. As discussed in Chapter 5, I believe that the short life-span and resultant low life-time reproductive output of Quolls compared to the Eutherian carnivores is the ultimate cause of the different behaviour of populations of the four species under conditions of increased mortality or reduced fecundity.

The results presented above indicate the mechanism by which the three Eutherian carnivores might supplant populations of *D. maculatus* over evolutionary time. In particular, the ability of populations of Eutherian carnivores to out-persist populations of *D. maculatus* (and by inference all other species of Dasyuromorphia), provides an insight into the mechanisms by which Eutherian carnivores have replaced marsupi-carnivores in Australia and South America over recent and geological time. These results also suggest that the future of Australia's marsupial carnivores in the wild is bleak. Even if we humans change our behaviour to better accommodate the needs of Quolls, their long-term survival rests on their ability to co-exist with the longer-lived, more stable populations of Cats, Dogs and Foxes.

9.5. Summary

- Dingoes, Foxes and feral Cats are potentially important predators on and competitors with *D. maculatus*. The Dingo exerts the greatest potential predatory effect; the feral Cat exerts the greatest potential competitive effect for prey. The rank-scoring approach I used suggests that paired combinations of the Eutherians and all three Eutherian carnivores together exert a much greater predatory and competitive impact on *D. maculatus*.

- The rainforest habitat of *D. maculatus* in north Queensland probably buffers the species against direct impacts from the Red Fox, however extensive areas of sympatry between *D. maculatus*, the Feral Cat and the Dingo are known within the Wet Tropics Area.

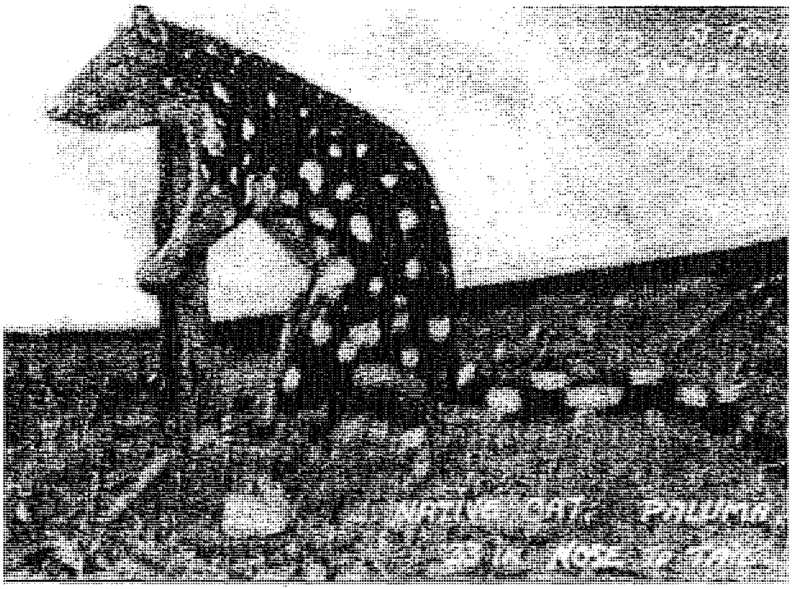
- The role of the Eutherian carnivores in hosts and vectors of pathogens to Quolls is unknown but potentially significant.

- Populations of all three Eutherian carnivores are inherently more able to persist through periods of increased mortality or reduced fecundity, than are populations of *D. maculatus*.

- The long-term future of *D. maculatus* appears to hinge on the availability of dense forested habitats in which the impacts of Eutherian carnivores and drought are buffered. The results of this Chapter that indicate predatory and competitive impacts by all three eutherian carnivores, and patterns from the fossil and historical record that demonstrate replacement of marsupial carnivore faunas by eutherian carnivores in each case that they have mingled, suggest that the evolutionary future of *D. maculatus*, and all carnivorous members of the Dasyuromorphia, is tenuous.

Chapter 10.

General Discussion: Conservation of the Spot-tailed Quoll and the future of Australia's carnivorous mammals



In previous chapters, I have highlighted the biological constraints experienced by, and the conservation status of *D. maculatus* in north Queensland. In this Chapter I present a conceptual model using a modification of the Pressure – State – Response model developed by the OECD and used in Australian State of the Environment reporting, for *D. maculatus*. I also discuss the future of Australia's carnivorous marsupials.

Chapter 10. General Discussion: Conservation of the Spot-tailed Quoll and the future of Australia's carnivorous mammals.

10.1. Preamble

In previous chapters, I have highlighted the biological constraints experienced by and the conservation status of, *D. maculatus*. In this Chapter I present a conceptual model of the conservation status of *D. maculatus* using a modification of the Pressure – State – Response model as developed by the OECD and used in Australian State of the Environment reporting.

10.2. Conservation of *D. maculatus*: a conceptual model

This model (Fig 10.1) explicitly lists the biological constraints on *D. maculatus* that were identified in previous chapters, the pressures (threats) on the species in north Queensland, and human community response required to ameliorate those pressures.

10.2.1. Ecological Constraints

The ecological constraints operating on *D. maculatus* have been identified in the preceding data chapters, are presented in Fig 10.1, and are summarised below.

10.2.1.1. Small population size

The life-history strategy of *D. maculatus* dictates that the species is restricted to the most equable, predictable and productive environments in the tropical north, resulting in a very limited distribution and concomitantly small population size (total adult population estimated at approximately 550 individuals Ch 8)). This small population size (which is the reason for the species being listed as Endangered (Chapter 8)), further compounds the problems of elevated extrinsic mortality associated with the species life history strategy (see below).

