

OVERVIEW OF THE IMPACTS OF FERAL CATS ON AUSTRALIAN NATIVE FAUNA

invasive species program



Australian Nature Conservation Agency

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by

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FOREWORD

Feral cats and native wildlife - what are the impacts? This question has been asked by researchers for many years, seemingly without much progress. On the one hand, we know that feral cats have caused extinctions on some islands and have caused the failure of reintroduction programs for endangered mammals in semi-arid areas. On the other hand, cats have been present in Tasmania, on Kangaroo island and in the northern parts of Australia for at least as long as anywhere else yet these places have retained virtually the full complement of their original fauna.

If a native population is declining, the cause of that decline should be identified before any remedial work is undertaken. Many different things, such as habitat modification or introduced species, could be a causal factor in such declines. As such it is highly desirable to identify the actual cause of a decline in the population before commitment is made to an extensive feral animal control campaign.

A series of national overviews were commissioned by the Invasive Species Program to determine the impacts of feral animals on our native wildlife. This overview brings together all of the existing information concerning the effects of feral cats on native species and identifies key gaps in knowledge. It will be an invaluable tool in clarifying the impacts of invasive species on the Australian environment and, perhaps more importantly, provides a strategic direction for future research and control of feral cat impacts.



Peter Bridgewater
Chief Executive Officer
Australian Nature Conservation Agency

SUMMARY

This report provides an overview of the impact of feral cats *Felis catus* on native fauna of the Pacific region, with particular reference to Australia and its island territories. In Australia, cats take a wide variety of native species of mammals, birds and reptiles, but show evident preference for young rabbits or small marsupials where these are available. Reptiles are taken primarily in and habitats, while birds often feature predominantly in the diet of cats on islands. Despite their catholic diet, population-level impacts of feral cats on native fauna have been poorly documented. There is considerable potential for competition to occur between cats and carnivorous species such as quolls and raptors, but no critical evidence has yet been adduced. There is also potential for amerisal impacts to occur, either via transmission of the pseudophyllidean tapeworm *Spirometra erinacei* or of the protozoan parasite *Toxoplasma gondii*, but evidence for deleterious effects in freeliving animals is not compelling. Direct predatory impacts have been inferred from anecdotal and historical evidence, more strongly from failed attempts to reintroduce native species to their former ranges, and most critically from the decimation of island faunas and responses of prey species following experimental removal of cats or reduction of cat numbers. Attributes of the biology of feral cats and their prey species derived from the literature review were used to develop a rank-scoring system to assess the susceptibility of native species to cat predation. Species listed federally as endangered or vulnerable were designated as being at zero, low or high risk of impact from cats according to their attribute scores, and their distributions mapped from primary sources and actual locality data. Based on the number of threatened species they contain, localities and regions within Australia were placed in order of priority for future research to clarify the precise impacts of feral cats. Although difficult and expensive to carry out, controlled and replicated field removal experiments are recommended to elucidate cat impacts in all mainland areas. Removal of cats should take place also on offshore islands and island territories, but only if pilot studies show that this will not release populations of alternative predator species such as introduced rats. If release appears likely, cats should be removed only as a component of an integrated control program that targets all relevant predators.

Disclaimer

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EXECUTIVE SUMMARY AND RECOMMENDATIONS

- 1) Population and community-level impacts of feral cats on native fauna have been little studied, but evidence from several studies indicates that direct predation is the most important process involved.
- 2) On the Australian mainland cats can impact on native mammals weighing up to about 2000 g, but impact falls most heavily on smaller species, especially those weighing <220 g. Vulnerability to predation is enhanced for species occupying open or otherwise unprotected habitats, and by behavioural traits such as saltatory locomotion. Cats can impact on birds up to about 1000 g, but impact again falls most heavily on smaller species weighing <200 g. Ground foragers and ground nesters are most vulnerable, especially in open habitats, although impact on hollownesting species is also possible.
- 3) On islands, cats have had major impacts on terrestrial mammals up to 3000 g and birds up to 3500 g, although smaller species are preferred. As in mainland situations, vulnerability to impact is increased if protective habitat is not available, if foraging, burrowing or nesting activities take place on the ground surface or other exposed sites and, for birds, if the island is occupied year-round.
- 4) In mainland areas and on some islands where introduced mammals (rabbits, *Mus domesticus*, some *Rattus spp.*) or native mammals (usually *Rattus spp.*) reach high densities, impacts of feral cats on susceptible native fauna may be increased by a 'subsidy' effect. Impacts may be intensified if other species of predators, such as foxes, are present.
- 5) Although long periods of apparently stable coexistence (i.e. several years) are possible between feral cats and potential prey, impact may still occur if 'rogue' individuals develop hunting skills for particular prey species at any time. The impact may be major if the prey population is small when predation begins.
- 6) In Australia, in contrast to other parts of the world, feral cats are not recorded to have impacted on any species of reptiles, amphibians, fish or invertebrates.
- 7) To clarify the impacts of feral cats more precisely, controlled and replicated field removal experiments should be carried out. Such experiments must be seen as constituting a very important scientific and conservation goal, and as the only means of reliably guiding management on the level of cat control that will achieve recovery objectives for endangered and vulnerable fauna.
- 8) Endangered and vulnerable species of native vertebrates that are potentially at most risk of impact from feral cats have been identified, and should be targeted for evaluation of response in cat removal experiments. However, to maximise returns from field experiments, responses of all other potentially impacted species should be monitored also.
- 9) The responses of non-native species of predators, such as foxes, and of prey, such as rabbits, should be monitored in all cat removal experiments to evaluate any indirect effects they may have on native species. Cat removal experiments carried out in fox- or rabbit-free regions will introduce no indirect effects, and hence should yield particularly clear insight into cat impacts alone.
- 10) On the basis primarily of the numbers of co-occurring endangered and vulnerable native species that are at risk of impact from feral cats, it is recommended that cat removal experiments be carried out at localities in eight regions. In decreasing order of priority, these are: 1) south-west Western Australia, 2) the Channel Country, 3) Top End, 4) Kimberley, 5) Tasmania, 6) Norfolk Island, 7) coastal Victoria, and 8) the Pilbara.

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1. INTRODUCTION

The domestic or house cat *Felis catus* (Carnivora: Felidae) is usually believed to be derived from the African or Arabian wildcat *Felis sylvestris lybica* (Randi & Ragni, 1991; Bradshaw, 1992). Circumstantial evidence suggests that domestication began about 8000 BP in the eastern Mediterranean (Zeuner, 1958; le Brun et al., 1987), and continued until 4000 BP in the Middle East and perhaps also in the valley of the Indus (Baldwin, 1975; Ahmad et al., 1980). Paintings and sculptures of cats from the Eighteenth Dynasty confirm that cats were fully domesticated and living in close association with humans in Egypt by 3600 BP (Clutton-Brock, 1981; Serpell, 1988). Domestic cats spread slowly from Egypt, but occupied much of Europe prior to the spread of the Roman Empire (Waldren et al., 1984; J. Clutton-Brock, cited as [pers. comm. in](#) Kitchener, 1991). In the last 2000 years domestic cats have been transported actively on sailing vessels to most parts of the world (Lumpkin, 1993), either for food, their ability to control ship-borne rodents, or as pets. In the Pacific region, transport of cats has taken place relatively recently. Domestic cats were brought by the first European settlers to eastern Australia and New Zealand in the late eighteenth century (Dieffenbach, 1843; Rolls, 1969), and were introduced to islands of the sub-Antarctic slightly later, in the early 1800s (Debenham, 1945). Several Polynesian islands, including Tonga and the islands of Hawaii, also received cats in the late eighteenth or early nineteenth centuries (Baldwin, 1980). Domestic cats were probably introduced to several islands in Micronesia by Spanish sailing ships as early as the sixteenth century, and could have been introduced to north-western Australia and New Guinea still earlier by Indonesian trading vessels (Baldwin, 1980). Cats have been introduced to several smaller islands of the Pacific region this century (e.g. Kirkpatrick, 1966), especially to islands off the coasts of Australia and New Zealand (Fitzgerald & Veitch, 1985; Dickman, 1992a).

Although initially confined to settled areas, cats in many parts of the Pacific region have established feral populations that persist in remote or little-disturbed localities. In contrast to domestic cats which obtain most or all of the resources they need to survive and reproduce from humans, feral cats have little or no interaction with humans and maintain self-perpetuating populations. In Australia, populations of feral cats were augmented in the nineteenth century by the planned release of thousands of cats outside of settled areas (Rolls, 1969). Releases were made to control mice at gold digs in south-eastern and western Australia (Howitt, 1855; Carnegie, 1898), and also in an attempt to control plagues of rabbits (Rolls 1969; Fuller, 1970) and native rats (Bennett, 1879). Until European colonisation of the Pacific region, Australia, New Zealand, Antarctica and the many Pacific islands contained no species of felids, and were relatively depauperate in medium-sized species of carnivorous mammals (Flannery, 1994). Hence the arrival of *Felis catus* probably represented an important ecological event. Recent studies of domestic cats in Australia and New Zealand have shown that many species of native vertebrates are killed by cats each year; and suggest that the impact of cats in settled areas is substantial (Fitzgerald, 1988; Paton, 1991). The impact of feral cats on native fauna has not been critically investigated, but numerous historical and circumstantial accounts suggest that cats can have large deleterious effects (e.g. Dickman, 1993a).

1.1 Scope of the report

In response to the common perception that cats may be threatening the survival of endangered native fauna, predation by feral cats was listed as a key threatening process under the *Endangered Species Protection Act 1992*. The Act allows for the preparation of Threat Abatement Plans (TAPs) to guide

actions needed to reduce threatening processes (Carter, 1994). The present report summarises information on the impact of feral cats that should assist in the TAP process. The aim of the report, as defined by ANCA, is to comprehensively review the available evidence and literature of the impact on Australian native wildlife by the feral cat, *Felis catus*. Scope items include:

- summarising and critically reviewing research findings on the impact of feral cats on Australian fauna and identifying specific localities and native populations where this impact is regarded as greatest.
- summarising and critically reviewing research findings on the impact of feral cats on native fauna in other countries in circumstances relevant to the Australian context, especially where control of cats has benefited wildlife (or has been shown not to benefit wildlife).
- providing a critique of research methods, including experimental design, and recommending practical methods and priorities for research in Australia to clarify the impact of feral cats on wildlife.
- providing a comprehensive bibliography.

The report begins by defining some commonly-used terms and concepts, and then considers briefly the findings of several studies of the effects of domestic cats on Australian native wildlife. In the next section, information is collated on feral cats especially in regard to diet and direct observations of predation; a review is made also of correlational, historical and experimental evidence for the impact of feral cats on native vertebrates in the Pacific region. Indirect impacts on native fauna, including disease, exploitation, competition and second-

third-order interactions with other - introduced species are also considered. Information from this review is used to identify attributes of native species that are likely to increase their susceptibility to impact from feral cats. Non-marine species of mammals, birds and reptiles that are listed federally as endangered and vulnerable (ANCA, 1994) are then categorised according to these attributes as at low risk or high risk of impact from feral cats, and species density maps of at-risk taxa are compiled. Based on the maps, localities with large numbers of susceptible species are identified and ranked in order of priority for more detailed investigation. Finally, recommendations are made for future research in these localities, both to clarify and ultimately minimise cat impacts.

The report does not seek to compare the impacts of feral cats with other threatening processes on native fauna. Although desirable, such an undertaking would be difficult and is beyond the scope of the present project. However, I note that feral cats and other threatening processes are likely to interact, and also that the impacts of cats alone are often difficult to evaluate. Moreover, in situations where cat numbers have been increased by human agency, such as in suburban or rural environments, impacts of cats may be seen as secondary to more pervasive and direct threats such as clearing, habitat fragmentation or human persecution. Where possible I acknowledge the impact of cats in the broader context of human activities and other threatening processes, but caution that no formal prioritisation of the importance of these impacts has been attempted.

DEFINITIONS

i). Felts *catus* **Linnaeus**, 1758. In several recent works the domestic cat has been identified as a subspecies of the wildcat Felts *sylvestris*, namely *Es. catus* (Corbet & Hill, 1991; Bradshaw, 1992). However, this is inappropriate on the grounds of taxonomic priority, in that Felts *catus* was the name given originally by Linnaeus to the domestic blotched tabby, with *F. sylvestris* being applied subsequently to the wildcat by Schreber (Pocock, 1951). Despite similarities in appearance between *F. catus* and *F. sylvestris*, especially the African wildcat *Es. lybica*, *F. catus* can be distinguished from its relative by its reduced brain size, smaller adrenal glands, relatively longer intestine, and neotenus traits such as retention of juvenile appearance, playfulness and docility into adulthood (Kitchener, 1991). In the present work, I follow Mahoney & Richardson (1988) and Jones (1989) in referring to the introduced cat of Australia and the Pacific region as Felts *catus*.

ii). **Domestic cat**. This is a pet or house cat living in close connection with a household where all its ecological requirements are intentionally provided by humans (Moodie, 1995). Domestic cats may still impact on native fauna by their predatory activities, but do not rely on hunting for food.

iii). **Stray cat**. This is a cat that relies only partly on humans for provision of its ecological requirements (Moodie, 1995). Stray cats may obtain food or shelter that has been provided intentionally or otherwise by humans, and include animals kept on farms for rodent control, dumped animals, and cats living in urban fringe situations such as garbage dumps. Moodie (1995) notes that urban strays, purposely fed by humans but which live independently in other ways, are often referred to, confusingly, as feral cats in the literature.

iv). **Feral cat**. This is a free-living cat which has minimal or no reliance on humans, and which survives and reproduces in self-perpetuating populations (Moodie, 1995).

Note that ii) to iv) provide operational definitions of cats that are based primarily on the degree of use that is made of human-derived resources. Individual cats can potentially move between categories during their lifetimes (Moodie, 1995), as has been exemplified by Newsome (1991).

v). **Impact**. The impact of any organism introduced to a new environment may be negative, positive or neutral with respect to its effects on native species. In the case of the cat, an immediate negative impact on native fauna could be brought about in three ways. In *competition*, impact would occur from depletion of important resources shared by the cat and by native species; in *predation* the impact would be from direct consumption of native species; and in *amensalism* the impact would occur via transmission of disease, parasites or pathogens to native species with no net effects on the cat (Dickman, 1992b).

It is important to note that, while each of these processes affects individuals, this may not translate to any detectable impact on native fauna at the level of either the population or community. For example, predation of native fauna by cats can be demonstrated readily by analyses of cat diet, but there may be no impact on populations of the prey species if harvesting rates are low, if non-reproductive individuals are consumed or if compensatory breeding or survival occur. In this report, I consider that cat-induced impact on native fauna is demonstrated only if it has detectable effects at the population level. These effects can be on population size or on extent of geographical range. Following initial review of the literature, I consider further that impacts can be classified as minor or major depending on the magnitude of their apparent effects. Formally, I define a **minor impact** of cats as **one which produces a decrease of 25% or less in the population size or geographical area occupied by a native species**, and a **major impact** of cats as **one which produces a decrease of 75% or more in the**

population size or geographical area occupied

by a native species. The latter definition includes cat-induced extinctions. The dichotomy between minor and-major impacts appears justified because of the apparent lack of 'intermediate' impacts in the literature. I note that impacts may be produced rapidly (e. g. within days) or over periods of many years, and can occur at the scale of local, regional or entire species populations, and hence distinguish these, where information is available. I note also that impacts may sometimes be attributed jointly to cats and to other threatening processes, and evaluate these where data permit.

Finally, although immediate impacts of cats on native fauna could- be potentially neutral or even positive, few appear to have been reported. Long-term, evolutionary impacts of cats (e.g. Marshall, 1962; Stone et al., 1994) have been little studied in the Pacific region, but could be expected to be small due to the recent arrival of cats. Hence, such impacts - are not considered further in this report.

3. IMPACTS OF DOMESTIC AND STRAY CATS

Although a detailed appraisal of the effects of domestic cats on native fauna is outside the brief of this report, a selective review is nevertheless appropriate. First, domestic cats have been subject to detailed studies of hunting behaviour that yield insight into the likely behaviour of their feral counterparts. Second, because domestic cats are usually well fed, they are likely to take 'optimal' prey and hence reveal prey preferences; hungry animals cannot afford to be choosy and may take whatever they can find (Richards, 1983; Stephens and Krebs, 1986). Third, more-detailed studies have been made on the infectious diseases, pathogens and parasites of domestic than of feral cats; these should provide insight into potential amensal effects on native fauna.

3.1 Competitive impacts of domestic and stray cats

Possible competitive interactions have been observed between stray cats and dogs in Japan (Hirata *et al.*, 1986) and between cats and opossums *Didelphys uirginiana* in New York City (Kieran, 1982), but equivalent observations from Australia have not been reported. Given that the shelter requirements of domestic cats are usually met, food is the most likely resource for which cats and native fauna might compete. Given further that the diets of domestic cats comprise many small vertebrates, in addition to human-supplied food (Leyhausen, 1979), potential competitive interactions would be most likely to occur between cats and carnivorous native species such as quolls *Dasyurus* spp., owls and nightjars. However, while urban populations of native carnivores have been reported (Marlow, 1972; Hoskin, 1991), there is no quantitative evidence that any have been affected by competition from cats; comments about the possible importance of competition (e.g. Brunner *et al.*, 1981; Edgar, 1983) are entirely speculative.