10.2.1.2. Short life span and low fecundity

The life history strategy of *D. maculatus* in particular its short life-span (3 years) and rigid breeding system (seasonality, monoestrus condition, constraints on litter size imposed by nipple number and subsequent low life-time fecundity), places a requirement upon populations for annually low levels of extrinsic mortality and predictably high breeding success each year (Chapters 5 and 9).

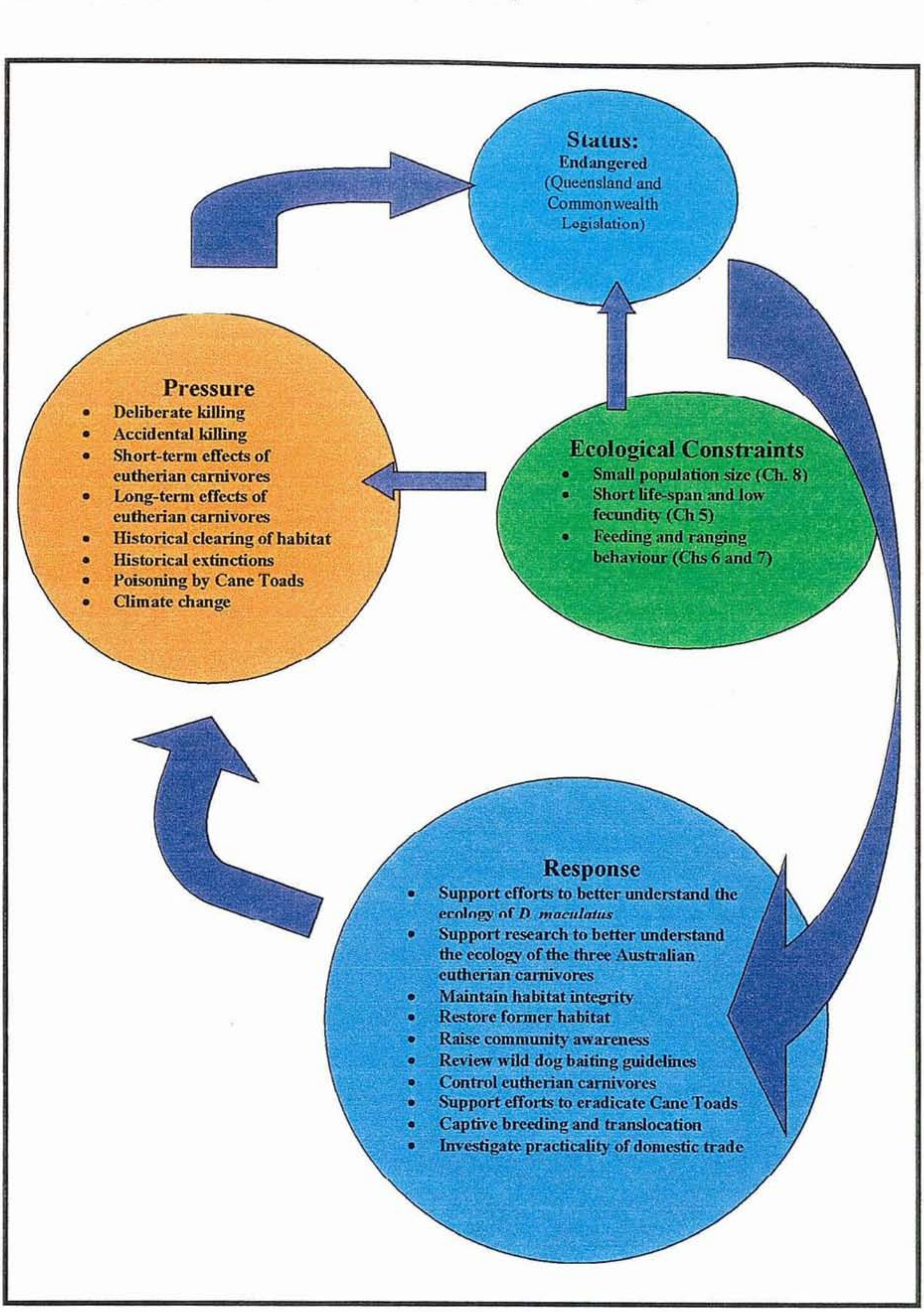


Fig 10.1. Modified Pressure – State – Response model for the conservation of *D. maculatus* in north Queensland.

10.2.1.3. Feeding and Ranging Behaviour

The behaviour of *D. maculatus* including its opportunistic carnivory (Chapter 6), wide ranging potential (Chapter 7), scent marking behaviour on roads (Chapter 7), and an apparent tendency to return again and again to a food source (Chapter 7), all render it particularly likely for individuals to come into contact with the agents of extrinsic mortality. These agents include humans who sometimes deliberately kill Quolls when they raid poultry yards and who accidentally kill Quolls with poisoned meat baits laid for Eutherian carnivores, and as road kills. Feral animals are another group of agents of extrinsic mortality of Quolls; for example there is strong anecdotal evidence that Quoll populations crash when Cane Toads colonise their habitats and the Quolls attempt to eat them (Burnett 1997).

The wide ranging abilities of Quolls (i.e. six km straight-line distances recorded over 24 hour period in this study (Ch. 7)), further suggest that within any population of *D. maculatus*, a large proportion of the population is capable of visiting a source of extrinsic mortality. Using the six km example, a poultry yard embedded in a matrix of Quoll habitat has the potential to attract Quolls from a circular area of nearly 40km^2.

10.2.2. Pressures (Threats)

10.2.2.1. Deliberate Killing

Deliberate killings of Spot-tailed Quolls occur in retaliation for their depredations upon domestic poultry, and to a lesser extent, when they enter houses, scavenging for food and food scraps.

I obtained 152 records of *D. maculatus* from north Queensland. Ninety-one of these records were of animals that were found at poultry yards or scavenging around houses (Appendix 8.2). The predilection of *D. maculatus* for poultry has been noted in many instances dating back to Goulds' observations from the late 1800s (Gould 1974). In this monograph he describes the species as, "a most dreaded enemy to poultry: it is consequently regarded by the settler as one of his greatest pests" (p110). A common theme during the closer settlement of Quoll habitat is of immediate Quoll depredations upon poultry, retaliation against Quolls and rapid disappearance of *D. maculatus* from those areas (Wet Tropics; Short (1988), Frawley (1987), and from personal communications with first settlers of post WWII selections on the Atherton Tablelands, Tom Conner pers. comm. (24/7/2001), Henry Tranter pers. comm. (3/7/2001): south-eastern Australia; Lunney and Leary (1988), Bennett (1990)).

A behavioural inclination for *D. maculatus* to return to a food source until it is depleted or the quoll is killed increases the risk that any Quoll raiding a human food source will eventually be killed. An example of this behaviour is illustrated by the photograph on the cover of this chapter. This Quoll raided a fowl yard at Paluma in the southern Wet Tropics area, where the species is probably now extinct. Over a three week period in the early 1940s, this individual killed 51 fowl before eventually being killed itself (Tom Conner pers. comm. 24/7/2001).

10.2.2.2. Accidental Killings

Accidental killings of Spot-tailed Quolls take the form of accidental poisoning during wild dog baiting campaigns, and road kills.

Poison Baiting

Circumstantial evidence suggests that accidental poisoning of Quolls occurs when they ingest baits laid for wild dog control (e.g. Belcher 1996). This is potentially one of the most serious yet manageable threats to *D. maculatus* in north Queensland. Sodium Monofluroacetate (1080) poison baits are used throughout Australia, including north Queensland, in the control of wild dogs and dingoes. Approximately one tonne of poisoned meat baits are laid on the southern Atherton Tablelands each year (Paul Davis, Land Protection Officer, Department of Mines, Energy and Resources, Atherton, pers. comm. 23/9/2000). 1080 kills by blocking the Krebs Cycle, the physiological process by which food is converted to energy. Captive and field studies on the larger south Australian subspecies of Spot-tailed Quoll have shown that the species readily finds and consumes meat baits that are laid for wild dogs (Murray 1999, Murray *et al.* 2000). Doses of 1.8mg/kg of animal weight result in 50% mortality of quoll populations (Murray 1999). In-line with Queensland guidelines, doses of 10mg of 1080/125g meat bait are used in the approximately 750kg of poison baits distributed on the Atherton Tablelands each year (Queensland Department of Natural Resources 1997). It is likely that an individual Spot-tailed Quoll would consume at least a single 125g bait in a feed (This is close to the average weight of a Bush Rat *Rattus fuscipes*). This equates to a dosage of 6g 1080/kg and 9g/kg per average sized north Queensland male and female *D. maculatus* respectively, which is three and six times the LD_{50} dose for 1080, identified by Murray (1999). This clearly places *D. maculatus* at risk of fatal poisoning in areas such as the Atherton Tableland where there is an extensive shared boundary between Quoll habitat and grazing/dairy country.

Road kills

Green and Scarborough (1990) attribute the majority of human induced mortality of the species in Tasmania today to road kills. Twenty-two of the 89 quoll sighting records (25%) from the Wet tropics Area for which I obtained relevant data were road kills (Appendix 8.2). This suggests that road kills are a significant source of mortality of Spot-tailed Quolls in the Wet Tropics Area. The breakdown of roadkills in the Wet Tropics Area is;

(1) Daintree Population (see Map 8.1)

- Four (4) roadkills on the Mt Windsor Road, in the Windsor Uplands.
- One (1) roadkill from the Mt Lewis Rd, in the Carbine Uplands.

(2) Atherton Population (see Map 8.1)

- Ten (10) roadkills on the Palmerston Highway where it passes through the South Johnstone Uplands.
- Four (4) roadkills from the Lamb Uplands including,
    - (i) three (3) roadkills from the Kennedy Highway where it passes through the northern reaches of the Uplands and,
    - (ii) 1 record from the Mt Haig Rd .
- Two (2) roadkills, 1 each from the Tully Falls Rd and the Maalan Rd in the Atherton Uplands.

Spot-tailed Quolls are behaviourally inclined to be found on roads. Therefore due to the roads play in scent marking (Ch. 7) and as sources of carrion, the incidence of roadkills of *D. maculatus* is potentially much greater than might be expected if road kills were a random event. Roads may also play a more insidious role in depleting Quoll populations by acting as routes of invasion into rainforest for Eutherian carnivores which may prey upon or compete with Quolls (Ch. 9) and Cane Toads (Seabrook and Dettman 1996) which may poison Quolls that attempt to eat them.

10.2.2.3. Short term effects of eutherian carnivores

All known core sub-populations of *D. maculatus* in north Queensland occur in at least partial sympatry with at least one Eutherian carnivore species. Six of these populations occur in at least partial sympatry with two species of Eutherian carnivore; the Cat and the Dingo. I have explored the potential for predatory and competitive interactions between Eutherian carnivores and *D. maculatus* in the wet tropics (Ch. 9) and shown that while the risk of predation in rainforest habitats is low, there is potential for dietary competition especially where more than one Eutherian carnivore co-occurs with *D. maculatus*. The full extent of this interaction depends to a great extent on the degree to which the Eutherian carnivores penetrate into the rainforest away from roads or other edges. There is no data on this aspect of Eutherian carnivore habitat use.