3.2 Predatory impacts of domestic and stray cats

In contrast to the dearth of evidence for competition, the predatory effects of domestic cats on native fauna have been much better documented. Perhaps the most well-known and dramatic example of predator impact concerns a species of wren *Xenicus lyalli* that was endemic to Stephens Island, New Zealand. This species was extirpated by the cat of a lighthouse keeper within months of settlement on the island in 1894 (Atkinson & Bell, 1973).

In Australia, there are two well-documented case studies of the predatory impacts of domestic cats. The first involves the sole remaining mainland population of the eastern barred bandicoot *Perameles gunnii* at Hamilton, Victoria. Distributed originally in south-western Victoria and south-eastern South Australia, the population of *P. gunnii* began to shrink in the 1840s following European settlement (Menkhorst & Seebeck, 1990; Seebeck *et al.*, 1990). Population reduction was caused by a suite of factors, including gross habitat modification, grazing and predation by introduced carnivores (Seebeck, 1979). The Hamilton population comprised ~1750 animals in 1982-83 (Moon, 1984), and as few as 150-300 in 1989 (Lacy & Clark, 1990), thus exhibiting an annual rate of decline of ~25% over this period. Population studies by Brown (1989) and Minta *et al.* (1990) have shown that individual fecundity is high, and suggest that the population decline is driven by excessive mortality, especially of juveniles (i.e. animals <500 g). Partitioning of mortality data shows that predation by cats causes 42% (Dufty, 1994) to over 50% of the deaths of juveniles; this rate may increase still further following flooding when animals are forced into open areas away from cover (Maguire *et al.*, 1990).

The relative importance of cats in the decline of *P. gunnii* has been emphasised in simulation studies that predict how demographic parameters should change under different management regimes

(Maguire et al., 1990). Beginning with a mean annual growth rate of the population, or R_0 , of 0.69, these authors show that provision of cover by fencing and planting of shrubs increases R_0 to 0.82, while rigorous control of cats increases it to 0.98. Additional measures to reduce road-kills would permit population increase with R_0 of 1.10. Because provision of cover can be expected to indirectly reduce predation, domestic and stray cats can be considered to have a more important depressive effect on the population growth of *P. gunnii* at Hamilton than any other factor. Under the definitions given above (Section 2), the impact of cats on the regional population of *P. gunnii* is clearly a major one.

The second case study involves a local population of the superb lyrebird *Menura novaehollandiae* at Sherbrooke Forest, Victoria. Regular surveys of birds in the 810 ha forest area have revealed a population decline from 130 *M. novaehollandiae* in the 1960s to only 60 in 1988 (Bradley & Bradley, 1990). Predation by domestic cats, dogs and foxes has been identified as the major cause of the population decline, with cats probably accounting for disproportionate mortality of juveniles, and dogs and foxes for disproportionate mortality of older birds (Larkin, 1989; H. Bradley, pers. comm.). The impact of cats alone in this situation is minor, but continuing.

In addition to studies of individual species, several reports have surveyed the range of native fauna taken by domestic cats. The first survey, by Paton (1990, 1991) was based largely on questionnaire responses obtained from cat owners in Adelaide and more rural parts of South Australia and Victoria. Based on information from 421 respondents, the survey showed that about 62% of cats took birds, 59% took mammals and 34% took reptiles; some took frogs and insects. Twice as many mammals (15.7) were returned on average by cats to their owners each year than either birds (8.0) or reptiles (7.8). Capture rates varied with locality, being least in suburban areas (22.1 individual prey taken per year) and greatest in rural areas (54.3 prey/year), presumably reflecting differences in prey abundance or accessibility, or in the opportunities for hunting by the cats. Paton (1991) noted that these capture rates are probably underestimates, as well-fed cats in a comparable study on a farm in Illinois found

that only half the prey captured were returned to the household (George, 1974). Unfortunately Paton (1991) did not distinguish native and introduced species. However, independent estimates from studies in Canberra and Hobart suggest that 22-46% of the take would be natives (Trueman, 1991; Barratt, 1994a, 1995); an estimate of 80% (ANPWS, 1992) appears to have little substantiation. In total, the consumption of native prey by domestic cats has been shown to comprise 48 species of mammals, 177 species of birds, 46 species of reptiles, 5 species of amphibians and many invertebrates, the vast majority weighing <100 g (Paton, 1994).

Rough extrapolations from the capture rate data suggest that the impact of domestic cats on native fauna is substantial. Given densities of cats in suburban Adelaide of 2/ha, densities of birds of 10-30/ha and an offtake by cats of 10-20 birds per year, predation by cats will remove at least 50% of the standing bird populations or destroy all the young being hatched (Paton, 1991, 1993). In such circumstances, populations could be maintained only by continuous immigration from surrounding areas where cat predation was less intense. Although overall densities of small native species of mammals, reptiles and amphibians are poorly known in either suburban or rural areas, it is likely that these are also liable to severe depletion by domestic cats. For example, three species in the marsupial genus *Antechinus* occur ubiquitously in wooded habitats in eastern Australia, but all are absent from towns and cities unless large areas of dense vegetation cover are available to limit predation (Steeves, 1990; Sumner & Dickman, 1996). In the Toohey Forest, Brisbane, the total absence of all small ground-dwelling native mammals has been attributed largely to depredation by cats (McRae & Smith, 1987). Although other factors, such as degraded habitat, may also deplete native small animals in developed areas, these examples represent apparently major impacts of cats on local species populations.

A second survey, using similar methods to those of Paton (1991), investigated the prey returned by over 200 cats in suburban areas of Canberra (Barratt, 1994a, 1995). About 75% of the cats were reported to hunt, and returned at least 76 species of vertebrates to their owners over the course of a year. Most

prey were the introduced rodents *Rattus rattus* and *Mus domesticus* (64% by frequency); native species of birds comprised 14% of the diet, introduced birds 10%, reptiles 7%, amphibians 1% and unidentified mammals and birds 4%. Predation on mammals was greatest on the edges of suburbs adjoining grassland, whereas native birds experienced highest predation in older suburbs adjoining forest. Using a density estimate of 3 cats/ha for outer suburban areas, Barratt (1994a, 1995) estimated that 9.7 individual prey were taken annually per cat, with a total of almost 480 000 being taken in Canberra each year. Rough estimates indicate that 10-25% of the standing crop of introduced birds, and 20-27% of the standing crop of native birds, is depredated each year. Impacts appear to be spread unevenly among species, with predation being relatively intense on the crimson rosella *Platycercus elegans* and weak on the introduced starling *Sturnus vulgaris* (Barratt, 1995).

A third survey (Anon., 1994) used telephone interviews with over 1000 householders who own cats in seven Australian cities to further investigate populations of domestic cats and their effects on wildlife. The results indicated that 56% of cats captured prey over the survey period of 12 months, and suggested further that introduced species comprised the bulk of vertebrates taken. Thus 41% of cats were reported to take introduced mammals such as rats, mice and rabbits, while 19% took introduced birds such as sparrows, starlings and mynas. In contrast, only 2% of cats were reported to take native mammals, while 7% took native birds and 17% took reptiles and amphibians. The average annual capture rate of 4.76 individual prey per cat (4.68 for Adelaide, 3.71 for Canberra) reported by Anon. (1994) is much less than the values of 22.1 and 9.7 given by Paton (1991) and Barratt (1994a). This value comprised 3.19 introduced species taken per cat per year, compared with 1.32 reptiles and amphibians, 0.23 native birds and only 0.02 native mammals. Using an estimated total domestic cat population of 1 397 000 in the seven cities surveyed (Anon., 1994), aggregate yearly losses of native species come to 1 846 900 reptiles and amphibians, 314 900 birds and 23 900 mammals.

Before accepting the estimates of Anon. (1994), several comments need to be made on the methodology of the survey. First, because respondents were telephoned and asked to remember on-the-spot how many prey their cats had returned over the previous 12 months, the reported rates of capture may be unreliable. D.C. Paton (pers. comm.) has pointed out that respondents whose cats took large numbers of particular prey would be inclined to underestimate the true number caught or to indicate uncertainty about what the number was; either bias would lead to underestimation of losses. Second, the take of native mammals has been underestimated by an unknown amount because no native species other than bats and possums were allowed for; all dasyurid, peramelid and burramyid marsupials and native rodents taken by cats were assumed to be introduced vermin. Third, ambiguity in the questionnaire about the species of birds captured (e.g. "doves", "mynas" and "little grey/brown ones") may reduce confidence in the reported take of native versus introduced species. However, J. Newby (pers. comm.) has indicated that bias is probably minimal or that native species were marginally overrepresented in the survey, as over 83% of birds returned by cats were identified clearly or assumed to be native if identity was uncertain. The study by Anon. (1994) indicates clearly that the annual take of native species by domestic cats is great, but provides little further insight into what impact this might have.

The fourth survey to investigate the impacts of domestic cats quantified the numbers and species of native fauna injured by cats that were presented to a single wildlife shelter in Melbourne (Seebeck et al., 1991). Over a period of 16 months, 364 individual animals were presented; 272 were native mammals and 92 were birds. Surprisingly, 242 of the mammals (89%) were common ringtail possums *Pseudocheirus peregrinus*. In a subsequent study, Dowling et al. (1994) presented the results of a more extensive survey of native species admitted to shelters, other animal welfare agencies and zoos throughout Victoria over a five year period between 1987 and 1992. Their records indicated that, of 2460 attacks on native species made by introduced predators, 1846 (75.0%) were by cats, 564 (22.9%) by dogs, and 50 (2.0%) by foxes. Cats were reported to

have injured at least 70 species of native birds, 22 species of mammals (including eight species of bats) and five species of reptiles, as well as a further, 10 species of introduced birds and mammals. In accordance with the earlier findings of Seebeck et al. (1991), most of the mammals reported by Dowling et al. (1994) as falling victim to cats were *P. peregrinus* (n = 923, 72.1%) with 76.6% of these possums being classified as sub-adults or dependent young weighing <500 g. One hundred and sixtyeight sugar gliders *Petaurus breviceps* (13.1% of mammals) were also injured by cats, the majority (64.2%) again being sub-adults or younger animals.

Despite some biases in the data of Dowling et al. (1994) arising from collection of species with human appeal (e.g. no insects or snakes were taken to shelters) and the omission of most cat victims that died before collection, the results of this study confirm that domestic cats are significant predators of native wildlife.

Moreover, there is some indication that small possums and gliders are taken preferentially and that young animals are at particularly high risk of injury. Seebeck et al. (1991) noted receipt of 39 *PR peregrinus* injured by cats within a week

at one wildlife shelter, perhaps indicating that predation is selective on this species. Such predation can cause extinction of local populations, as has been observed in Victoria (Dowling et al., 1994) and parts of Sydney (B. Smith, pers. comm.).

Several further studies on a smaller scale to those outlined confirm that domestic cats can have minor or major effects on local populations of native vertebrates. In remnant bushland of the Lane Cove Reserve, Sydney, Stephens (1978) reported that wildlife was taken by at least 55% of the domestic cats she studied, and that rats and mice comprised most prey returned to householders. Small native species such as the brown antechinus *Antechinus stuartii* were found to be much less abundant at Lane Cove than in the larger and less disturbed bushland of Kuringai Chase National Park, leading Stephens (1978) to conclude that cats have had a major impact on small mammals at Lane Cove. A limited sample of 11 cat faeces collected from this area in 1991 showed that *P. peregrinus* comprised the major prey by volume (63.2%);

rodents and rabbits comprised 28.5% and birds and other materials 8.3% (C.R. Dickman, unpub.). The population of *P. peregrinus* at Lane Cove declined by 48% between 1989 and 1992 (J. Stephenson, pers. comm.).

Elsewhere in Sydney, at North Head, domestic and stray cats have contributed to a decline in numbers of one of the last populations of the long-nosed bandicoot *Perameles nasuta* remaining in the city area. Bandicoots comprised 28.2% by volume in a sample (n = 20) of cat faeces and stomachs collected from this area, and were found as victims of cat attacks on six occasions (Scott, 1994; C.R. Dickman, unpub.). Between 1991 and 1994 the population declined by at least 25% (C.R. Dickman, unpub.), despite continuous production of young by females from winter to late summer each year (Scott, 1994). Several other examples of the depredations of domestic cats on native fauna have been reported (Jones & Everding, 1991; Trueman, 1991; Ward, 1994; see also review in Rathore, 1992), but provide little further insight into levels of impact.

The findings of the Australian studies, reviewed above, are supported and amplified by work from North America and Europe. Thus, domestic and stray cats have generally been found to take a very broad range of vertebrate and invertebrate prey (Borkenhagen, 1979; Mitchell & Beck, 1992); when live prey is limiting, scavenge, carrion and household refuse may be taken in large amounts (McMurray and Sperry, 1941; Dards, 1981). At the population level preferred prey usually are small mammals, birds and lizards, especially those with body weights < 100 g. Preference for small size was confirmed in a simple but elegant study by Childs (1986), who showed that cats in urban Baltimore take young Norway rats *Rattus norvegicus* weighing <200 g while the majority of rats available in the population (90.8%) weigh >200 g. At the individual level, some cats specialise in hunting particular prey species. Often these are species of birds or terrestrial mammals (Bradshaw, 1992), but unusual prey such as bats (Churcher & Lawton, 1989) and grasshoppers (Hochstrasser, 1970) may also be targeted. Specialisations are often short-lived, perhaps reflecting temporary increases in the availability of prey (D.C. Paton, pers. comm.).

Except for the Stephens Island wren, impacts of domestic cats on fauna outside Australia appear usually to be minor and local. However, domestic cats have been shown to deepen and prolong troughs in populations of both California voles *Microtus californicus* (Pearson, 1964, 1966) and rabbits *Oryctolagus cuniculus* (Liberg, 1984), and to dampen population changes in field voles *M. agrestis* in areas where populations are cyclic (Hansson, 1988). In early experiments, Elton (1953) also showed that domestic cats could prevent *Rattus norvegicus* from reinvading farm buildings, after rats had first been eliminated by poisoning. However, cats were unable to eliminate established populations of rats. Finally, Churcher & Lawton (1987) estimated that between a third and a half of all deaths of house sparrows *Passer domesticus* in a British village could be attributed to domestic cats, thus bringing about a sustained reduction in the local population size. Churcher & Lawton (1989) later alluded to 'supercats' elsewhere in Britain that brought home up to 400 prey items a year, but refrained from commenting on what impact such cats could be expected to have.

3.3 Amensal impacts of domestic and stray cats

A major survey of the diseases and parasites of domestic cats in Australia (Moodie, 1995) revealed over 100 described species of pathogens. At least 50 of these are host-specific and hence could have no direct effect on native fauna. However, many pathogens are not host-specific, and at least 30 of the species listed by Moodie (1995) for cats have been found also in native fauna. Because pathogens carried by domestic cats are likely to be transmissible to their feral counterparts, the impacts of cat-transmitted diseases and parasites are considered in more detail in section 4 (impacts of feral cats). However, brief comment is warranted here on the protozoan parasite *Toxoplasma gondii*, which causes toxoplasmosis, both because it is the most important disease that cats transmit to wildlife (and to humans), and also because it has been subject to most study in cats and native species (Dubey & Beattie, 1988).

The cat and related felids are the only definitive hosts for *T. gondii* (Dubey, 1986). Infection is usually spread by excretion of oocysts, the sexual stage of the parasite, and subsequent ingestion of oocysts by native mammals and birds leads to chronic infection with cysts in muscle and nervous tissue (Hartley & Munday, 1974). Infection can also be acquired in cats and native fauna by ingestion of tissue cysts in carcasses up to several days after death of the host, and also by ingestion of intermediate hosts such as invertebrates which ingest oocysts from soil (Ruiz & Frenkel, 1980). Symptoms of toxoplasmosis in native fauna include poor coordination, blindness, lethargy, respiratory and enteric distress, and often sudden death (Patton et al., 1986; Canfield et al., 1990). Toxoplasmosis occurs in the population of *Perameles gunnii* at Hamilton, Victoria, and is one of the factors contributing to the decline of the population. Determination of cause of death of 100 juvenile and adult bandicoots from 1982=89 showed that three had died from generalised active toxoplasmosis, and that deaths of a further seven were associated with toxoplasmosis (Lenghaus et al., 1990). Many animals had quiescent infections, indicating that the level of exposure to *T. gondii* in the *P. gunnii* population greatly exceeded 10%. Mortality due to toxoplasmosis may have been underestimated by Lenghaus et al. (1990) if carcasses of infected animals had not been found. In contrast to the predatory impact of cats, the effects of toxoplasmosis appear to be greatest on adults. Lenghaus et al. (1990) found no evidence of toxoplasmosis in pouch young and in only a small but unspecified number of juveniles. By extrapolation from studies on *P. gunnii* in Tasmania (Obendorf & Munday, 1990), infection of animals at Hamilton probably occurs by ingestion of earthworms and insects which in turn acquired their oocysts from cat faeces deposited in the soil. Using the available figures, the impact of toxoplasmosis on *P. gunnii* would be a minor one at the regional level.

3.4 Summary: impacts of domestic and stray cats

Domestic and stray cats occur in environments that have been modified substantially by human activity, so their impacts on native fauna are often difficult to distinguish from impacts such as those of other introduced species or of habitat change. Surveys in several cities have shown that large numbers of native vertebrates are killed each year by cats, and provide indicative evidence of impact. However, the same surveys also indicate heavy depredation on introduced species. It is not clear whether use of alternative introduced prey might alleviate predation on native species, exacerbate it by supporting higher densities of cats, or have no effect.

In a small number of studies there is compelling evidence that domestic and stray cats have minor or major impacts on native wildlife, sometimes at the level of regional populations but most usually on local

populations. The evidence is confined almost solely to demonstrations of direct predatory impacts, but indirect impact via transmission of toxoplasmosis has been shown in one species and is possibly more important than has been reported. Several conclusions can be drawn about predation by domestic and stray cats:

- i). A very wide range of native faunal species is taken, but there is some evidence of preference for mammals, then birds, other vertebrates and then invertebrates.
- ii). Prey up to 1-2 kg may be taken occasionally, but preference is shown for prey weighing <200 g, and especially for prey weighing <100 g.
- iii). Although predation appears often to be opportunistic, especially at the population level, individual cats sometimes develop hunting skills and preferences for particular species of prey.

These findings are used to focus the review of impacts of feral cats on native fauna.

4. IMPACTS OF FERAL CATS

Concern about the depredatory effects of feral cats was expressed over 130 years ago by Gould (1863), and has been echoed by many authors since (e.g. Troughton, 1932; Rolls, 1969; Potter, 1991). Jones (1925 pp. 258-259) considered them to be an "unmitigated curse" and " ...a terrible scourge, when we consider the vast numbers of the more rare, interesting and beautiful members of our native fauna that are annually destroyed by them." Unfortunately there are no critical studies of the impact of feral cats on native fauna in Australia, although two controlled field removal experiments on cats are currently being carried out (D. Risbey, J. Short, pers. comm.; C.R. Dickman & P.S. Mahon, unpub.). However, it is still possible to draw strong inferences about the impacts of feral cats from historical, circumstantial and observational evidence, as well as from case histories of island wildlife following the introduction and establishment of feral cats. In the following review I use these different kinds of evidence to evaluate the impacts of feral cats on Australian native fauna, focussing particularly on predatory impacts, where evidence is most extensive.

4.1 Competitive impacts of feral cats

Competitive interactions between feral cats and native fauna have been alluded to by several authors (e.g. Brooker, 1977; Caughley, 1980; Johnson & Roff, 1982; Cross, 1990), but compelling evidence for competition has not been obtained (Dickman & Read, 1992). If competition does occur, it could be expected to affect species that are ecologically most similar to cats and which overlap with cats in their use of food, habitat, shelter or other resources. Among native mammals, quolls *Dasyurus* spp. share the greatest similarity in diet with feral cats and coexist with them in forest and woodland habitats in eastern, western and northern parts of the continent. The spotted

tailed quoll *D. maculatus* is the most carnivorous of the four Australian species and hence overlaps most in diet with feral cats; it eats a wide variety of small vertebrates, including terrestrial and arboreal marsupials such as bandicoots and possums (Alexander, 1980). The diet of the western quoll *D. geoffroii* also comprises some small vertebrates, up to the size of rabbits (37.6% by volume), but the bulk of the diet (43.8%) is invertebrates (Soderquist & Serena, 1994). Neither the eastern quoll *D. viverrinus* nor the northern quoll *D. hallucatus* eat many vertebrates; hence overlap in diet with feral cats is minimal (Fleay, 1962; Blackhall, 1980). The diets of other large dasyurids are either too poorly known to permit comments about possible competition (i.e. the New Guinea quolls *D. albopunctatus* and *D. spartacus*; Flannery, 1990a), or too different from the diet of feral cats (i.e. Tasmanian devil *Sarcophilus harrisii*; Green, 1967) to suggest that competition might occur.

Apart from diet, eastern and western quolls show considerable overlap with feral cats in habitat and den requirements, at least in wooded environments (Godsell, 1982; Serena & Soderquist, 1989; Serena *et al.*, 1991). Spotted-tailed quolls and feral cats co-occur in forest, especially where annual rainfall exceeds 600 mm (Mansergh, 1984), but the den requirements of this quoll are too poorly known to comment further on likely overlap. Although large dasyurids are potentially most likely to compete with feral cats, it is possible that competition occurs at times for food between cats and predatory birds. On subAntarctic Marion Island, predation by cats on burrowing petrels has reduced the prey base for sub-Antarctic skuas *Catharacta clonnbergi*, leading to a minor reduction in their population size and breeding success (Hunter, 1990). In North America, predation by cats has also been shown to diminish prey for raptors during winter, thus exerting a minor competitive effect on the raptor populations (George, 1974). Although no equivalent studies have been carried out in

Australia, feral cats could reduce prey populations for nocturnal species such as barn owls *Tyto alba* (Smith & Cole, 1989; Dickman et al., 1991), powerful owls *Ninox strenua* (Tilley, 1982), masked owls *Tyto novaehollandiae* (Mooney, 1993), sooty owls *T. tenebricosa* (Beruldsen, 1986) and letter-winged kites *Elanus scriptus* (Hollands, 1977). Competition for food was posited explicitly by Smithers & Disney (1969) between cats and boobook owls on Norfolk Island. Cats could also reduce prey for more diurnal species such as the brown goshawk *Accipiter fasciatus* (Aumann, 1988) and peregrine falcon *Falco peregrinus* (Olsen et al., 1993) and other diurnal species that take similar prey to cats. During plagues of the native long-haired rat *Rattus villosissimus*, rats can comprise the staple diet of both feral cats and letterwinged kites, with dietary overlap approaching 100% for periods of several months (C.R. Dickman, unpub.). Rat plagues may stay at particular locations for 1-2 years (Predavec & Dickman, 1994), and allow populations of predators to increase dramatically. If competition occurs between cats and kites, it could be expected to be during brief 'crunch' periods when the predators are at high densities and the rats are declining. Unfortunately, this expectation is yet to be tested.

Conceivably, competitive interactions could occur for particular resources, such as food, between feral cats and larger reptiles. Some elapid snakes and goannas ingest a range of small vertebrates similar to that taken by feral cats, and hunt in the same habitats where cats occur (Shine, 1991; King & Green, 1993). Despite such possibilities, however, there has been no research implicating competition between cats and reptiles. Weavers (1989) showed that lace goannas *Varanus varius* take cats as part of their diet and suggested that the reverse might also occur; in such complex situations competition may not be an important interaction and would be difficult to demonstrate.

In summary, there is considerable potential for feral cats to inflict competitive impacts on Australian native fauna. This potential derives from similarities in resource use between cats and several species of larger, predatory vertebrates. However, critical evidence for competition has not been

adduced in any study involving cats. Thus conclusions cannot yet be drawn about the importance and prevalence of the competitive impacts of feral cats on any elements of the native fauna.

4.2 Predatory impacts of feral cats

Before effective assessment can be made of the predatory impacts of feral cats in Australia, it is first necessary to evaluate what feral cats eat and how they hunt. Studies of cats on the mainland and on islands are evaluated separately because of evident differences in the diets of cats in these two situations.

4.2. Diets of feral cats: mainland only

A summary of dietary data, collated from 22 studies of feral cats in 20 localities throughout mainland Australia, is presented in Appendix 1. In accordance with the findings for domestic and stray cats (section 3), mammals comprise the major prey of feral cats in most localities. Introduced rabbits, *Oryctolagus cuniculus* and house mice, *Mus domesticus* predominate in semi-arid and some arid habitats, whereas marsupials are predominant in temperate forest, urban and suburban habitats. During plagues, mice may form up to 100% of the diet of feral cats, whereas rabbits may form up to 89% by weight (Jones & Coman, 1981). There is some evidence that larger male cats are able to take larger rabbits (e.g. Hart, 1994), although at Yathong in semi-arid New South Wales small rabbits, <50 days old comprised 73% of the diet of both mature and immature cats while adult rabbits comprised only 8.3% (Catling, 1988). Interestingly, cats in some rabbit-infested inland regions appear to be larger than those in rabbit-free areas in northern and eastern Australia (P. Wagner, pers. comm.), perhaps indicating prey-based selection for larger body size, or greater longevity.

In temperate forest and suburban habitats the common ringtail possum *P. peregrinus* is consistently highly represented in the diets of feral cats. Triggs *et al.* (1984) found that *P. peregrinus* was the only arboreal marsupial taken by cats at Croajingalong National Park, Victoria, while Coman & Brunner (1972) and Brunner *et al.* (1991) found that it was the most highly represented marsupial by volume

or frequency in cat droppings and stomachs. These latter studies, as well as Jones & Coman (1981), showed that other arboreal marsupials such as brushtail possums *Trichosurus vulpecula*, sugar gliders *Petaurus breviceps* and greater gliders *Petauroides uolans* may also be taken frequently by feral cats. Smaller native species such as the brown antechinus *Antechinus stuartii* (35 g), bush rat *Rattus fuscipes* (125 g) and swamp rat *R. lutreolus* (120 g), form a consistent part of the diet of feral cats, particularly in temperate forest habitats where they are most likely to be abundant. Bats appear to be eaten rarely by cats, although several individuals have been found on occasion in stomach samples (e.g. Chapman & Kitchener, 1978).

In wet-dry tropical and arid habitats where rabbits do not occur, native rodents become an important part of the diet of feral cats. At two sites in the Top End of the Northern Territory, Cameron (1994) found that native *Rattus* species (*R. tunneyi*, *R. colletti*, *R. villosissimus*; 60-150 g) comprised 75-86% by volume of stomach contents of feral cats. At two sites in and western Queensland, the long-haired rat *R. villosissimus*, spinifex hopping-mouse *Notomys alexis* (30 g) and sandy inland mouse *Pseudomys hermannsburgensis* (12 g) comprised the major part of the diet of cats (> 60% by volume in droppings) during different years (C.R. Dickman, unpub.).

In most studies cited in Appendix 1, birds, reptiles and invertebrates have been represented as consistent but minor parts of the diet of feral cats. In general, birds are represented most highly in temperate forest, urban and suburban habitats, as well as in some localities in arid Australia. Small species such as wrens *Malurus spp.*, robins *Petroica spp.* and thornbills *Acanthiza spp.* have all been recorded, as have larger species such as galahs *Cacatua roseicapilla*, magpies *Gymnorhina tibicen* and several species of parrots *Psephotus spp.* Young (300-500 g) of larger species such as malleefowl *Leipoa ocellata* and wedge-tailed eagle *Aquila audax* are taken occasionally (Brooker, 1977; Priddel & Wheeler, 1994). Emu *Dromaius nouaehollandiae* has also been recorded (Jones & Coman, 1981), presumably having been taken either as scavenger or as young birds. Unfortunately not all studies identified

the avian prey of cats to species. However, there is some tendency for larger, ground-feeding species such as parrots, quails and magpies to be taken more frequently than smaller passerines.

Reptilian prey tended to be taken mostly in and habitats, but their representation was sporadic. Nocturnal species such as geckos and flap-footed lizards were often recorded, as were diurnal species of skinks, dragons, goannas and snakes. Surprisingly, very small and partly fossorial species such as *Lerista spp.* (<2.0 g) were sometimes recorded, as were highly venomous elapid snakes such as young dugites *Pseudonaja nuchalis*. Because individual reptilian prey were often small (about 90% of species listed in the original studies summarised in Appendix 1 weigh <10 g), their representation by percentage volume in cat stomachs or droppings masks the numbers that may be taken. For example, a minimum of 19 skinks was taken from the stomach of a single cat at Kinchega, NSW (Jones & Coman, 1981), 13 geckos have been recovered from another stomach sample from coastal woodland in WA (C.R. Dickman, unpub.), and over 30 dragons were taken from a single cat stomach from Roxby Downs, South Australia (D.C. Paton, pers. comm.). In total, 38 species of mammals have been recorded in the diet of feral cats, as well as 47 species of birds, 48 species of reptiles and 3 species of amphibians (Paton, 1994). Reptiles (36 species) feature particularly in and areas (Boscacci *et al.*, 1987; G. Edwards, pers. comm.). Other food categories listed in Appendix 1 are of minor or variable importance.

Reviews of the diet of feral cats in mainland areas in other parts of the world reveal great similarities with the situation in Australia (Corbett, 1979; Fitzgerald & Karl, 1979; Liberg, 1984; Fitzgerald, 1988; Kitchener, 1991). In all studies, mammals have consistently comprised the major part of the diet throughout the year, with other vertebrates, especially birds, comprising only a minor component. Rabbits and murid rodents, especially *Rattus* species, appear to be favoured prey, and together comprise the bulk of the diet of feral cats in some localities over long periods (e.g. Fitzgerald & Karl, 1979).

4.2.2 Diets of feral cats: islands

Few studies of the diet of feral cats have been made on islands off the coast of Australia. However, several investigations have been conducted on islands elsewhere in the Pacific region, and these are summarised in Appendix 2. On islands such as Macquarie, Raoul and Stewart, cat diets are similar to those in most mainland areas of Australia (Appendix 1) and comprise mostly introduced rabbits and rats. The range of food categories taken on islands is generally less than that on the Australian mainland and reflects the absence of prey such as marsupials and, on some islands, amphibians, large reptiles or bats. Because of restricted availability of usually preferred prey, cats on some islands make extensive use of alternative food sources. On the tiny (28 ha) Herekopare Island, New Zealand, for example, there are no introduced or native species of mammals. Prior to elimination of feral cats there in 1970, fairy prion *Pachyptila turtur* comprised the bulk of the diet with other sea birds and occasional land birds making up most of the remainder (Fitzgerald & Veitch, 1985). Terrestrial orthopterans, wetas, appeared to be important to individual cats, with two stomachs being found each to contain over 100 insects. On Great Barrier Island, New Zealand, the endangered chevron skink *Leiopisma homalonotum* is taken by feral cats (Towns & McFadden, 1993). On Christmas Island, the introduced black rat *R. rattus* comprises almost one third of the diet of feral cats by weight (Tidemann *et al.*, 1994). However, 21% of the diet is comprised of the large (350 g) flying-fox *Pteropus melanotus*, while the large (524 g) imperial pigeon *Ducula whartoni* comprises a further 28% (Tidemann *et al.*, 1994).

Studies of diet of feral cats on islands elsewhere in the world support the conclusion from Appendix 2 that insular cats often have a restricted diet comprising unusual prey. On sub-Antarctic Marion Island petrels are major prey, with many chicks of the great-winged petrel *Pterodroma macroptera* being taken directly by cats from nesting burrows (van Aarde, 1980). In the Galapagos cats sometimes take birds of similar or larger mass than themselves, such

as frigate birds *Fregata spp.*, pelicans *Pelecanus spp.* and flightless cormorants *Phalacrocorax spp.* (Konecny, 1987). Iguanids feature prominently in the diet on islands of the Caribbean (Rand, 1967), while on Aldabra Atoll, Seychelles, hatchlings of the green turtle *Chelonia mydas* are seasonally predominant (Seabrook, 1990).

4.2.3 Hunting behaviour of feral cats

The hunting behaviour of feral cats has been described in some detail by Corbett (1979) and Leyhausen (1979), and provides further insight into how prey are selected. Cats hunt solitarily, and pursue either a mobile strategy where movement occurs toward the prey, or a sedentary strategy where the cat lies in wait until a potential prey animal appears. Initial detection of prey using either strategy is usually by hearing, with vision being used subsequently to precisely locate the prey (Bradshaw, 1992). Once located, a cat will adopt a crouching posture and run rapidly toward the prey, making use of available cover to avoid detection. Stalking continues until the cat is close enough to spring. Small prey, such as small birds, small mammals and invertebrates, are pounced on with both fore paws and killed with a bite to the back of the head or thorax (Pellis & Officer, 1987). Larger prey, such as young rabbits, may be held by the cat's jaws and struck repeatedly by the forepaws until a killing bite can be delivered. For still larger prey the cat will fall on its side and rake the body of the prey with its hind claws, while holding the prey immobile in its jaws and fore paws. Alternative methods of prey capture are the 'downward pounce' which is directed at small prey that are moving in long grass or other cover, and 'fishing' using an extended forepaw to extract prey from within crevices or under cover (Bradshaw, 1992).

Cats pursuing a mobile hunting strategy are usually adult or dominant individuals, whereas sedentary hunters are often younger subordinates (Corbett, 1979). However, the strategy adopted depends also on the prey being hunted, with cats of any age adopting a mobile strategy if the prey is mobile or a sedentary strategy if the prey is concentrated within a burrow system or expected to move to near where the cat is positioned.

4.2.4 Predatory impacts: what constitutes acceptable evidence?

In terms of the definition advanced above (section 2), acceptable evidence for impact would be any demonstration that cats have caused a decline of 25% or more in the population abundance or geographical distribution of any native species.

Unfortunately, unambiguous evidence of this kind does not exist. In most situations where cats appear to have caused a population or distributional decline the magnitude of the decline has not been quantified, or factors other than cats may also be implicated. However, very strong inferences can be made in certain situations that cats were the primary cause of decline of a native species; in other situations strong circumstantial evidence implicates cats as the most likely cause of the decline. In the section below I present five categories of evidence that cats have produced impacts on native fauna, beginning with the weakest but most prevalent evidence (anecdotal) and concluding with the strongest evidence (experimental) that is available.

Predatory impacts: anecdotal evidence.