In non-rainforest habitats, such as much *D. maculatus'* range in southern mainland Australia and where *D. maculatus* is historically known from north Queensland, the role of Eutherian carnivores as a threatening process is potentially much greater due to their presumed greater dispersion throughout those habitats.

10.2.2.4. Long-term effects of Eutherian carnivores

Historical data (Ch. 3) and the greater extinction proneness of Quoll populations under regimes of increased mortality and decreased recruitment compared to Eutherians (Ch. 9) suggest that in the longer term, Eutherian populations may replace Quoll populations by default during resource bottlenecks or other times of increased mortality or reduced recruitment.

Additionally, the evolutionary potential of Australia's feral cat gene pool received a boost in the mid 1990s with the introduction of *Felis catus* x *Felis bengalensis* F4 hybrids into Australia. *Felis bengalensis*, the Bengal Cat, is an arboreal and water-loving inhabitant of rainforest environments in Asia (Nowak and Walker 1991) and threatens to introduce those qualities that are lacking in *F. catus* into their feral populations. While it has been argued that the high cost of individuals will ensure that animals are not allowed to stray, it is naive to consider that the spread of *Felis bengalensis* genes will remain under human control over even the medium term (100s of years) let alone longer evolutionary time scales (1000s - 10 000s years).

10.2.2.5. Historical clearing of habitat

Habitat able to support core populations of *D. maculatus* naturally expands and contracts over geological time (e.g. Nix and Switzer 1991). Alienation of habitat as discussed here though, is much less subtle, consisting of clearfelling of areas for agriculture and grazing. Approximately 80 000 hectares of former habitat for *D. maculatus* was cleared on the Atherton Tableland between the late 1800s and the 1988 (Winter *et al.* 1987, Collins 1994). While clear felling affects Spot-tailed Quoll populations directly through habitat loss, the secondary effects of clearing maybe more insidious, and include the creation of habitats suited to Eutherian carnivores, Cane Toads, and humans. Because of the Quoll's high mobility (Chapter 7), these secondary edge effects can affect Quolls for many kilometres into the forest because animals make routine or occasional forays to forest edges.

Most remaining habitat of *D. maculatus* is unsuitable for agriculture and occurs within the protected Wet Tropics World Heritage Area of North Queensland (Chapter 8). Continued habitat clearance is thus no longer a threat to the species. Forestry practices which may decrease the carrying capacity of habitat through the depletion of key prey species (for example ringtail possums) and of natal den sites are also no longer a threat because of the protection status afforded to quoll habitat by World Heritage Listing.

10.2.2.6. Historical extinctions of populations of *D. maculatus*

I have documented the probable historical extinction of *D. maculatus* in the Mt Spec Uplands, and its localised extinction from cleared areas of the Atherton Tablelands (Chapter 8). It is also possible that populations of the species have become extinct at other sites in north Queensland from which it has not been recorded for over 50 years (see Chapter 8).

Historical extinctions result in a decrease in the size of the north Queensland metapopulation of *D. maculatus*. A decrease in numeric size of the population leads to further pressure on the conservation status of the species due to the effects of the small population paradigm (e.g. see Caughley and Gunn 1996).

10.2.2.7. Poisoning by Cane Toads

Northern quoll populations have been shown to crash following Cane Toad colonisation of their habitat (Burnett 1997). Western quolls have been shown to be susceptible to toad toxin (Covacevich and Archer 1975) and Spot-tailed quolls have been found to eat frogs in Tasmania (Green and Scarborough 1990). It therefore seems likely that Spot-tailed quoll mortality rates are increased by colonisation of their habitat by Cane Toads.

Watt (1993) noted that in south-eastern Queensland, quoll populations were numerically highest in areas from which toads were absent. In north Queensland, quoll populations are also most abundant in areas which lack toads although this effect may be confounded by other altitudinal and human impacts (Chapter 8).

10.2.2.8. Climate change

Because of their role as top order predators (Chapter 6), Spot-tailed Quolls are expected to be the most vulnerable of the Wet Tropics mammal species to perturbations of the rainforest food web brought about by climate change. In addition, their small population size and their relictual mountaintop distribution (Chapter 8) suggest that they will also be amongst the most susceptible of the Wet Tropics mammal species to any further restriction of the highland altitudinal zone.

Increased atmospheric CO_2 levels are an integral component of the Greenhouse scenario and may also have implications for the Wet Tropics food web. For example, Lawler (1993) contends that increases in atmospheric CO_2 levels within the range predicted in the Greenhouse scenario by the year 2030, will impact on Eucalyptus leaf-eating, *Pseudocheirus peregrinus* populations, by reducing the nutrient value of leaves which are an important component of their diet. The extent of the impact of this change on rainforest ringtail populations, which are a very important component of the diet of *D.*

maculatus is unknown, as are the extent of food web perturbations caused by other changes in primary productivity.

Based on current models, the extent of astmospheric warming in Australia is expected to be between approximately 1^0C and 4^0C by the 2050's and between 2 and 5.5^0C by the 2080's (Commonwealth of Australia 2000). This warming effect is expected to be greatest in inland areas, but I expect that due to the very small altitudinal extent of upland rainforest (core habitat of *D. maculatus*) in north Queensland, even a minor increase in temperature here will represent a significant loss of core habitat for *D. maculatus*. Concomitant with this postulated decrease in habitat availability in highland adapted species is the increase in habitat availability of species which are currently restricted below certain altitudes, including the Cane Toad *B. marinus*.

10.2.3. Responses

A range of responses are required to deal with the pressures which operate on populations of *D. maculatus* in north Queensland (Fig. 10.2). These responses include: (i) supporting studies of the ecology of *D. maculatus* and (ii) the three Eutherian carnivores; (iii) maintaining existing habitat; (iv) restoring alienated habitat; (v) raising community awareness about Quolls and the pressures they face; (vi) reviewing wild dog baiting guidelines; (vii) examining methods for long-term control of Eutherian carnivores and; (viii) supporting efforts to eradicate Cane Toads. Other responses that I recommend here include; (ix) an investigation into the practicality and role of captive breeding and translocation of Quolls and; (x) development of a domestic animal industry based around threatened species and in particular *D. maculatus*.

These responses include research and management components that are listed separately beneath each Response, below. In most instances, research is still required to better direct management responses.

PRESSURE	**RESPONSE**	**PRIORITY**
All pressures	Support research to better understand ecology and habitat use by *D. maculatus*	A
Short-term effects of Eutherian carnivores	Support research to better understand the resource use and life-history strategy of Eutherian carnivores	A
Short-term effects of eutherian carnivores Long-term effects of eutherian carnivores Poisoning by Cane Toads Climate change	Maintain integrity of existing habitat	A
Short-term effects of eutherian carnivores Poisoning by Cane Toads Climate change Historical clearing of habitat Historical extinctions	Restore former habitat	B
Deliberate killing Accidental killing Short-term effects of eutherian carnivores	Raise community awareness	A
Accidental killing Short-term effects of eutherian carnivores Long-term effects of eutherian carnivores	Review Queensland baiting guidelines	A
Short-term effects of eutherian carnivores Long-term effects of eutherian carnivores Historical clearing of habitat Climate change	Control Eutherian carnivores	B
Poisoning by Cane Toads Climate change Historical clearing of habitat	Support efforts to eradicate Cane Toads	B
Historical extinctions	Captive breeding and translocations	B
All pressures	Investigate practicality of adoption of *D. maculatus* into domestic pet trade	A

Fig 10.2. The relationships between the pressures and responses listed in Fig 10.1. See text for full descriptions of each pressure and of each response.

10.2.3.1. Support research to better understand the ecology and habitats of *D. maculatus*

PriorityA: A better understanding of the ecology and habitats of *D. maculatus* in north Queensland is essential for targeted research and management plans that will contribute to the amelioration of pressures acting on populations of the species.

Required research includes:

- Development of a model of the Quoll/Human interaction on the Atherton Tablelands in particular the extent and nature of that interaction.
- A refinement of knowledge of the distribution and abundance of the Spot-tailed Quoll in north Queensland including survey of areas from which Quolls were known early in the 1900s, but from which no records have been had in the past 50 years (includes Big Tableland, Mt Finnegan, Cardwell Range, Paluma, Great Basalt Wall and Eungella areas) (links with 10.2.3.3).

10.2.3.2. Support research to better understand the resource use and life-history strategy of Eutherian carnivores.

Priority A: A proper understanding of the life-history response of Eutherian carnivores is required to fully understand their long-term role with respect to *D. maculatus*. A refined understanding of their resource utilisation, in particular their dispersion through rainforest habitats that support Quolls is also required to better understand their potential short-term impacts.

My research of the potential impacts of Eutherian carnivores on *D. maculatus* provides a first approximation because the detailed knowledge required for a more comprehensive assessment has not been collected.

Research required to attain this knowledge includes:

- Examination of habitat utilisation including the dispersion of Eutherian carnivores throughout Quoll habitat.

- Collection of habitat specific schedules of birth and death for Dingoes, Feral Cats and Foxes in order to more confidently model the responses of these species to specific environmental conditions and to efforts to control them (links with10.2.3.7).

10.2.3.3. Maintain integrity of existing habitat

Priority A: The maintenance of existing habitat is crucial to the survival of *D. maculatus*.

Existing habitat manages itself and the best that we can do is to not interfere with the natural processes in rainforest ecosystems. Maintenance of habitat integrity (i.e. vegetation structure and floristics) buffers the effects on populations of *D. maculatus* from a range of pressures including the effects of; (1) Eutherian carnivores, (2) Cane Toads and (3) climate change. Although there is no firm data, it appears that within forest systems, Eutherian carnivores and the Cane Toad reach their highest abundances in disturbed areas and along roads. Maintenance of habitat integrity may alleviate some of the impacts of climate change, by providing areas for Quolls to move into in the event of wide-spread environmental change.

Maintenance of existing habitat will have flow on benefits to all other upland rainforest fauna, including approximately 30 species rare and threatened fauna that are found in the Australia's wet tropical rainforests (*Commonwealth of Australia Environment Protection and Biodiversity Conservation Act 1999*; *Queensland Nature Conservation (Wildlife) Regulation 1994*).

Research requirements

Research requirements include:

- Development of a refined model of Spot-tailed Quoll habitat (Links with 10.2.3.1)
- Development of a model of the anticipated impacts of Global warming in order to identify which existing habitat areas are most at risk, and which are likely to be important corridors and reservoirs for *D. maculatus* under predicted enhanced Greenhouse scenarios.

Management requirements

Management requirements include:

- Maintenance of existing habitat requires that road construction, upgrading of disused roads, dam building, powerline construction and other infrastructure developments are excluded from areas known to support populations of *D. maculatus*. In particular, road or other infrastructure development on the Mt Windsor Tableland, the Mt Carbine Tableland (Mt Lewis and Mt Spurgeon Roads), and the Lamb Range (Mt Haig and Mt Edith Roads) needs to be limited. Similar conditions need apply to areas identified as important refuges and movement corridors under conditions of the enhanced Greenhouse effect.
- Maintenance of existing Quoll habitat may also require the control of Eutherian carnivores dependent upon the results of research on habitat use by these species (see 10.2.3.2.).