The ecological literature on Australian wildlife abounds with comments about the likely predatory impacts of feral cats on native species. These impacts include reduced population sizes and ranges, but are also suggested to have general unspecified effects (Table 1). Because anecdotal observations do not provide conclusive evidence of cat impacts but instead often represent authors' opinions and best guesses, I have not attempted a comprehensive tabulation of anecdotal evidence. Table 1 has been compiled largely from perusal of studies reported in *Australian Wildlife Research* (1990), *Wildlife Research* (1991-1994), *Australian Mammalogy* (1990-1994), and references therein, simply to provide an indication of the type and extent of anecdotal evidence that is available.

Most studies listed in Table 1 acknowledged that effects ostensibly attributable to cat predation could have been produced by other factors, or noted that cat predation alone could have negligible impact. Few studies provided any quantitative assessments of impact. An interesting exception to this is a study by Saunders (1991), that showed that cats killed 7% of nestling red-tailed black cockatoos *Calyptrorhynchus magnificus*

(n = 428) over 11 breeding seasons at a locality in the wheatbelt of Western Australia. In one year, cats killed 17% of nestlings within nest hollows. Even in this study, however, it was not clear whether losses of nestlings to cats had a detectable impact at the population level. Despite the obvious problems of accepting anecdotal evidence in any study of cause and effect, several observations may nevertheless be drawn from the tabulated studies. First, most studies that imputed any predatory impacts of cats dealt with small to medium-sized mammals, or birds (Table 1, see also Stephens, 1992). The largest species depredated were the allied rock-wallaby, *Petrogale assimilis* (4 kg) and bridled nailtail wallaby *Onychogalea fraenata* (4.5 kg). However, because cats were not observed killing individuals of either species and were recorded eating mostly young wallabies (Spencer, 1991; Horsup & Evans, 1993), the maximum prey size taken by cats may be considerably less than 4.5 kg. Indeed, current work on *O. fraenata* indicates that cats are the major cause of mortality of juveniles <2 kg, although adult females up to 3 kg may be taken on occasion (D.O. Fisher, pers. comm.).

Second, reptiles, amphibians and fish are very rarely considered to be impacted by predators. For those few species that could be affected (Table 1, see also Thompson, 1983), it is usually unclear whether cats or red foxes *Vulpes vulpes* pose the more serious threat. In 12 recent reviews that I consulted on the ecology, status and conservation of these three classes of lower vertebrates, ten failed to list cats as a threatening factor at all (Grigg *et al.*, 1985; Michaelis, 1985; Burbidge & McKenzie 1989; Kennedy, 1990; Ferraro & Burgin, 1993; Ingram & McDonald, 1993; Osborne *et al.*, 1993; Richardson, 1994; Sadlier, 1994; Tyler, 1994); two studies (Woinarski, 1993; Sadlier & Pressey, 1994) mentioned cats specifically but noted that their impact, if any, was not clear. Third, there is no anecdotal evidence that cats have predatory impacts on invertebrates. Although this is not surprising in view of the generally low representation of invertebrates in the diet of feral cats (Appendix 1), cat predation is not considered to be a threatening process for any species (Hill & Michaelis, 1988; Greenslade & Crawford, 1994; Yen & Butcher, 1994).

Table 1. Anecdotal reports of predatory impacts of feral cats *Felis catus* on native vertebrates in Australia.

<i>Taxa affected</i>	<i>Location</i>	<i>Impact¹</i>	<i>Role of cats² in impact</i>	<i>Source</i>
Mammalia				
<i>Perameles gunnii</i>	Tasmania	RD	Major	Green (1974)
<i>Isoodon obesulus</i>	Tasmania	RD	Major	Green (1974)
<i>I. obesulus</i>	Kings Park, WA	LE	Major	Tingay & Tingay (1982)
<i>Myrmecobius fasciatus</i>	Southern Australia	RE	Minor	Friend (1990)
<i>Lagorchestes conspicillatus</i>	Northern Australia	LD	Minor	Ingleby (1991)
<i>Petrogale lateralis</i>	Central WA	LD	Minor	Pearson (1992)
<i>P. assimilis</i>	NE Qld	LD	Major ?	Spencer (1991)
<i>Onychogalea fraenata</i>	Central Qld	LD	Major ?	Horsup & Evans (1993)
<i>Leporillus</i> spp	Southern Australia	RE	Minor	Copley (1988)
<i>Pseudomys novaehollandiae</i>	NE Tasmania	LD	Major	Pye (1991)
Small mammals	Murray mallee	LD	Major	Stephens (1992)
Small mammals	Kangaroo I, SA	LD	Major	Inns <i>et al.</i> (1979)
Small mammals	Warburton, WA	LE	N	Burbidge & Fuller (1979)
Small mammals	Murray-Darling	RE	Minor	Allen (1983)
Small mammals	Central Australia	RE	Major	Finlayson (1961)
Small mammals	Arid Australia	RD	Minor	Morton (1990)
Aves				
<i>Calyptorhynchus magnificus</i>	Wheatbelt, WA	LD	Minor	Saunders (1991)
<i>Pedionomus torquatus</i>	NSW, Vic.	RD	N	Baker-Gabb (1990)
<i>Amytornis striatus</i>	Western NSW	RD	Minor ?	Brickhill (1990)
<i>Pezoporus wallicus</i>	SE Australia	RD	Minor	Meredith (1984), McFarland (1991)
Birds	Murray mallee	RD	Major	Stephens (1992)
Birds	Western NSW	RD	Major,	Bennett (1891)
			Minor	Smith <i>et al.</i> (1994)
Birds	Arid Australia	RD	Minor	Reid & Fleming (1992)
Reptilia, Amphibia				
<i>Egernia kintorei</i>	Central Australia	LD	N	Cogger <i>et al.</i> (1993)
<i>Litoria aurea</i>	Murray mallee	LD	N	Stephens (1992)
<i>L. raniformis</i>	Murray mallee	LD	N	Stephens (1992)

Notes. ¹ LD = local decline, LE = local extinction, RD = regional decline, RE = regional extinction.

² Minor and major refer to magnitude of impact attributed to feral cats, as defined in section 2; N = role of cats not specified or not possible to deduce from source. Because of the anecdotal nature of all listed reports, it is emphasised that assessments of impact should be regarded as tentative.

Anecdotal evidence therefore suggests that small mammals and birds are more likely to experience negative impacts from cat predation than other wildlife taxa. However, as noted by Braysher (1993), other taxa have also been subject to less relevant research than mammals or birds, and it is possible that more pervasive cat-impacts remain to be discovered.

Predatory impacts: historical evidence.

Historical evidence for cat-induced impacts on wildlife has been used to explain extinctions of several species of native mammals and birds that occurred shortly after European settlement in Australia (Baynes, 1979; Dickman, 1993a; Smith & Quin, 1996). Some of these extinctions, in the first half of the nineteenth century

(Table 2), occurred before the introduction of rabbits and foxes, before the establishment of a broad-scale pastoral industry and other deleterious changes (Dickman *et al.*, 1993), hence eliminating these factors as causative agents in the extinction process. However, important premises for the argument that cats caused early extinctions in Australia are that cats were early invaders themselves and that they were capable of having significant, broad scale effects. These premises are reviewed below.

Evidence for the early arrival of cats in Australia was presented first by Finlayson (1943) and subsequently by Tindale (1974) and Baldwin (1980). These latter authors noted that Aborigines in central Australia and northern Western Australia use a variety

Table 2. Extinctions of native mammals on the mainland of Australia, pre-1900, showing dates of last records.

Species (body weight, g)	Date of last record	Source	
Rodentia			
<i>Pseudomys</i> sp.	Pre	1900	Watts & Aslin (1981)
Alice Springs mouse, <i>P. fieldi</i> (50)		1895	Spencer (1896)
Gould's mouse, <i>P. gouldii</i> (50)		1857	Kreffft (1866)
<i>Notomys</i> sp.	Pre	1900	Watts & Aslin (1981)
Darling Downs hopping-mouse, <i>N. mordax</i> (50)		1840s	Mahoney (1977)
Big-eared hopping-mouse, <i>N. macrotis</i> (60)		1844	Mahoney (1975)
Short-tailed hopping mouse, <i>N. amplus</i> (100)		1896	Brazenor (1936)
White-footed rabbit-rat, <i>Conilurus albipes</i> (200)		1875	Flannery (1990b)
Marsupialia			
Unnamed potoroid	Pre	1900	Baynes (1987)
Broad-faced potoroo, <i>Potorous platyops</i> (800)		1875	Kitchener (1983)
Eastern hare-wallaby, <i>Lagorchestes leporides</i> (2500)		1890	Flannery (1990b)

Mean body weights taken from Burbidge & McKenzie (1989)

of apparently unrelated words to describe cats, and suggested that cats have been known to them for a long time. In the central desert region, most Aboriginal people interviewed by Burbidge *et al.* (1988) considered that cats have always been present while some indicated that cats had moved into central Australia from the west. Cats could have been introduced accidentally to the north-western coast in the seventeenth century from the wrecks of Dutch ships (Tindale, 1974); alternatively they could have arrived earlier, possibly around the fifteenth century, via mariners from Indonesia (Baldwin, 1980). A pre-European rock painting in Arnhem Land, that may depict a striped cat (Clegg, 1978) provides further tentative support for an early arrival of cats to northern Australia.

In eastern Australia, the first cats were probably introduced by European settlers in the late eighteenth century. Cats were commonly taken on European trading and exploration vessels of the eighteenth and nineteenth centuries (Cook, 1967; Dartnall, 1978), the first recorded arrivals at Sydney Cove being brought on the First Fleet by Richard Johnston. If European exploration of eastern Australia commenced before the arrival of the First Fleet (Boyd *et al.*, 1993), it is conceivable that cats arrived on the east coast prior to 1788. Irrespective of the precise time of arrival on the east coast, similarities in coat colour patterns between cats in several cities in eastern Australia and in England support the notion that cats were brought at some early time from Europe (Moffatt, 1968; Dartnall, 1975).

If populations of feral cats became established during the early period of European settlement in Australia, reports of their presence would be expected in the diaries and journals of overlanders and other early explorers. However, I have been unable to find such reports. In northern and western Australia, where cats are likely to have been introduced earliest, detailed accounts of the land and biota by Grey (1841), Giles (1875) and Gregory & Gregory (1884) all fail to mention cats. I have been similarly unable to find references to feral cats in the detailed journals of Sturt (1833, 1848), Stuart (1865) and Krefft (1866). Feral cats were noted eventually in Western Australia by Carnegie (1898), by Carruthers (1892), and the Elder Expedition (Lindsay, 1893), but not until the closing years of the nineteenth century.

The virtual absence of observations of feral cats by early European explorers is surprising given the historical and anthropological evidence discussed earlier. The diaries of the early explorers were usually detailed, so it is unlikely that feral cats were observed but not recorded. It is more likely instead that cats were present but not observed, either because they were distributed patchily or because their population densities were low. In parts of northern and western Australia, for example, cats have not been recorded in several detailed fauna surveys (Dahl, 1987; Johnson, 1964; Burbidge & McKenzie, 1978; Friend *et al.*, 1991), but have been sighted or considered common in others (Miles & Burbidge, 1975). (

If this speculation is correct, there is tentative support for the premise that feral cats were present during the demise of several species of native mammals and birds early in the nineteenth century. Could they be considered causative agents of the demise?

Except for the dwarf emus of King and Kangaroo Islands which had been hunted to extinction by about 1827 (Blakers *et al.*, 1984), most of the early recorded extinctions in Australia involve native rodents (Table 2). Three species are known only from sub-fossil deposits, and possibly represent extinctions that occurred during the period of Aboriginal rather than European settlement. The first, *Pseudomys* sp., has been found in large numbers in caves and Aboriginal middens on the basalt plains of western Victoria and appears to have favoured open forest habitats near permanent water (Wakefield, 1964a). Although the time of disappearance of this species is not known, it was listed by Wakefield (1964b) with other mammals that have disappeared from the basalt plains since the arrival of Europeans. The hopping-mouse *Notomys* sp. is known only from the Flinders Range, South Australia, and has been identified from material estimated at 100-300 years old (Watts & Aslin, 1981; Tunbridge, 1991). The species probably inhabited open tussock grassland on clay soils. Finally, an unnamed species of potoroid was recorded by Baynes (1987) from the southern Nullarbor of Western Australia and South Australia. This species appeared to occupy both treeless steppe and lightly wooded mallee heath. It has been recorded in deposits with both feral cats and red foxes (Baynes, 1987), suggesting that its demise post-dated European settlement. Among species recorded alive by Europeans, the Darling Downs hopping-mouse *Notomys mordax* and big-eared hopping-mouse *N. macrotis* appeared to be rare at the onset of European settlement and were extinct by the 1840s (Mahoney, 1975, 1977). The habitat at which the single specimen of *N. mordax* was taken was probably low open forest dominated by brigalow *Acacia harpophylla*, whereas the habitat of *N. macrotis* was either coastal heathland or open forest and woodland (Watts & Aslin, 1981).

Further early losses include Gould's mouse *Pseudomys gouldii* and, over most of its range, the Alice Springs mouse *P. feidi* (Table 2). Gould's mouse had a particularly extensive geographical range, and by 1857 had been collected at localities as distant as eastern and south-western New South Wales and the Moore River in Western Australia; subfossil material is known also from the Flinders Range in South Australia (Smith, 1977). The habitats occupied by *P. gouldii* are poorly known, but included plains and sandhills of the interior as well as open forest (Gould, 1863). *Pseudomys feidi*, as discussed here, follows Baynes (1990) in synonymising this species with the Shark Bay mouse *P. praeconis*. This species occurred extensively over the western and zone from the southern Nullarbor and Shark Bay in Western Australia to Uluru in the Northern Territory (Baynes, 1990), and principally occupied open habitats. It was last collected alive on the coast of Western Australia in 1858 and near Alice Springs in 1895, but still occurs on Bernier Island where cats are absent (Watts & Aslin, 1981).

Several further species listed in Table 2 were apparently declining in range and abundance when first collected by Europeans, but nevertheless survived into the second half of the nineteenth century. These include the white-footed rabbit-rat *Conilurus albipes*, short-tailed hopping mouse *N. amplus* and broad-faced potoroo *Potorous platyops*, as well as the long-tailed hopping-mouse *N. longicaudatus* which persisted until 1901 (Dickman *et al.*, 1993).

Two factors suggest that most of these species would have been particularly prone to cat predation. First, except for *P. platyops* and the eastern hare-wallaby *Lagorchestes leporides*, all mammals that were extinct prior to 1900 weighed 200 g or less (Table 2). This is the size range of prey most preferred by cats (section 3). Second, the saltatory mode of locomotion and the primarily open habitats occupied by the now-extinct species would have made them particularly conspicuous to hunting cats (Dickman, 1992c). Reasons for the declines of the larger *P. platyops* and *L. leporides* are unclear due to the paucity of specimens and localities that are known. However, the pattern of demise of the latter species, at least, appears to differ from that of the smaller rodents that became extinct in that it was tolerably

abundant' over much of its range in the 1840s (Gould, 1863), and declined sharply to extinction only after 1860. Because this period coincides with the onset of intense pastoral activity in the rangelands of eastern Australia, as well as changes in fire regimes and, latterly, peaks in rabbit numbers (Dickman *et al.*, 1993), cats were probably not important in the final demise of this species.

Regional declines of both mammals and birds in western New South Wales have also been interpreted to have arisen from cat predation. Thus, 10 of 13 species of mammals that were last recorded in the Western Division of the state in 1857 or before weighed <220 g and occupied mostly open habitats, whereas 10 of 12-14 species surviving beyond 1857 weighed >350 g (Dickman *et al.*, 1993). One small species that apparently persisted beyond 1857, until 1880, was the pig-footed bandicoot *Chaeropus ecaudatus* (~200 g); this was reported to be 'exceedingly rare' in 1857 by Krefft (1866). Four of six species of birds now extinct in the Western Division were also last collected in the 1840s (Sturt, 1848). These were probably affected by habitat degradation through overgrazing, but the black bittern *Dupetor flavicollis* and Lewin's rail *Rallus pectoralis* were extirpated also by cats (Smith *et al.*, 1994). Six further species of birds that declined or became extinct last century in western New South Wales were listed by Smith *et al.* (1994) as being affected by predators; since foxes crossed the Murray from Victoria only in 1893 (Dickman *et al.*, 1993), the effects of cats were presumably predominant. As with the mammals that declined, seven of the eight species of birds that decreased are small (<200 g), and all are ground foragers or ground nesters. Three of the eight species use marshy or riparian habitats, whereas the remaining five occur predominantly in open plains country (Blakers *et al.*, 1984).

In summary, there is some evidence that cats have historically had deleterious impacts on native mammals and birds in Australia. Cats were present at least from the early days of European settlement and represent the only obvious threat in the first half of the nineteenth century that could have caused the decline and extinction of native fauna over broad geographical areas. The species that declined were small, ground-dwelling and mostly occupants of open habitats, and

hence would have been particularly prone to predation from cats. However, it must also be noted that there is at present little evidence that cats were present in all localities and regions from which native species declined, or that they were present during the periods of decline. Such evidence is needed before more definite conclusions can be drawn about the historical impact of cats on native fauna.

Predatory Impacts: evidence from reintroduction programs.

In an attempt to maintain or reconstitute original faunas, organisms are sometimes moved from parts of their geographical ranges where they still persist to other parts from which they have become locally extinct. In many cases local extinctions will have been caused by human activity or its consequences, but they may arise also from natural catastrophes such as fires or floods (IUCN, 1987).

Reintroduction programs can provide useful inferences on the impact of cats, or other threatening processes, in two ways. First, if a reintroduction succeeds only after it has identified and removed a particular threatening process, such as feral cats, that process can be inferred to have some impact on the species that is reintroduced. Second, if a reintroduction fails, intensive monitoring of the fate of the translocated individuals often reveals the nature of the threatening process that prevents establishment occurring.

Inferences drawn about the importance of a threatening process through reintroduction programs are likely to be valid for the organisms that are physically moved, but some caution is needed before concluding that the process caused local extinction in the first place. This is partly because threatening processes may change over time, but also because animals translocated to a new area will have adapted to local conditions in their area of origin that may differ from those of the reintroduction site. This may be particularly obvious in situations where donor and receptor sites differ in essential food or shelter resources, or where 'naive' organisms are moved from predator-free situations such as islands to predator-infested sites elsewhere. However, with these caveats in mind, the results of reintroduction programs can provide useful insight into the potential impacts of threatening processes such as cats.

The results of 25 attempts to reintroduce macropods were reviewed recently by Short *et al.* (1992), and indicated that successful reintroduction depends critically on the control of introduced predators. Thus in the presence of predators only one of 12 reintroductions (8%) was successful, whereas reintroductions to sites without predators (all islands) succeeded in nine of 11 attempts (82%). In the one case where a species survived reintroduction to an area containing predators, conditions were unusually conducive to success. The species involved, the brush-tailed bettong *Bettongia penicillata*, was shifted only 13 km within the Perup Nature Reserve in Western Australia. Predator numbers were chronically low and reduced still further by poison baiting at the time of translocation of bettongs, while thickets of dense vegetation were available for refuge. Of the studies discussed by Short *et al.* (1992), cats were implicated with foxes or dingoes *Canis familiaris dingo* in the failure of four reintroductions and alone in the failure of two; foxes or dogs/dingoes alone were incriminated in a further five failures. With foxes, cats prevented the reintroduction of three species of macropods including larger species such as the brush-tailed rock-wallaby *Petrogale penicillata* (6800 g) and tammar wallaby *Macropus eugenii* (4200 g); as sole predators cats decimated only the smaller rufous hare-wallaby *Lagorchestes hirsutus* (1660 g) and banded hare-wallaby *Lagostrophus fasciatus* (1880 g). Cats have been implicated in the failure of further reintroductions of macropods in South - Australia (Copley, 1995), and appear to have been the sole cause of failure of Project Desert Dreaming, in which the burrowing bettong *Bettongia lesueur* (-1000 g) was reintroduced to the Gibson Desert of Western_ Australia (Christensen & Burrows, 1995).

The cat-caused failure of one reintroduction program, involving *L. hirsutus*, is particularly instructive and has been discussed in detail by Gibson *et al.* (1994). In this study, hare-wallabies were taken from a formerly extant population in the Tanami Desert (Lundie-Jenkins, 1993), bred in captivity, and excess animals returned to two sites in the Tanami. At the Yinapaka release site, animals were established successfully in a 100 ha enclosure in December 1986. In August 1990 11 animals were captured and equipped with radiocollars, and released a week later into

the wild. In December 1990 and January 1991 seven of these 11 animals were killed by cats, together with a juvenile male. Five of 20 animals released later in 1991 at Yinapaka were also killed within weeks by cats. Losses of hare-wallabies stopped only after removal of four feral cats from the site. At the Lungkartajarra release site, captivebred *L. hirsutus* were established in two 0.25 ha pens between November 1989 and - September 1991, equipped with radiocollars and allowed to disperse 10-30 days later. Between October 1991 and January 1992 14 of 25 collared animals were killed by cats. The killings stopped after February 1992 - following removal of four feral cats (Gibson *et al.*, 1994). Interestingly, cats killed different sex and age classes of *L. hirsutus* in about the same proportions as those released, suggesting that predation was opportunistic (Gibson *et al.*, 1994). Furthermore, not all cats killed. Hare-wallabies persisted with cats for some time before killings began (Lundie-Jenkins *et al.*, 1993); killings then occurred within only 2-4 weeks before specific cats were removed. These observations suggest that killings were made by one or two cats, perhaps residents, that achieved a first kill by chance and then selectively hunted further hare-wallabies. In addition to macropods, many other species of native animals have been subject to reintroduction programs. For native mammals, reintroductions have been usually successful if cats were absent in the receptor sites but only variably successful if cats were present (Table 3). Unfortunately, cat-free sites often lacked other conspicuous threats, whereas sites with cats also contained other predators such as foxes or dogs; hence impacts of cats alone are difficult to specify. Of the failed reintroductions listed in Table 3, predation by cats was identified tentatively as the major cause of failure only for golden bandicoots *Isodon auratus* (Christensen & Burrows, 1995). However, feral cats were, suspected to be hindering establishment of the numbat *Myrmecobius fasciatus* at Karroun Hill, Western Australia (Friend & Thomas, 1995), and were shown to be a major cause of failure in two of three releases of brush-tailed phascogale *Phascogale - tapoatafa* in Gippsland (Soderquist, 1995).

In contrast to the situation for mammals, there have been relatively few managed reintroductions of birds, reptiles or

Table 3. Reintroductions of native mammals (excluding macropods) to areas with and without feral cats *Felis catus* in Australia.

Species	Location ¹	Result ²	Other threats ³	Source reintroduced
(a) Cats absent or reduced in numbers				
<i>Perameles gunnii</i>	Gellibrand Hill Park, Vic.	Success	Fox, dog (small numbers)	Backhouse <i>et al.</i> (1995)
<i>P. gunnii</i>	Hamilton community Parklands, Vic.	Success		Backhouse <i>et al.</i> (1995)
<i>P. gunnii</i>	Mooramong, Vic.	Success	Fox, dog (small numbers)	Backhouse <i>et al.</i> (1995)
<i>Myrmecobius fasciatus</i>	Yookamurra, SA	Success?		Friend (1994)
<i>Trichosurus vulpecula</i>	Katarapko I, SA	Success	Exotic plants	Papenfus (1990)
<i>Phascolarctos cinereus</i>	Goat I, SA	Success?	Exotic plants	Robinson <i>et al.</i> (1989)
<i>Lasiorhinus latifrons</i>	Wedge I, SA	Success	Sheep, settlement	Robinson (1989)
<i>Pseudomys australis</i>	Yookamurra, SA	Success?		Copley (1995)
<i>Leporillus conditor</i>	Yookamurra, SA	Failure		Copley (1995)
<i>L. conditor</i>	Reevesby I and St. Peter I, SA	Success	Sheep, exotic plants <i>Mus domesticus</i>	Copley (1995)
<i>L. conditor</i>	Salutation I, WA	Success		K. Morris (pers.comm.)
(b) Cats present				
<i>Dasyurus geoffroii</i>	Dwellingup, WA	Failure	Hunters, dog or pig	Serena <i>et al.</i> (1991)
<i>D. geoffroii</i>	Julimar, WA	Failure?	Fox, dog?	K. Morris (pers.comm.)
<i>Phascogale tapoatafa</i>	Gippsland, Vic.	Partial success	Fox, goanna, raptors	Soderquist (1995)
<i>Myrmecobius fasciatus</i>	Boyagin NR, WA	Success	Fox (small numbers)	Friend & Thomas (1995)
<i>M. fasciatus</i>	Karroun Hill NR, WA	Success	Fox, dingo, raptors	Friend & Thomas (1995)
<i>Isodon auratus</i>	Gibson Desert, WA	Failure	Fox, dingo (small numbers)	Christensen & Burrows (1995)
<i>Pseudocheirus peregrinus</i>	Ku-ring-gai Chase NP, NSW	Failure	Fox, dog	Smith (1995)
<i>Trichosurus vulpecula</i>	Ku-ring-gai Chase NP, NSW	Failure	Fox	Smith (1995)
<i>T vulpecula</i>	Dandenong Ranges, Vic.	Failure	Fox, dog?	Pietsch (1995)
<i>T vulpecula</i>	Five localities in mainland SA	Success in 4/5 localities	Fox, dog	Papenfus (1990)
<i>Phascolarctos cinereus</i>	Six localities in mainland SA	Success in 5/6 localities	Fox, dog	Robinson <i>et al.</i> (1989)
<i>Lasiorhinus latifrons</i>	Five localities in mainland SA	2 successes, 3 unknown	Fox?	Copley (1995)

Notes. ¹ Locations are shown in Roman type if the reintroduction was certainly to habitat within the species' former range, and in italic if the reintroduction was probably within the species' former range.

² 2 indicates that the result of the reintroduction is uncertain because of insufficient data or insufficient time to determine the outcome.

³ Other threats were sometimes not stated in the original sources, but habitat change due to human activity was evident in all studies. Reintroductions of macropods are described by Short *et al.* (1992) and Copley (1995); see text.

amphibians in Australia. Since 1911 some 17 species of birds have been released on Kangaroo Island, South Australia (Robinson, 1989). Although only four species are known to have persisted, no records are available for many others (Copley, 1995). Similarly poor records have been kept of 12 species of birds

released on Maria Island, Tasmania, between 1969 and 1971 (Rounsevell, 1989). In well-monitored reintroduction programs, involving species such as *Leipoa ocellata* and the noisy scrub-bird *Atrichornis clamosus* feral cats are regarded as having minimal or no impact on the success of the program (Priddel & Wheeler, 1994; Danks, 1995).

In summary, predation by feral cats has been implicated as the cause of failure of several reintroduction programs on mammals, especially those involving small species of macropods (<2000 g), dasyurids and peramelids. There is some evidence that individual cats have disproportionate effects on translocated individuals, so that reintroduction programs can fail even when cats are at low density. There is little evidence that other species of vertebrates have been affected by cats in reintroduction programs, but few relevant studies have been carried out. Although the effects of feral cats on reintroduced species are usually difficult to distinguish from those wrought by other threats, the red fox appears in many studies to be the most important and pervasive cause of program failure.

Predatory impacts: evidence from islands.

Because of their physical isolation, many islands off the coast of Australia and elsewhere in the Pacific region have been subject to little disturbance from human activities. Islands that have been isolated for long periods (i.e. pre-Pleistocene) often have taxa that are endemic to them, while many islands isolated by sea-level rises at the end of the Pleistocene retain biota that disappeared from the adjacent mainland after the onset of European settlement. However, some islands have also suffered limited disturbance, such as the introduction of cats. Feral cats occur on at least 40 islands off the coast of Australia (Dickman, 1992a), seven off the coast of New Zealand (Veitch, 1985) and several dozen elsewhere in the Pacific (King, 1973, 1984). While they are usually not the only agent of disturbance that has been introduced, cats may be the most obvious or important agent that can be identified. Changes in island faunas after the introduction of cats can therefore provide compelling evidence of impact.

Australian offshore islands.

In the Australian region cats have caused or contributed to population declines and extinctions on many offshore islands (Table 4). Among the best documented case studies are the loss of brush-tailed bettongs from St Francis Island, South Australia, and the losses of several small and medium-sized mammals from Dirk Hartog Island, Western Australia.

When St Francis Island was settled in the 1860s it was reported to be 'swarming' with bettongs (Jones, 1924). Cats were introduced to exterminate the animals because of the damage they caused to the settlers' vegetable garden, and by the early 1900s the bettongs were extinct. Although the demise of *B. penicillata* was probably hastened by clearing of much of the original vegetation (Robinson & Smyth, 1976), there appears little doubt that cats were a major causal agent in this island extinction.

Dirk Hartog Island has had a history of visitation by Europeans since 1616, and has been held under pastoral lease for sheep since 1899 (Burbidge & George, 1978). The precise time of introduction of cats is not known. However, they were reported as becoming numerous in 1916-17 (Carter, 1917), perhaps indicating that introduction coincided with establishment of the sheep station. Burbidge & George (1978) report local knowledge that the 'wallabies', thought to be *Lagostrophus fasciatus* and burrowing bettong *Bettongia lesueur* became extinct in the 1920s. However, as some doubt has been cast recently on the former presence of *L. fasciatus* on Dirk Hartog (Baynes, 1990), the local reports may refer to *B. lesueur* alone. A further eight species of native mammals have been recorded as sub-fossils from Dirk Hartog (Table 4). Except for *Bettongia lesueur* (1500 g), *B. penicillata* (1300 g) and *Dasyurus geoffroii* (1075 g), body weights of these species averaged 220 g or less. Of the terrestrial mammals originally present on Dirk Hartog, only three small species (< 30 g) remain (Table 4).

Although Dirk Hartog remains a pastoral station and has also supported large populations of goats (Burbidge & George, 1978), strong comparative evidence implicates cats in the wave of extinctions. Bernier and Dorre Islands, to the north of Dirk Hartog, do not have cats and have retained their original faunas almost intact; only the desert mouse *Pseudomys desertor* has disappeared from Bernier (Ride *et al.*, 1962; Ride, 1970). Both Bernier and Dorre have been subject, to intermittent human occupation and sheep grazing; goats were also present on Bernier for nearly 90 years, and caused considerable damage to the island's vegetation before their eradication in the mid 1980s (Morris, 1989). House mice were present on Bernier Island around the

Table 4. Impacts of feral cats *Felis cat us* and other threats on native terrestrial mammals and birds on islands off the coast of Australia.

Island	Area (ha)	Species	Effects	Other threats	Source				
St Francis, SA	809	<i>Bettongia penicillata</i>	Ex	Habitat change, <i>Rattus rattus</i> (Ex) (1976)	Robinson & Symth				
		<i>Isoodon obesulus</i>	S						
		<i>Macropus eugenii</i>	Ex						
		24 species of birds	S						
Reevesby, SA	344	<i>Macropus eugenii</i>	Ex	Habitat change, Robinson <i>et al.</i> (1985); sheep, exotic plants, Mus <i>domesticus</i>	Robinson (1989)				
		<i>Leporillus conditor</i>	Ex						
		<i>Pelagodroma marina</i>	D?						
		Other sea and land birds	S						
Flinders, SA	3 642	<i>Macropus eugenii</i>	Ex	Habitat change, Robinson (1989)					
Kangaroo, SA	435 000	<i>Phascogale tapoatafa</i>	Ex	Habitat change, Ford (1979); settlement, 8 sp. Inns <i>et al.</i> (1979); exotic mammals, Robinson (1989)					
		<i>Dasyurus maculatus</i> (?)	Ex						
		11 other species native mammals	S						
		<i>Leipoa ocellata</i>	Ex?						
Hermite, WA	1 010	214 other species native birds	S	6 sp. exotic birds + many introduced native species					
		<i>Lagorchestes conspicillatus</i>	Ex	<i>Rattus rattus</i>	Burbidge (1971, 1989); Burbidge & McKenzie (1989)				
		<i>Isoodon auratus</i>	Ex						
		<i>Hydromys chrysogaster</i>	S						
		<i>Malurus leucopterus</i>	Ex						
		<i>Eremiornis carteri</i>	Ex						
		<i>Chrysococcyx basalis</i>	Ex						
		<i>Pachycephala rufiventris</i>	Ex						
		<i>Ephthianura tricolor</i>	Ex						
		<i>Charadrius mongolus</i>	S						
		35 other species native birds	Ex						
		Dirk Hartog, WA	54 360			<i>Bettongia lesueur</i>		Habitat change, Burbidge & George (1978); Baynes (1990)	
						<i>B. penicillata</i>	Ex		
						<i>Lagostrophus fasciatus</i> (?)	Ex		
<i>Dasyercus cristicauda</i>	Ex								
<i>Dasyurus geoffroi</i>	Ex								
<i>Parantechinus apicalis</i>	S								
<i>Sminthopsis dolichura</i>	Ex								
<i>Perameles bougainville</i>	Ex								
<i>Leporillus conditor</i>	S								
<i>Pseudomys albocinereus</i>	Ex								
<i>P. fieldi</i>	S								
<i>P. hermannsburgensis</i>	Ex								
<i>P. shortridgei</i>	S								
84 species native birds	S								
Angel, WA	880	<i>Zyomys argurus</i>		Fox	Burbidge & McKenzie (1989)				
Dolphin, WA	3 200	<i>Petrogale rothschildi</i>	D	Fox	"				
		<i>Dasyurus hallucatus</i>	S						
		<i>Zyomys argurus</i>	S						
Gidley, WA	845	<i>Z. argurus</i>	S	Fox	"				
Legendre, WA	1300	<i>Z. argurus</i>	S	Fox	"				
		<i>Rattus tunneyi</i>	S						
Garden, WA	1 170	<i>Macropus eugenii</i>	S	Naval base, settlement	"				
		60 species native birds	S						
Rottneest, WA	1550	<i>Setonix brachyurus</i>		Habitat change, settlement, Mus <i>domesticus</i> , <i>Rattus rattus</i>	Burbidge & McKenzie (1989); Saunders & de Rebeira (1983, 1989)				
		113 species native birds	S						

Table 4. cont

<i>Island</i>	<i>Area (ha)</i>	<i>Species</i>	<i>Effect</i>	<i>Other threats</i>	<i>Source</i>
North Stradbroke Qld		Not specified	D	Habitat change, settlement, fox, dog; cane toad	Sinclair (1989)
Muttonbird, NSW	8	<i>Pelagodroma marina</i>	D?	- Fox, dog	Smith & Dodkin (1989)
Broughton, NSW	138	4 other species sea birds	S?		"
		<i>P. marina</i>	D	Settlement, rabbits,	"
		6 other species sea birds	S?	<i>Rattus rattus</i>	

Notes. S = stable, D = declined, Ex = extinct, ? indicates that an effect is suspected but not quantified. Tammar wallabies *Macropus eugenii* were probably extinct prior to settlement on St. Francis and Reevesby Islands, and hence may not have been eliminated by cats (Robinson & Smyth, 1976; Robinson 1989). On Hermite Island, Burbidge (1971) emphasised the disappearance only of *E. carteri* and *M. leucopterus*. However, the four other named species of birds have not been recorded since 1912 and may thus be presumed extinct.

beginning of the twentieth century but, unlike on Dirk Hartog, persisted for only a few years (Ride *et al.*, 1962). However, mice are considered to be poor competitors with native fauna on islands (Dickman; 1992a), and are unlikely to have contributed to any of the extinctions on Dirk Hartog.