10.2.3.4. Restore former habitats

Priority B: Although important in the longer term, the restoration of former habitats is a lower priority than the management of existing habitat for *D. maculatus*.

Restoration of former habitats includes replanting of cleared habitats especially where replanting acts to reconnect areas of known or potential Quoll habitat. Revegetation needs to proceed hand in hand with other pressures including control of Eutherian carnivores and Cane Toads and deliberate and accidental killing by humans. Restoration of former habitats might also include control of the above pressures in relatively intact habitats from which *D. maculatus* has disappeared (e.g. Mt Spec Uplands) prior to relocation there (see 10.2.3.9). Restoration of former habitats buffers the effects on populations of *D. maculatus* from a range of pressures including the effects of: (1) Eutherian carnivores, (2) Cane Toads, (3) historical extinctions, (4) historical clearing and (5) climate change.

Maintenance of existing habitat will have flow on benefits to all other upland rainforest fauna, including approximately 30 species rare and threatened fauna that are found in the Australia's wet tropical rainforests (*Commonwealth of Australia Environment Protection and Biodiversity Conservation Act 1999*; *Queensland Nature Conservation (Wildlife) Regulation 1994*).

Research Requirements

Research requirements include:

- Rigorous investigation of the habitat requirements of *D. maculatus* in order to ensure that restoration works are resulting in Quoll-suitable habitats (links with 10.2.3.1 and 10.2.3.3).
- Monitoring of Quoll populations in areas adjacent to and within alienated habitats is required in order to determine the uptake of these restored habitats by *D. maculatus*.

Management Requirements

Restoration of habitats that have been alienated by clear felling requires tree planting and protection of remnant vegetation (mostly on freehold land) on the Atherton Tablelands. Areas adjacent to the forests of the eastern and southern margins of the Tablelands are adjacent to extant populations of *D. maculatus* and are the priority areas for restoration of Quoll habitat. The tenuous forest connection that links the main body of rainforest on the southern side of the Tablelands with the isolated forests of the Herberton Range is also a high priority area for revegetation.

Restoration of habitats from which Spot-tailed Quolls have disappeared but in which plant communities are relatively intact, for example, the comparatively intact wet sclerophyll belt that runs the western length of the wet tropics rainforests and the Mt Spec uplands, requires the control of Eutherian carnivores, mitigation of wild dog baiting effects, and raising community awareness in order to prevent deliberate and accidental killing of Quolls by humans (see below).

10.2.3.5. Raise community awareness

Priority A: Raised community awareness of the conservation values of *D. maculatus*, and of the value of private land for conservation of the species is critical in the long-term as human land-use pressure increases adjacent to the core habitats of *D. maculatus* in the Wet Tropics..

Raising community awareness is a key response to most pressures operating on populations of *D. maculatus:* (1) accidental killing, (2) deliberate killing, (3) restoring former habitats, (4) maintaining existing habitats and (5) controlling domestic Eutherian carnivores.

Research Requirements

Research requirements include:

- An investigation into the nature and frequency of Spot-tailed Quoll/Human interactions on the Atherton Tablelands in order to target awareness raising activities at sections of the community where that is most needed (links with 10.2.3.1).
- Monitoring of Quoll related community enquiries to QPWS and other management agencies and response of the community to public talks and displays.

Management Requirements

Awareness raising among the community needs to be conducted in a consistent manner and requires that community requests for information or other assistance are dealt with promptly. The establishment of a single contact point for community queries is essential in order to meet these aims.

A community awareness raising project has commenced on the Atherton Tablelands this year. It is run by a local community group with Threatened Species Network funding and the project aims are; "to reduce the incidence of accidental and deliberate killings of Spot-tailed Quolls on the Atherton tablelands by raising public awareness about Quolls and their endangered status, and the importance of private land for conservation of this species".

Activities to date include:

- the establishment of a Quoll web site (www.infocus.to/quolls);
- establishment of a community contact point for dissemination of Quoll related information based out of the Atherton Office of the Queensland Parks and Wildlife Service;
- development of displays for community markets;
- a series of talks to 10 schools and six community groups on the Atherton Tablelands;

- a brochure which highlights the main threats to Spot-tailed Quolls on the Atherton Tablelands from human activities (Appendix 10.1), and;
- a pamphlet which describes ways of reducing predation from Quolls on poultry (Appendix 10.2).

10.2.3.6. Review Baiting guidelines

Priority A: Poision baiting is possibly one of the most serious yet manageable threats to *D. maculatus*. For this reason it needs to be addressed as a top priority.

Revision of Queensland and other States and Territories wild dog baiting guidelines after identification and experimentation with alternative techniques will buffer the effects of accidental killing of Quolls when they take poison baits laid for dogs/dingoes.

Research Requirements

Research requirements include:

- A review of wild carnivore baiting strategies from around the globe,
- Identification of other potential models for wildlife friendly carnivore baiting guidelines,
- Identification, experimentation and adoption of a best practice system for baiting feral Eutherian carnivores but not native wildlife, in particular Quolls.

Management Requirements

Quoll friendly baiting guidelines need to be implemented on all properties that lie adjacent to the Wet Tropics Area, in particular, properties on the eastern and southern Atherton Tablelands within the Atherton, Eacham and Herberton Shires.

10.2.3.7. Control Eutherian carnivores

Priority B: Further resolution of the impacts of the Eutherian carnivores (10.2.3.2) is required prior to the implementation of a Eutherian carnivore control program for the benefit of *D. maculatus* and thus control itself is a lower priority at this stage.

Local control of Eutherian carnivores will buffer the short-term effects of Cats, Dingos and Foxes on Quoll populations. Control of these predators is also integral to the maintenance of existing habitat and the restoration of former habitats and will be of benefit to most other native fauna.

Due to the evolutionary significance of *Felis bengalensis* hybrids a policy of compulsory sterilisation of all *F. catus* x *F. bengalensis* hybrids before import into Australia and of those already in Australia is required. A policy restricting the import of any new strains of canid or felid into Australia is also required.

Research requirements

Research requirements include:

- Review and evaluate strategies for controlling Eutherian carnivores in a way that doesn't impact on populations of *D. maculatus* or other fauna (links with 10.2.3.6).
- Examine dispersion and abundance of eutherian carnivores throughout Quoll habitat, in particular, throughout deep rainforest (links to 10.2.3.2.).
- Examine the extent and nature of incursions by free-ranging domestic eutherian carnivores into Quoll habitat.
- Collect life-history data, especially birth and death rates of Eutherian carnivores for use in population viability analyses (links with 10.2.3.2).

Management Requirements

Management requires:

- A sustained, Quoll friendly control program for Eutherian carnivores throughout the range of *D. maculatus* in north Queensland. Control of all Eutherians should be conducted simultaneously, to avoid increases in some species through competitive or predator release. For example evidence suggests that Red Fox numbers increase when Dingo numbers are reduced (Jarman 1986), and that Cat numbers similarly increase when Fox and Dingo populations are reduced (Christensen and Burrows 1994).

  Areas of known sympatry between *D. maculatus* and feral cats are priority areas for cat control and include:

1. The summit area of Mt Bartle Frere,
2. The summit area of Mt Bellenden Ker,
3. The western Mt Windsor Tableland,
4. The road network of the South Johnstone forestry area,
5. The Mt Lewis Rd and,
6. The cleared areas of the Atherton Tablelands.

Areas of narrow allopatry and probable sympatry between *D. maculatus* and the Red Fox are priority areas for fox control and include:

1. The cleared areas of the Atherton Tablelands especially in the southern and eastern portions, and,
2. The Kuranda/Speewah area.

Areas of sympatry between *D. maculatus* and Dingos are priority areas for Dingo control and include all areas from which core sub-populations of *D. maculatus* are known.

10.2.3.8. Support efforts to control Cane Toads

Priority B: The impacts of Cane Toads on *D. maculatus* are unproven and thus control of Cane Toads in the Wet Tropics area is a lower priority at this stage although the likely whole of ecosystem benefits of Cane Toad removal justify their control irrespective of their impacts on Quolls.

Control of Cane Toads will ameliorate the potential effects of Cane Toads on *D. maculatus*, and in turn will ameliorate this one aspect of the effects of historical habitat clearing and climate change.

Research Requirements

Research requirements include:

- Research into the distribution and abundance of Cane Toads throughout Quoll habitat.
- Research into the efficacy of hand removal of Cane Toads from upland roads in the Wet Tropics Area. A road-based toad monitoring and removal program should consist of a monthly or two monthly series of road traverses commencing at the start

of the storm season in October and probably ceasing each year by April or May. The actual design of this removal program is dependent upon the results of monitoring.

Management requirements

Six road systems pass through core quoll habitat in the Wet Tropics Area and these would form the basis of a Cane Toad control program. These roads include;

(i) the Mt. Windsor Tableland Road (15km),
(ii) the Mt. Spurgeon (10km) and Mt. Lewis (42km) Roads on the Carbine Tableland,
(iii) the Mt. Edith (15km) and Mt. Haig (15km) Roads on the Lamb Range,
(iv) the South Johnstone Forestry area road network (c. 100km) in the Palmerston area and,
(v) the Tully Falls/Koombooloomba Rd in the Tully Falls area.

10.2.3.9. Captive Breeding and Translocation

Priority B: Captive breeding and translocation is possibly one of the most important tools for the conservation of *D. maculatus*, although more information is required on genetics and distribution of the species before translocation can be undertaken.

Captive breeding and subsequent translocations will ameliorate the effects of historical and future extinctions of *D. maculatus*.

Research requirements

Research requirements include:

- Refinement of models of distribution of *D. maculatus* in the Wet Tropics (links to 10.2.3.1).
- Documentation of genetic variability of *D. maculatus* in the Wet Tropics Area.
- Development of effective animal husbandry techniques for *D. maculatus* (links with 10.2.3.10).

Management requirements

- If possible, Quolls for the initial captive breeding stock should be sourced from populations that are experienced with Cane Toads and closer settlement with humans. If there is any genetic basis for survival in sympatry with these agents of mortality, this will ensure a greater chance of survival of translocated animals.
- Captive bred Quolls will be translocated to areas of their former range from which the species is now extinct, (i.e. Mt Spec), and other areas that they may prove to have disappeared from dependent upon further studies (see 10.2.3.1.).
- The removal of animals from the wild for establishment of a captive stock must not adversely affect wild populations. This may be achieved by taking sub-adults during their early dispersal phase (November-January), when natural attrition is high.
- A stud book of all captive bred Quolls needs to be developed, to ensure that the genetic diversity of wild populations is maintained within the captive population, and so that translocations of captive born young into the wild contribute to genetic diversity of the wild population (links with 10.2.3.10).