In addition to these well-documented studies, cats can be implicated strongly in losses of mammals and birds from Hermite Island in the Monte Bello group (Burbidge, 1971), and probably also in the loss of the greater stick-nest rat *Leporillus conditor* from Reevesby Island in the Sir Joseph Banks group (Robinson, 1989). Birds appear to have fared better than mammals on Australian offshore islands, although the white-faced storm-petrel *Pelagodroma marina* has declined on three islands (Table 4). The exposed burrows, nocturnal activity and clumsy movements of this species on land perhaps increase its proneness to predation by cats.

Despite such clear effects of cats in the studies described, impacts of cats on other island faunas are not always so obvious. First, it is often difficult to separate the effects of cats from those of other threats, particularly when loss of habitat has been extensive or when other predators such as foxes and dogs have been introduced. Second, for many islands there is uncertainty about when cats were introduced and when native fauna declined. For example, on the Bass Strait islands many extinctions of native mammals are known to have occurred (Table 5), but the timing of the losses is uncertain. Some native species were recorded as subfossils of unknown age, and visits to the islands to sample native animals have not been frequent (Whinray, 1971; Hope, 1973,

1974). Feral cats were present on King Island in 1887 (Campbell, 1888) and could have contributed to the demise there of the spotted-tail quoll *Dasyurus maculatus* which was last recorded in 1923 (Courtney, 1963). However, the quoll was actively persecuted by settlers (Green & McGarvie, 1971) and, like the endemic King Island emu *Dromaius minor* may have been exterminated directly by human hunting pressure. Green & McGarvie (1971) report the demise of a further five species of birds from King Island, and attribute their loss to human predation or habitat alteration. Similar losses have occurred also on Flinders Island' (Green, 1969).

Taken together, the studies summarised in Tables 4 and 5 show that cats can decimate insular populations of native mammals and birds, but also that apparently stable coexistence may be possible. For example, the golden bandicoot *Isodon auratus* disappeared from Hermite Island after the introduction of cats, but the ecologically similar southern brown bandicoot *I. obesulus* persisted with cats on St Francis Island (Robinson & Smyth; 1976) and occurs - presently with cats on Kangaroo Island (Inns *et al.*, 1979). Detailed ecological studies on insular species with stable populations are sparse, but suggest that native species can coexist with cats if refugia are available. For terrestrial mammals in a 'critical' weight range' (CWR) of 35-5500 g, for example, rockpile habitats usually provide important shelter from predation (Burbidge & McKenzie, 1989). In Tasmania, where no native mammals except the thylacine *Thylacinus cynocephalus* have become extinct since European settlement, utilisation of dense

Table 5. Status of native terrestrial mammals on islands of the Bass Strait with populations of feral cats *Felis catus*.

	Flinders 133 000 ha	King 110,000 ho	Cape Barren Deal 44,500 ho	2000 ha	Clarke 11,500 ho
Monotremata					
<i>Ornithorhynchus anatinus</i>		P			
<i>Tachyglossus aculeatus</i>	P	P	P		
Marsupialia					
<i>Antechinus minimus</i>	P	P		(Ex)	P
<i>Dasyurus maculatus</i>	Ex	Ex	(Ex)	(Ex)	
<i>Sarcophilus harrisii</i>	(Ex)				
<i>Isoodon obesulus</i>	Ex				
<i>Vombatus ursinus</i>	P	Ex	Ex		
<i>Pseudocheirus peregrinus</i>	P	P	Ex	(Ex)	Ex
<i>Trichosurus vulpecula</i>	P	P	P		
<i>Cercartetus nanus</i>	P	P		P	
<i>Potorous tridactylus</i>	P	P	P?		
<i>Thylogale billardierii</i>	P	P	Ex	(Ex)	Ex
<i>Macropus rufogriseus</i>	P	P	P	P	P
<i>M. giganteus</i>				Ex	Ex
Rodentia					
<i>Rattus lutreolus</i>	P	P			
<i>Pseudomys higginsii</i>		(Ex)	P	(Ex)	
<i>Hydromys chrysogaster</i>	P				

Results are based on data presented by Hope (1973, 1974). P = present, Ex = extinct since European settlement, (Ex) = extinct, possibly prior to European settlement (recorded as sub-fossil only). All islands have been subject to habitat change for pastoral activity and settlement. Rabbits occur on Deal and Clarke Islands and have been present historically on Flinders; *Rattus rattus* occurs on all except Clarke Island, *Mus domesticus* on all except Clarke and Deal Islands; feral pigs occur only on Flinders Island. Foxes are absent from all islands.

vegetation appears to be particularly important for the persistence of species such as the long-nosed potoroo *Potorous tridactylus* (Heinsohn, 1968) and long-tailed mouse *Pseudomys higginsii* (Stoddart & Challis, 1993).

The generally greater stability of birds on Australian offshore islands (Table 4) perhaps also reflects use of dense vegetation, or nest and roost sites that are inaccessible to cats, such as sea cliffs. However, bird populations may also be able to sustain relatively high levels of predation on islands providing that immigration equals or exceeds losses (Saunders & de Rebeira, 1985, 1986).

New Zealand offshore islands.

Because New Zealand has only three species of native mammals, the bats *Chalinolobus tuberculatus*, *Mystacina tuberculata* and the now-extinct *M. robusta*, impacts of cats have been confined largely to depredation on native birds and reptiles. Research on the impact of cats on insular populations is quite extensive and has been summarised previously (Merton, 1970; King, 1984; Veitch, 1985; Fitzgerald, 1988, 1990); hence only a brief review of major results is provided here.

Along with the Norway rat *Rattus norvegicus*, cats were introduced to New Zealand in the late eighteenth century (Wodzicki & Wright, 1984). Between about 1840 and 1931 cats were introduced to 15 islands off the coast of both North and South Islands; they have since been implicated in the extinction of at least six species of island endemic birds (including the Stephens Island wren) as well as of some 70 local populations of insular birds (King, 1984). The species that have succumbed to cat predation include tiny species, such as the Stephens Island wren (<10 g) to much larger species such as sooty shearwaters *Puffinus griseus* (~800 g) and kakapo *Strigops habroptilus* (up to 3500 g). Accounts of cats on two adjacent islands, Stewart and Herekopare, are instructive and illustrate the predatory impact of cats in the New Zealand region. The accounts are based primarily on Karl & Best (1982) and Fitzgerald & Veitch (1985).

Stewart Island (174 600 ha) lies off the southern coast of South Island. Visitation by whalers and sealers in the early 1800s and subsequent European settlement caused some change in habitat and also allowed the

establishment of feral cats and *R. norvegicus*. A second species of rat, *R. exulans*, was present on Stewart prior to European settlement, while *R. rattus* was first recorded in 1911. At least five species of birds have disappeared from Stewart Island, the South Island kokako *Caiiiaeas cinerea cinerea*, Stead's bush wren *Xenicus longipes variabilis*, Stewart Island snipe *Coenocorypha aucklandica iredalei*, South Island saddleback *Philesturnus carunculatus carunculatus* and yellowhead *Mohoua orchrocephala*. A sixth species, the brown teal *Anas aucklandica chlorotis*, has not been seen since 1972. A seventh species, the kakapo *Strigops habroptilus*, was rediscovered in 1977 in a small area of about 10 000 ha (King, 1984). Kakapo are an unimportant component of the diet of feral cats and occur in only ~5% of cat scats. However, impact on kakapo is severe. Between 1980 and 1982 about 60% of male birds were killed by cats. Between the 1981-82 season and late 1983 the population was estimated to have declined from 50-150 to just 20 birds (King, 1984). Despite their large size, kakapo are vulnerable to cats because they are flightless, ground-dwelling, breed once every two years and have altricial young (Karl & Best, 1982). They also roost on the ground by day in the open or under low shrubbery, and rely primarily on cryptic camouflage to escape detection. In addition to their major impact on kakapo, cats on Stewart Island take other species of birds that feed or nest on the ground. These include parakeets *Cyanoramphus spp.*, pipit *Anthus novaeseelandiae*, blue penguin *Eudyptes minor* crested penguin *E. pachyrhynchus* and sooty shearwater (Karl & Best, 1982). A continuing decline in population size of the New Zealand dotterel *Charadrius obscurus* on Stewart Island has also been attributed to predation from feral cats; the island population now numbers only 60-65 birds and is considered endangered (Dowding & Murphy, 1993). Although some of the smaller species may be depredated also by rats, rats are themselves the staple prey of cats on Stewart Island (Appendix 2). The relationship between cats, rats and birds is obviously complex. However, it appears that rats may 'subsidise' the impact of cats on birds by supporting larger populations of cats than would otherwise occur. Impacts of cats are equally severe on ground-dwelling species of land birds and sea

birds on other New Zealand islands, either alone (Cheeseman, 1887) or with other predators such as rats (Merton, 1970; Dowding & Kennedy, 1993) or wekas *Gallirallus australis* (Taylor, 1979).

Herekopare Island (28 ha), lying 8 km off the east coast of Stewart Island, contrasts with most other New Zealand islands in that it lacks mammalian prey. Cats were introduced to Herekopare probably in the mid-1920s, and persisted on the island for about 45 years until they were eradicated in 1970 (Fitzgerald & Veitch, 1985). No other predatory or introduced species occurred on Herekopare with the cats, although wekas from Stewart Island were present intermittently. The island is not settled and has thus experienced little change in vegetation, although increased coverage of the tree nettle *Urtica ferox* since 1911 may have reduced the area available for petrels.

Exterminations of birds by cats were being recorded in the early 1940s (Richdale, 1942) and by 1970 six species of land birds were confirmed to be locally extinct: yellowcrowned parakeet *Cyanoramphus auriceps*, fernbird *Bowdleria punctata*, robin *Petroica australis rakiura*, brown creeper *Finschia novaeseelandiae*, banded rail *Rail us philippensis* and snipe *Coenocorypha aucklandica iredalei* (Fitzgerald & Veitch, 1985). Two species of sea birds, diving petrels *Pelecanoides urinatrix* and broad-billed prions *Pachyptila vittata*, formerly present in enormous numbers on Herekopare, were also exterminated.

As on Stewart Island, ground-dwelling birds and nesting sea birds on Herekopare appeared to be particularly vulnerable to cat predation. Of the six species of land birds that disappeared only the brown creeper feeds above ground, whereas four of six native land birds that survived the introduction of cats are arboreal foragers (Fitzgerald & Veitch, 1985). Two further species of ground foragers, the red-crowned parakeet *C. novaeseelandiae* and tomtit *Petroica macrocephala*, also succumbed initially to cat predation but later recolonised while cats were still present. Elimination of the diving petrels was perhaps facilitated by three aspects of their biology (Fitzgerald & Veitch, 1985). First, they were the smallest petrels on Herekopare (~120 g). Second, chicks are fed nightly by both parents and have a longer nesting period than other

petrels, and so are vulnerable to cats for longer. Third, diving petrels and prions returned to Herekopare to lay eggs earlier in spring than other sea birds, and hence became available to cats at the end of a lean winter period.

In summary, studies on New Zealand islands provide compelling evidence that cats can severely depress and extirpate native birds. Ground feeding and ground nesting species appear to be particularly vulnerable, and even species weighing up to $3\frac{1}{2}$ kg are not immune. Low intensity predation by cats can still have a major impact on population size, as in the case of the kakapo, if abundant alternative prey are available to support high cat densities.

Other Pacific Islands.

As in the New Zealand region, impacts of cats on islands elsewhere in the Pacific region have fallen most heavily on birds. Cats are suspected or known to have depleted breeding populations of sea birds and endemic land birds on islands of the central and south Pacific (King, 1973; Perry, 1980; Wodzicki, 1981; Rauzon, 1985; Kirkpatrick & Rauzon, 1986), including the islands of Hawaii (Tomich, 1969), as well as on Norfolk and Lord Howe Islands off the coast of eastern Australia (Smithers & Disney, 1969; Recher & Clark, 1974; Forshaw, 1980; Schodde *et al.*, 1983; Hermes *et al.*, 1989). Cats are considered to be a particularly serious threat to birds on many subAntarctic islands on the southern fringes of the Pacific (Johnstone, 1985), especially when other introduced species such as rats and rabbits provide alternative prey if birds are seasonally absent.

The introduction of cats to sub-Antarctic Macquarie Island has been well documented (Cumpston, 1968), and provides a particularly instructive example of their predatory impact. Along with wild dogs, cats were introduced by sealers to Macquarie Island (12 000 ha) soon after its discovery in 1810. Dogs are not recorded after 1820, but cats persisted on the island on a diet that presumably comprised both sea birds and endemic land birds. No further species were introduced until 1872, when wekas were imported from Stewart Island. Cats remained in low numbers until the 1880s, but increased dramatically following the introduction of rabbits in 1879. Two species

of endemic land birds, the Macquarie Island parakeet *Cyanoramphus novaezelandiae erythrotis* and banded rail *Rallus philippensis macquariensis*, which were apparently numerous in the 1870s, then declined precipitously and were extinct by 1890. The sudden demise of these species has been interpreted as being a direct consequence of increased predation from cats and secondarily from wekas, rather than from any direct effects of rabbits themselves (Taylor, 1979). Prior to the arrival of rabbits, cats presumably faced severe shortages of food over winter due to the seasonal migration of most seabirds, and this would have minimised their predatory impact. However, with rabbits available year round to sustain a larger population, Taylor (1979) has proposed that more consistent and intensified predation on the land birds would have led to their demise.

Subsequent studies of burrow-nesting petrels on Macquarie Island have shown that the grey petrel *Procellaria cinerea* no longer breeds on the island and that Antarctic terns *Sterna vittata* nest only on offshore stacks (Jones, 1977). Breeding populations of Antarctic prions *Pachyptila desolata* appear stable, white-headed petrels *Pterodroma lessoni* and sooty shearwaters *Puffinus griseus* are declining, while blue petrels *Halobaena caerulea*, diving petrels *Pelecanoides urinatrix* and fairy prions *Pachyptila turtur* persist in very low numbers (Brothers, 1984). Although cats have been implicated in the declines of these species, their impact is difficult to separate from that of wekas and also that of black rats, introduced in 1910. Rabbits <600 g comprise the bulk of the diet of cats on Macquarie, but many Antarctic prions and white-headed petrels are taken also (Jones, 1977). Despite the arguments of Taylor (1979), winter still appears to be a period of food shortage for cats; few rabbits <600 g are available, prions and white-headed petrels migrate, and wekas, rats and scavenged material feature prominently in the diet (Jones, 1977). The introduction of myxomatosis to Macquarie Island in late 1978 has greatly exacerbated the shortage of food in winter by causing a large (>90%) reduction in the rabbit population; wekas also have disappeared, and rodents are now a particularly important part of the diet over this period (Rush, 1992). It is perhaps no coincidence that the three

most abundant species of petrels, the Antarctic prion, white-headed petrel and sooty shearwater are all absent from Macquarie Island in winter, while those that have declined most dramatically, the grey, blue and diving petrels, as well as fairy - prions, were either winter breeders or resident throughout the year (Brothers, 1984; Brothers *et al.*, 1985).

In contrast to the grim situation for some petrels, surface-nesting albatrosses and skuas are seldom taken by cats (Jones, 1977). Although some nest on rock stacks off Macquarie Island that are inaccessible to cats, these species also tend to be large and have defence mechanisms that presumably reduce cat predation (Jones, 1977).

Similar patterns of cat impact have been reported on other islands. On Hog Island in the Indian Ocean, cats were introduced in the late nineteenth century and have since exterminated several species of burrownesting seabirds and small surface-nesting species. Only surface-dwellers large enough to repel cats and larger burrowing species that dig deep burrows have survived (Derenne & Mougin, 1976). Similar impact has been recorded on sub-Antarctic Marion Island with cat-induced declines of diving petrels and storm petrels (van Aarde, 1980), as well as on Dassen and Robben Islands off the coast of South Africa (Cooper *et al.*, 1985; Berruti, 1986; Brooke & Prins, 1986). On Iles Kerguelen in the southern Indian Ocean rabbits are eaten year round and form the staple diet of cats in winter (Derenne, 1976). As on Macquarie Island blue petrels have declined in abundance; other species weighing <250 g and the winter-breeding grey petrel have also been reduced. Only larger and more aggressive species such as white-chinned petrels *Procellaria aequinoctialis* appear unaffected by cats, as do species that occupy wet sites which cats avoid (Derenne, 1976; Weimerskirch *et al.*, 1988). On islands where rabbits are not available, cat populations may be boosted by other mammalian prey. Furet (1989) found that house mice comprised the sole diet of feral cats during winter on Amsterdam Island in the southern Indian Ocean, and that young Norway rats <100 g were selected at other times. Few birds occur on the island, apparently because of the depredatory effects of the subsidised cat population.

In summary, there is extensive evidence that cats can have deleterious impacts on endemic land vertebrates and breeding bird populations on both offshore and oceanic islands. Insular faunas that have evolved for long periods in the absence of predators appear particularly susceptible to cat predation (Dickman, 1992c). In the Australian region, impact is greatest on terrestrial mammals weighing <3000 g and possibly also on the burrow-dwelling white - faced storm-petrel. Only one insular species of bat has been lost (*Nyctophilus howensis*, from Lord Howe Island), and the cause of its demise is unknown (McKean, 1975). Cat impact is reduced on islands providing rock outcrops or dense vegetation but increased where habitat is altered or simplified. In the New Zealand and broader Pacific-region cats impact on birds up to 3500 g but have greatest effects on birds <1000 g. Land - species that feed and nest on the ground are particularly vulnerable, as are smaller (<800 g) and less aggressive species of sea birds that nest on the ground surface or in shallow burrows. Impact on some islands, especially in the sub-Antarctic, is intensified by the presence of introduced rodents or rabbits, which support cat populations through periods of winter food stress.

Predatory impacts: field experiments.

Field experiments involving the removal or reduction of cats have the greatest potential to quantify the effects of predation on prey populations. In semi-arid New South Wales experimental reduction of the numbers of cats and foxes has demonstrated that these predators can jointly maintain rabbits at low population densities, but have little or no suppressive effect when densities are high (Newsome *et al.*, 1989; Pech *et al.*, 1992). Unfortunately, no equivalent experiments have been completed to determine the effects of cats on native fauna. Two studies are under way, at Heirisson Prong, Western Australia, and the Simpson Desert, western Queensland, but have not run long enough to have produced results.

In the absence of properly controlled and - replicated experiments, inferences about the impact of cats can still be obtained by assessing the responses of prey populations at specific sites before and after cat removal. Such inferences should of course be treated with some caution: many factors other than cats are likely to affect the size of any

population at different times, making it difficult to determine whether cat removal has been causal or coincidental in producing population change.

With this caveat in mind, it does appear that removal or reduction of cats from a site is usually followed by increases in the population size or reproductive success of known species of prey (Table 6). Population increases in some species have been spectacular. For example, the stitchbird *Notiomystis cincta* on Little Barrier Island, New Zealand, increased over six fold from less than 500 individuals to 3000 in just a few years following removal of cats (Griffin *et al.*, 1988). Breeding success of three species of petrels on Marion Island, South Africa, increased similarly by 17 to 49 percentage points in just two years in cat-free exclosures compared with control sites (van Rensburg, 1986; van Rensburg & Bester, 1988). Further increases in population size and diversity of birds have been reported on Mangere and Cuvier Islands, New Zealand, following removal of cats (Veitch, 1985), but details are not available. Only Rauzon (1985) has suggested that birds do not always respond positively to removal of cats. However, results are difficult to evaluate in this study because of differences in bird survey methods before and after removal of cats.

In summary, known prey species have usually increased after removal or reduction of cats in the few studies where such removals have been attempted. Where the response has been quantified, the impact of cats has been major. Although other factors may have influenced population increases for some species at some times, the consistency of response following cat removal provides some of the most compelling evidence for impact that is available.

4.3 Amensal impacts of feral cats

4.3.1 Pathogens

Transmission of pathogens by an invading species to susceptible natives can have more profound effects on the natives than any direct impact of the invader itself. Wellknown examples of such impact include the decimation of the lowland native bird fauna of Hawaii by malarial parasites carried by introduced birds (van Riper *et al.*, 1986), and

declines of cervids in North America due to a meningeal helminth carried by white-tailed deer (Schmitz & Nudds, 1994). Similar impacts have not been demonstrated on native fauna in Australia. However, cats and other introduced carnivores carry a wide range of disease and parasitic organisms (Newsome & Coman, 1989; Wilkinson, 1990), and some of these, such as *Toxoplasma gondii*, are suspected to have caused population declines in several species of native mammals (Shepherd & Mahood, 1978; Mahood, 1980). To identify possible amensal impacts of cats on native fauna, I used the review of Moodie (1995) to list all pathogens recorded from cats in Australia that are not known to be specific to cats and which could potentially transfer to native hosts. I then reviewed literature on native vertebrates to record species in which those pathogens had been identified.

In general, coincidence of disease and parasitic organisms in cats and native fauna appears to be small (Table 7). Some sharing of parasitic arthropods (especially Ixodes ticks) and general bacterial and fungal infections is apparent, but few cat viruses, protozoan or helminth parasites have been recorded in native fauna. Native birds, reptiles and amphibians have least cat pathogens, while rodents, bats and monotremes share fewer diseases and parasites with cats than do marsupials.

It should be noted that detailed surveys of pathogens are not available for all groups of native vertebrates, especially reptiles and amphibians, hence some underestimation of the coincidence of pathogens may have occurred. However, such bias is likely to be minimal. First, actual frequencies of coincident pathogens will be less than those tabulated if any organisms identified only to generic level in cats or native fauna differ specifically. Second, many pathogens recorded in native species are likely to have been picked up accidentally. For example, three species of fleas *Ctenocephalides felis*, *Echidnophaga gallinacea* and *Pulex irritans*, have been recorded from the brushtail possum *Trichosurus vulpecula*, but appear to be passengers and may not represent valid host records (Dunnet & Mardon, 1974). Third, detailed recent studies of monotremes (Whittington, 1992) and macropodid marsupials (Speare *et al.*, 1989; Arundel *et*

Table 6. Apparent effects of removal or reduction of feral cats *Felis catus* on terrestrial species of mammals and birds.

Species	Location	Removal or Reduction ¹	Effect	Source
Superb lyrebird	Sherbrooke, Vic.	Reduction	Pop. increase	H. Bradley (pers. comm.)
<i>Menura novaehollandiae</i>	Tidbinbilla,	Removal	Pop. increase	Lambie (1988);
Freckled duck	ACT			Osborne & Williams (1991)
<i>Stictonetta noevoso</i>	Tidbinbilla,	Removal	Pop. increase	Lambie (1988);
Musk duck	ACT			Osborne & Williams (1988)
<i>Biziura lobato</i>	Tidbinbilla,	Removal	Mixed ²	Lambie (1988);
Magpie goose	ACT			Osborne & Williams (1991)
<i>Anseranas semipalmato</i>	Yathong,	Reduction	Pop. increase	Newsome <i>et al.</i> (1989);
Rabbit	NSW			Pech <i>et al.</i> (1992)
<i>Oryctolagus cuniculus</i>	Reevesby I,	Removal	Pop. increase	Copley (1991)
Cape Barren goose	SA			
<i>Cereopsis novaehollandiae</i>	North West I,	Removal	Pop. increase	Domm & Messersmith (1990)
Banded rail	Qld			
<i>Rallus philippensis</i>	North West I,	Removal	Pop. increase	Domm & Messersmith (1990)
Silvereeye	Qld			
<i>Zosterops lateralis</i>	Kourarau,	Reduction	Pop. increase	Gibb <i>et al.</i> (1978)
Rabbit	NZ			
<i>O. cuniculus</i>	Little Barrier	Removal	Pop. increase	Veitch (1985)
Stitchbird	I, NZ			
<i>Notiomystis cincta</i>	Macquarie I,	Reduction	Not specified	Brothers & Copson (1988)
Seabirds	sub-Antarctic			
Great-winged petrel	Marion I,	Removal	Increased breeding success	van Rensburg & Bester (1988)
<i>Pterodroma macroptera</i>	S. Africa			
White-chinned petrel	Marion I,	Removal	Increased breeding success	van Rensburg & Bester (1988)
<i>Procellaria oequinoctialis</i>	S. Africa			
Salvin's prion	Marion I,	Removal	Increased breeding success	van Rensburg & Bester (1988)
<i>Pachyptila vittata</i>	S. Africa			
Three sp. seabirds	Baker I,	Removal	Pop. increase	King (1973)
(not specified)	central Pacific			
Lesser frigatebird	Jarvis I,	Removal	Pop. increase	Rauzon (1985)
<i>Fregata ariel</i>	central Pacific			

Notes. ¹Removals described by King (1973), Rauzon (1985) and Veitch (1985) were eradications of cats from islands; others were removals from smaller areas by use of cat-proof exclosures.

²Magpie geese increased following removal of cats, but decreased subsequently due to predation by ravens on eggs. Cats were the primary predators in most studies. However, foxes were also removed or reduced in the studies at Tidbinbilla, Sherbrooke and Yathong, while ferrets *Mustela furo* were excluded in the study by Gibb *et al.* (1978) at Kourarau.

al., 1990; Beveridge *et al.*, 1992) have found that helminth communities, at least, tend to be highly specific within species or genera (cf. Beveridge *et al.*, 1989), and that sharing of taxa with cats is virtually non-existent. Finally, many pathogens recorded in cats in Table 7 occur rarely, and some are likely to have transferred to cats from native species. Examples are fleas *Echidnophaga spp.* and the nematode *Cyathospirura dasyuridis* which is found commonly in quolls (Coman, 1972; Gregory & Munday, 1976).

Although feral cats may contribute to the dissemination or maintenance of some pathogens in populations of native fauna, impacts are difficult to discern. Several common pathogens such as *Salmonella*, *Leptospira* and *Sarcocystis* are frequently carried by free-living hosts without obvious clinical signs; infestation of mammals with *Pasteurella spp.* may become apparent only after individuals have been bitten by afflicted cats (Munday *et al.*, 1978; Munday, 1988). Infection by other organisms may produce clinical signs only in components of host populations or at certain times of year.

Table 7. Coincidence of non-specific pathogenic organisms recorded from cats *Felis cat us* in Australia and from native vertebrate fauna.

Pathogen group	No. pathogen species found in cats		No. pathogen species found in native vertebrates ²		Rodents & Bats	Reptiles & Birds Amphibians	
	D	F	Monotremes	Marsupials			
Viruses	3	0	0	0	0	0	0
Bacteria	>40	?	1(5)	8(5)	3(3)	3(2)	(1)
Fungi	>17	?	3(1)	2(1)	2(1)	1(2)	(2)
Protozoa	21	4	1	1(4)	1	1	0
Helminths	26	15	1	4(2)	2(1)	(1)	1
Arthropods	19	10	3(1)	7(3)	3(3)	(1)	0

Notes. ¹Data from Moodie (1995). Pathogens are listed only if recorded from domestic cats (D) or feral cats (F) in Australia and if known or suspected not to be host-specific on felids. The numbers of species listed are minima as pathogens could not always be identified below genus; numbers in the D and F columns are not additive as some pathogens have been recorded in domestic and feral cats.

²Data from Arundel *et al.* (1977), Presidente (1984), Speare *et al.* (1984), Bryden (1988), Speare *et al.* (1989), Walton & Richardson (1989), Hand (1990), Sprott *et al.* (1990), Whittington (1992) and Obendorf (1993). For native vertebrates, unbracketed numbers represent numbers of pathogens conspecific with those in cats; bracketed numbers represent congeneric pathogens where the specific identify was not clear or not stated.

Despite difficulties in quantifying impacts, two pathogens warrant further comment. Both use the cat as a definitive host, and both can produce severe clinical signs in a wide range of native species.

Spirometry erinacei is a large pseudophyllidean tapeworm that infests the gut of carnivores and which may have been introduced to Australia around the time of European settlement (Whittington, 1992). It is carried by foxes and dingoes (Coman, 1973a, 1978) and is the most prevalent helminth parasite of feral cats in eastern Australia (Gregory & Munday, 1976; Ryan, 1976; Coman *et al.*, 1981 a; cf. Milstein, 1993). Prevalence rates of 33-76% have been reported for cats from different parts of New South Wales, with mean and maximum incidences per cat of 20 and 625 parasites, respectively (Ryan, 1976). Eggs passed in faeces develop into the first intermediate stage, procercooids, within aquatic copepods or other small freshwater crustaceans (Arundel, 1977). A second intermediate stage, the plerocercoid, develops if the copepod is ingested. Plerocercoids migrate to the body cavity or within the soft tissues of hosts and cause a condition called sparganosis. Plerocercoids have been recorded in dasyurid marsupials, monotremes, some native rodents, snakes and frogs; they may produce no obvious clinical symptoms, but can cause muscular haemorrhage, damage to soft tissue such as the lung, and potentially death (Munday, 1988; Reddacliff & Spielman, 1990; Whittington, 1992). The life cycle of the parasite is completed when an infected intermediate host is eaten by a carnivore.

Despite its potentially damaging effects, the impact of *S. erinacei* at the population level is not known for any species. However, given the high prevalence of infection by this parasite in feral cats, it may be inferred that rates of infection are high also in small native species that act as intermediate hosts. Whittington (1992) noted that opportunities for transmission of *S. erinacei* may be particularly great in semi-arid areas, where mammals congregate at permanent water holes and are likely to ingest infected crustaceans. The possible importance of *S. erinacei* as a pathogen of native species, and the role of feral cats as vectors, clearly warrant further study.

The second and possibly more important cat vectored pathogen of native fauna is *Toxoplasma gondii*. This parasite was almost certainly introduced to Australia by cats prior to or at about the time of European settlement. Unlike infection by *S. erinacei*, which is chronic, infection of cats by *T. gondii* usually results in a single acute phase when oocysts are excreted, before immunity develops. Exposure to infection in cats, as judged by the presence of antibodies to *T. gondii*, has been shown to vary from zero in inland Western Australia to 96% in Tasmania (Hartley & Munday, 1974; Speare, 1985); prevalence rates of 14% and 44% have been recorded, respectively, from western New South Wales and central Victoria (Coman *et al.*, 1981b). Infection of native fauna by *T. gondii* produces symptoms such as lethargy, poor coordination and blindness, and can cause death. Antibodies and other

signs of infection have been recorded in at least 30 species of native mammals (Moodie, 1995) and several species of birds (Harrington, 1978; Orosz *et al.*, 1992). Prevalence of antibodies in infected populations has been reported to range from 3.3% in red-necked wallabies *Macropus rufogriseus* to 90% in water-rats *Hydromys chrysogaster* (Hartley & Munday, 1974). In macropods antibody prevalence may be higher in young (<1 year) than in older animals, with the disease becoming more manifest under stress (Johnson *et al.*, 1988). Prevalence of infection is usually greater in cool, temperate regions in southern Australia than in northern or central areas (Smith & Munday, 1965; Speare, 1985), although the presence of toxoplasmosis has been established in free-living kowari *Dasyuroides byrnei* in and western Queensland (Attwood *et al.*, 1975). The impact of toxoplasmosis on populations of native species has been much discussed, but remains largely speculative. Several species of larger carnivorous marsupials are known to have declined in abundance in eastern Australia around the turn of the century (Jones, 1923; Green, 1967) and toxoplasmosis has been suggested as the causative organism (Caughley, 1980). Populations of two species, *Dasyurus maculatus* and *Sarcophilus harrisii*, have since recovered, but the thylacine *Thylacinus cynocephalus* and the mainland form of *D. viverrinus* are now extinct. Caughley (1980) suggested that a remnant population of *D. viverrinus* survived in Sydney until the 1960s because transfer of toxoplasmosis from domestic cats might be lower than from feral cats elsewhere. More recently, Freeland (1994) implicated toxoplasmosis in postsettlement declines of rodents and species from several families of marsupials, and noted further that the infection could cause death both directly and indirectly by increasing the susceptibility of hosts to predation. Such increased vulnerability may be exacerbated in populations that are small or stressed (Obendorf & Munday, 1983; Lenghaus *et al.*, 1990). Despite the potential impact of cat-vectored toxoplasmosis on native fauna, the actual effects of the disease have not been quantified, and arguments for its importance are sometimes neither critical nor compelling. For example, survival and transmission of

T. gondii is favoured more in mesic than in arid environments, yet most early extinctions of native mammals in Australia took place in the arid zone. The simultaneous declines of carnivorous marsupials in the early 1900s on the mainland of eastern Australia and in Tasmania are similarly difficult to interpret as being due solely to toxoplasmosis, simply because the infection cycle would have been present for at least a century. It is possible that declines were precipitated by other factors such as the increasing use of rabbit poison in the early years of the century. The partly scavenging *D. viverrinus* and *S. harrisii* would have suffered much greater secondary poisoning from rabbit carcasses than the more predatory *D. maculatus* (Edwards, 1924). The persistence of *D. viverrinus* in Sydney may have been facilitated more by the limited use of rabbit poison in the urban environment than by reduced exposure to toxoplasmosis, especially as high prevalence of antibody (52.5%) has been demonstrated in the city's domestic cats (Speare, 1985).

There is no doubt that toxoplasmosis can kill a wide range of native mammals and some birds in captive situations, nor that clinical symptoms and mortality may occur in wild populations under stress. However, these observations do not permit the conclusion that toxoplasmosis has caused past extinctions or that it currently has widespread deleterious effects on native fauna. These uncertainties could be resolved by effective screening for toxoplasmosis in declining populations (e.g. Lenghaus *et al.*, 1990), and by screening tissues of specimens of now-extinct species held in museums to check for the presence of *T. gondii* cysts (G. McKay, pers. comm.).