10.2.3.10. Investigate the practicality and scope of bringing Quolls in to the domestic animal trade.

Priority A: This may be the only option for the medium-term survival of *D. maculat*us and is a potentially important way of subsidising captive breeding for translocation and an important tool for raising public awareness.

The development of a well managed domestic animal trade in Spot-tailed Quolls will not ameliorate any of the pressures listed above, but it will circumvent them by ensuring a robust and genetically diverse captive stock of Quolls in captivity. These stocks will provide a bank of animals that can be used for translocations into the wild, and will ensure that the species survives should large-scale and uncontrollable forces send wild populations extinct (e.g. climate change, fire ants, or other introduced animals).

I also argue that exposure of the public to native animals through a native animal pet industry will contribute to raising community awareness about the aesthetic and conservation values of native animals and the need to conserve their habitats.

Because there is only a very poorly developed native animal pet industry in Australia, any such moves in that direction for *D. maculatus* would require the development of a base-line model for the development and maintenance of such an industry, as well as a model specific to the needs of *D. maculatus*.

Research requirements

Research requirements include:

- Development of quoll husbandry techniques (links with 10.2.3.9).
- Development of a model for a sustainable native pet industry.
- Development of a model for the captive breeding and distribution among the public of Quolls, and the accountability of State agencies and private individuals in dealing with Quolls.

Management requirements

Management requirements include:

- Development of a model for a sustainable native animal pet industry. Such a model needs to be economically and environmentally sustainable and needs to be developed within the following constraints:
  (i) Self-funding so as not to draw funding away from other conservation works,
  (ii) Well policed to ensure that Quolls are housed comfortably and are not taken from the wild and,
  (iii) That no pressure is placed on populations of native fauna as a consequence of high abundance of free-ranging Quolls.

- A stud book of all captive bred Quolls needs to be developed, to ensure that the genetic diversity of wild populations is maintained within the captive population, and so that translocations of captive born young into the wild contribute to genetic diversity of the wild population (links with 10.2.3.10).

10.3. A future for Australia's marsupial carnivores?

Carnivorous marsupials have been a feature of the Australian fauna for at least the past 25-30 million years. Over that time two Orders and four families have contributed at least 41 species to the Australian carnivore guild. The diversity of marsupial carnivores was halved at around the time of the Glacial Maximum (25 – 35 000 years ago), when both carnivorous Diprotodontian lineages became extinct, leaving only the six Australian Dasyuromorphian carnivores extant. These six species have not fared well since the advent of Europeans to Australia. The Thylacine is now extinct, the Devil is restricted to the island of Tasmania, and all four quoll species have undergone dramatic collapses of their range. At the same time, the three species of feral Eutherian carnivore have expanded their ranges so that they are now the only mammalian carnivores across most of mainland Australia.

This pattern reflects that which occurred in Australia over the past 4000 years when Thylacines replaced the Thylacine and Devil on the Australian mainland. It also reflects the sequence of events on the South American continent when Eutherian carnivores gained access across the Panama Ismuth during two episodes of its formation. Each time that Eutherians crossed into South America, a suite of marsupial carnivores was replaced by the invading Eutherian carnivores. Today that entire family, the Borhaeyenidae is extinct and the only truly carnivorous marsupial is the Quoll-sized Thick-tailed Opossum, *Lutreolina crassicaudata*.

I have shown in Chapter 3 that this pattern of replacement of marsupials by Eutherians is explicable in terms of various phylogenetic and biogeographic constraints. Phylogenetic constraints include constraints on specialisation and radiation of marsupial faunas compared to Eutherians. These constraints include constraints on radiation of molar morphology, on morphological radiation caused by the marsupial requirement for rapid early development in order to survive early extra-uterine existence, and the smaller and less developed brain that constrains the evolution of novel social and hunting behaviour.

Biogeographic constraints on the survival of Australia's (and South America's extinct) marsupial carnivores in sympatry with Eutherian carnivores include the long history of evolution and isolation and the smaller land-mass of both Australia and South America compared to the northern continents and Africa. It has been argued that both of these factors lead to an environment in which competition is less intense (Briggs 1996) and in which the gene pool is less diverse. When confronted with suites of invading species with similar niches from larger and connected land-masses, Australia's (and South America's pre-contact) fauna finds itself at a disadvantage and in danger of replacement.

Thus, even if we can turn around the decline of *D. maculatus* and other members of the genus *Dasyurus* by managing human imposed pressures, their longer term survival must hinge upon either; (i) the unlikely scenario that we are able to eliminate the Eutherian carnivores from the Australian continent, or (ii) upon the equally unlikely scenario of their being able to exist in sympatry with Australia's flourishing Eutherian carnivore fauna, not only in the immediate future but over the next 100 000's of years.

Because of the virtually identical life-history strategy of all the *Dasyurus* species (Chapter 2), the results of this thesis are applicable to all members of the genus. The drastic decline in range of all Australian *Dasyurus* species (Chapter 2), and examples of local extinction of various species over very short intervals following changes in human landuse (e.g. Jones 1993, Lunney and Leary 1988, Bennett 1990) are all explicable in the context of the model expounded above. Without focussed conservation action each of Australia's *Dasyurus* species is threatened with extinction.

The genus *Dasyurus* represents the last vestige of a marsupial carnivore heritage which has endured Ice Ages, the arrival and flourishing of Aboriginal cultures, and until now, the environmental pressures of European Australia and the global economy. With three out of four species now listed as Vulnerable or Endangered (Chapter 2), the future of this group is tenuous. Much more is at stake in the conservation of *Dasyurus* species than the survival of a genus, they represent the last of a long line of marsupial carnivores, and with their passing would disappear the last echoes of a much different time, when pouched carnivores stalked the Australian landscape.