4.3.2 Other indirect effects

As noted above (section 3), a measurable impact of cats on one native species can potentially have unmeasured (and often unsuspected) but far-reaching effects on other species. Broadscale effects are more likely if an ecologically 'important' or keystone species is impacted, particularly if the presence of that species facilitates the presence of other species of native fauna or flora. Unfortunately, keystone species are difficult to identify, and I know of no unequivocal examples among the broad array of native species that are eaten by feral cats (Appendix 1). Possible contenders include honeyeaters and small mammals that act as

pollen vectors for a wide range of proteaceous and myrtaceous plant species (Hopper, 1980; Goldingay *et al.*, 1987; Paton, 1988); mycophagous mammals that facilitate dispersal of the spores of mycorrhizal fungi (Claridge & May, 1994); and the mulgara *Dasyercus cristicauda* that may increase the diversity of coexisting small mammals by suppressing competitively dominant species that would otherwise exclude smaller subordinates (unpub. obs). More detailed consideration of keystone species is not warranted at this point because of uncertainty about their precise ecological roles. However, because of the obvious potential for feral cats to disrupt community function by impacting on keystone species, their identification should be a priority for future research.

4.4 Summary: impacts of feral cats

Evidence from many sources shows that feral cats have minor or major impacts on native fauna and that direct predation is the most important process involved. Competition and amensal impacts probably occur, but their effects at the population level are not adequately known for any species. Competitive impacts would be inflicted by cats primarily on large, predatory species of marsupials and birds, whereas amensal impacts are most likely to occur via transmission from cats to native species of the protozoan parasite *Toxoplasma gondii* and the helminth *Spirometra erinacei*. Indirect community-level impacts may also occur via removal of keystone species, but none has yet been demonstrated. Direct predatory impacts on native fauna have been identified tentatively from circumstantial and historical evidence, but more convincingly from studies of species reintroductions and from introductions and removals of cats from islands. Several conclusions can be drawn from these studies about the predatory impacts of feral cats:

i). Mammals comprise the major part of the diet of feral cats on the mainland of Australia and elsewhere. Depending on the locality and habitat, young rabbits, rodents or marsupials may predominate. Other vertebrates, especially birds, are taken consistently at most localities, while reptiles may feature prominently in arid areas.

ii). Similar prey are taken, where available, on islands, although birds, reptiles and sometimes invertebrates can feature prominently if mammals are not available.

iii). On the Australian mainland cats can impact on native mammals weighing up to about 2000 g, but impact falls most heavily on smaller species, especially those weighing < 220 g. Vulnerability to predation is enhanced for species occupying open or otherwise unprotected habitats, and by behavioural traits such as saltatory locomotion. Cats can impact on birds up to about 1000 g, but impact again falls most heavily on smaller species weighing <200 g. Ground foragers and ground nesters are most vulnerable, especially in open habitats, although impact on hollow-nesting species is also possible.

iv). On islands, cats have had major impacts on terrestrial mammals up to 3000 g and birds up to 3500 g, although smaller species are preferred. As in mainland situations, vulnerability to impact is increased if protective habitat is not available, if foraging, burrowing or nesting activities take place on the ground surface or other exposed sites and, for birds, if the island is occupied yearround.

v). In mainland areas and on some islands where introduced mammals (rabbits, *Mus domesticus*, some *Rattus spp.*) or native mammals (usually *Rattus spp.*) reach high densities, impacts of feral cats on susceptible native fauna may be increased by a 'subsidy' effect. Impacts may be intensified if other species of predators, such as foxes, are present.

vi). Although long periods of apparently stable coexistence (i.e. several years) are possible between feral cats and potential prey, impact may still occur if 'rogue' individuals develop hunting skills for particular prey species at any time. The impact may be major if the prey population is small when predation begins.

vii). In Australia, in contrast to other parts of the world (e.g. Iverson, 1978), feral cats are not recorded to have impacted on any species of reptiles, amphibians, fish or invertebrates. These conclusions, as well as some additional factors considered in section 5, are used in section 6 to identify native species and regions within Australia where feral cat impacts can be considered to be greatest.

5. FACTORS THAT MODIFY IMPACT

The review of empirical research in section 4 identifies several aspects of the biology of native species that increase their vulnerability to predation from feral cats. In this section I consider further aspects of the interaction between feral cats and native fauna that are likely to increase or ameliorate cat impacts.

5.1 Density of cats

Although the relationship between the abundance of cats and prey species is likely to be complex (see *Intensity of predation*, below), impacts of feral cats should generally increase with increasing cat density. This is intuitively obvious, but is also supported by observations that impact increases when cat numbers are enhanced by subsidy effects (section 4). Unfortunately, few estimates of cat density are available in Australia (Table 8); comparisons between studies are also hampered by differences in methodology or in the seasons when estimates were made. However, perusal of Table 8 suggests that insular populations of cats can achieve very high densities, while mainland populations are relatively sparse. Densities appear to be particularly low in parts of the Top End and Cape York (Table 8; L.K. - P. Leung, pers. comm.), perhaps reflecting the absence of rabbits. Higher densities may be maintained locally in northern areas where native species of *Rattus* occur (Cameron, 1994). Jones (1983) noted that availability of food determines density, and that cat densities of > 1 /km² could be expected in favourable mainland habitats. Densities appear to be particularly variable over time in arid environments (Table 8), and presumably reflect the 'boom-or-bust' cycles of productivity that are driven by unpredictable rain.

Despite the paucity of absolute density estimates, relative densities of cats have been reported by several authors. A coarse-resolution map of cat abundance throughout Australia (Wilson *et al.*, 1992) shows that

sightings of feral cats are most frequent near human habitation and in a scattering of temperate and semi-arid localities in Victoria and New South Wales; a few local hot spots of high density occur in all other states except South Australia and Tasmania. To some extent frequent sightings near developed areas will represent observer bias, while sightings in open areas should be easier to make than those in closed habitat. More detailed regional surveys, based on counts of tracks, indicate that cat abundance can be relatively high in eucalypt forest and also in coastal thicket (Newsome & Catling, 1979; Catling & Burt, 1994). Entry of cats into areas of dense vegetation is possibly facilitated by tracks or roads (Bennett, 1991). Cats are also reported commonly in areas of arid and semi-arid grassland, open forest and woodland (e.g. Gibson, 1986; Boscacci *et al.*, 1987; How *et al.*, 1991), but are uncommon in closed forest, alpine and sub-alpine areas and wet heath (Newsome & Catling, 1979; Gordon, 1991; T.M. Bubela, pers. comm.).

Overall, these observations suggest that, while cat numbers can vary seasonally and locally within regions, abundance is usually higher in inland environments dominated by open habitats than in temperate or tropical environments dominated by closed forest or wet heath. Abundance in eucalypt forest in eastern and south-western Australia is probably intermediate between these extremes, although variation between regions is apparent (Table 8; Catling & Burt, 1994). Regional surveys generally support the broad-scale mapping of cat abundance of Wilson *et al.* (1992); a version of their map incorporating new information from studies cited above and in Table 8 is used in section 6.

5.2 Density and distribution of native fauna

Other factors being equal, small, disjunct and low density populations of native species are likely to be particularly susceptible to impact

Table 8. Population densities of feral cats *Felis cat us* in Australia

Location	Habitat	Density cats/km ²	Source
Althorpe I, S.A.	Open scrub	20-30	Copley (1991)
Kangaroo I, S.A.	Open forest	0.7	Paton (1994)
Great Dog I, Tas.,	Mixed forest, grassland	56.9	Hayde (1992)
North West I, Qld.	Open forest	1001	Domm & Messersmith (1990)
Kapalga, NT	Open forest, woodland	0.03	Ridpath (1990)
Hattah-Kulkyne, Vic.	Mallee	0.74 (winter)	Jones & Coman (1982)
		2.4 (summer)	Jones & Coman (1982)
Victoria		>0.9	Coman (1991)
Brindabellas, ACT	Open forest,	0.2	C.R. Dickman (unpub.)
	tall open forest		
Cradle Mountain -	Tall open forest,	0.15-0.2	M.E. Jones (pers. comm.)
Mt. St. Clair, Tas.	button grass		
Yathong, NSW	Mallee, spinifex	<1.0 (drought)	Newsome (1991)
		4.7 (non-drought)	
Shark Bay, WA	Coastal heath, shrubland	0.1-3.0	J. Short (pers. comms)
Royal N.P., NSW	Open forest	1.0	Mahood (1980)
Gnalta, NSW	Grassland	2.0	Mahood (1980)
Gibson Desert, WA	Mulga, spinifex	0.03 (drought)	Burrows & Christensen (1994)
	0.13 (non-drought)		
Hamilton Downs, NT	Mulga woodland	0.14 (winter)	G. Edwards &
		0.51 (autumn)	R. Paltridge (pers. comm.)
Connel's Lagoon, NT	Mitchell grassland	6.32	R. Paltridge (pers. comm.)

Notes. ¹ 105 cats were removed from this sand coy island of 105 ha over the course of a year. Because of recruitment following initial culling, the density value given is almost certainly an overestimate.

² This high mainland density estimate was obtained during a plague of long-haired rats. Density estimates for domestic cats are not shown, but may be very high (200 cats/km²; Paton, 1991) in comparison with the tabulated values for feral populations.

from feral cats. At the national level, such species have been identified on schedule 1 (Endangered) and schedule 2 (Vulnerable) of the *Endangered Species Protection Act 1992*, updated to July 1994 (ANCA, 1994). A species is considered to be endangered if

- it is likely to become extinct unless the circumstances and factors threatening its abundance, survival or evolutionary development cease to operate; or
- its numbers have been reduced to such a critical level, or its habitats have been so drastically reduced, that it is in immediate danger of extinction; or
- it might already be extinct, but is not presumed extinct.

A species is vulnerable if:

- within the next 25 years, the species is likely to become endangered unless the circumstances and factors threatening its abundance, survival or evolutionary development cease to operate (ANCA, 1994).

Species of mammals, birds and reptiles listed on these schedules are considered further in

section 6. However, because of lack of evidence for any impact of cats on amphibians and fish (section 4), species in these groups are omitted from further analysis.

5.3 Intensity of predation

In the most simple situation, the intensity of predation can be modelled as the response of a single species of predator to changes in the density of a single species of prey. At the population level, the numerical *response* describes how the density of the predator population changes in response to changes in prey density, whereas at the individual level the functional *response* describes the change in the number of prey eaten per predator at different prey densities. The numerical response may or may not be densitydependent at low densities of prey, but is asymptotic and hence inversely densitydependent at high prey densities. For cats the asymptote is potentially very high; densities of up to 2350 cats/km² have been recorded in situations with abundant food (Izawa et al., 1982).

Functional responses have been classified into three types (Holling, 1959). Thus if prey density is plotted on the abscissa against the consumption rate of the predator on the axis, type I responses are usually linear, type II responses are simple convex curves, while type III responses are sigmoidal or s-shaped. Type II and III functional responses are asymptotic at higher prey densities, indicating that the predator has a decreased per capita effect on prey at increasing prey densities. At low prey densities a type II response by the predator results in an inversely density-dependent effect on prey, whereas a type III response results initially in a density-dependent effect that gives way to inverse density-dependence at higher prey densities. Type III responses can be generated when increases in prey density allow predators to increase their efficiency in searching for the prey or decrease the time taken to handle the prey once it is encountered (Murdoch, 1969). However, type III responses may also be generated by predator switching where, provided that alternatives are available, specific prey are eaten disproportionately less at low than at high densities. Switching can result from predators becoming more efficient at finding and handling abundant prey, from development of a search image for abundant prey, or from concentration by the predator on habitats or microhabitats where prey capture and handling are most efficient (Murdoch & Oaten, 1975). Where switching occurs, predator density may be independent of the density of particular prey species and hence result in suppression of prey numbers at low levels (Caughley & Sinclair, 1994). If both functional and numerical responses are considered together as the *total response* of predators to changes in prey density, several stable and unstable points can occur (Caughley & Sinclair, 1994). Of particular interest is the 'predator pit', a situation where a predator can regulate a prey species at low density for long periods (Newsome, 1990). Entry into the pit can be due to predation but, in Australia, is more likely to be environmentally modulated by food scarcity and drought (Newsome *et al.*, 1989; Newsome, 1990). Escape from the pit may follow predator reduction or exceptional recruitment by the prey population (Pech *et al.*, 1992).

Despite theoretical discussion on the impact of cats on native fauna (Kinnear, 1991; Barratt, 1994b), there has been no empirical measurement of the intensity of cat predation on any native species. However, studies on rodents and lagomorphs overseas (Pearson, 1966; Keith *et al.*, 1984) and on rabbits in Australia (Pech *et al.*, 1992) suggest that a Holling type III functional response may be expected, with consequent regulation of susceptible native species at low densities. The broad range of native species taken by cats (Appendix 1) is possibly indicative of prey switching, and hence could be taken as further evidence for a type III response. However, in situations where cats target particular species, where predation is subsidised by alternative species of prey such as rabbits (or pet food for domestic cats) and switching does not occur, a type II functional response may be expected. In this situation, low density populations of native species are likely to be eliminated. These simple considerations suggest that already-small or depleted populations of native species are most likely to be impacted by cats. Impacts may be minor or major if the functional response is type III, but will inevitably be major if a type II response is exhibited. Impacts are likely to be exacerbated in remnant or simplified habitats where both refugia and prey species diversity are reduced, and where cat numbers are subsidised by abundant alternative prey.

5.4 Fecundity of native species

Native species with low fecundity will be impacted more than fecund species for any given rate of predation by feral cats. Highly fecund species are more likely to escape the predator pit and show expansion of population size and geographical distribution than species with low fecundity. Fecundity is the rate of production of offspring. For simplicity in the following section it will be measured as the average number of offspring produced per female per year.

5.5 Behaviour of predator and prey species

Several aspects of the behaviour of native species are likely to modify their susceptibility to predation from feral cats. First, cats are primarily nocturnal hunters (Bradshaw, 1992), and hence should impact more heavily on night-active than diurnal species. Some diurnal prey such as most birds and many reptiles are clearly still taken (Appendix 1), and may be impacted if their nocturnal refuges are conspicuous and accessible to cats, or if cats extend their hunting period into the early morning or late afternoon.

Second, colonial species such as burrowing petrels, sugar gliders and ringtail possums appear to be impacted more severely than species that nest, roost or forage alone (but cf. Thiollay, 1988). Aggregations of prey are relatively conspicuous; they should permit cats to readily form a search image, speed learning of techniques for prey capture and handling, and be more likely to elicit 'surplus killing' in which only some prey killed are eaten (George, 1978).

Third, terrestrial and scansorial species appear to be more susceptible to feral cats than fossorial or arboreal species. Although cats have been observed entering the burrows of several species of petrels, burrowing bettongs, bilbies and other digging species (Carnegie, 1898; Jones, 1977), truly fossorial species such as blind snakes (*Ramphotyphlops spp.*) and the marsupial mole *Notoryctes typhlops* appear to be eaten only rarely. Similarly, although cats are expert climbers, native species that are active primarily in the upper strata of forested environments such as Leadbeater's possum *Gymnobelideus leadbeateri* and some bats are seldom depredated. Species that use open terrestrial areas are likewise more conspicuous and at greater risk of predation than occupants of structurally complex environments such as dense heath or rock piles (above, and section 4).

Fourth, species that attract attention or lack effective anti-predator behaviour are especially likely to be taken by feral cats. Because cats usually detect prey by sight or sound, species that are visually conspicuous, that have jerky movements or vocalise frequently are likely to be most at risk. Anti

predator behaviour has been little studied in most native species that might be taken by cats (cf. Dickman, 1991; Soderquist, 1994). However, there is little evidence that small marsupials and native rodents are able to recognise and avoid the odour of cat faeces (Dickman, 1993a), or that strategies such as remaining motionless (e.g. bridled nailtail wallaby, *Onychogalea fraenata*; Horsup & Evans, 1993) or being cryptically camouflaged (e.g. button-quail, *Tu. mix spp.*) are very effective. Aggressive defence reduces cat predation on larger species of petrels and skiuas (Jones, 1977), the bandicoots *Isodon obesulus* and *I. macrourus* (pers. obs) and Tasmanian devils (M. Anderson, pers. comm.).

The impact of cat predation is also likely to be minimised in mobile species that migrate in response to changes of weather or season. The spectacular migrations of many species of seabirds from islands of the sub-Antarctic result in reduced cat predation when the birds are away from the cat-inhabited areas, reduced per capita predation and predator-satiation when the birds return and, in the absence of alternative prey, small populations of cats that are limited by shortages of food in winter. Although few data are available, it might be expected that migratory birds within Australia also experience reduced predation by cats than comparable species that remain as year-round residents (Schodde, 1982; Fullagar *et al.*, 1988).

Finally, an aspect of the behaviour of cats that may increase impact is their ability to move long distances (up to 200 km; Newsome, 1991) in response to changing environmental conditions. In their studies of vole dynamics, Anderson & Erlinge (1977) classified predators as resident generalists, resident specialists and nomadic specialists, and noted that their effects on prey would differ because of differences in their functional and numerical responses. For example, resident generalists could be expected usually to show type III functional responses, switching to alternative prey according to shifts in prey densities. In contrast, nomadic specialists could be expected to show a rapid numerical response to changes in prey density, tracking spatial shifts in numbers of their preferred prey and maintaining prey populations at low levels over large areas (Korpimaki & Norrdahl, 1991).

In relatively predictable temperate or semiarid environments, adult feral cats tend to be sedentary (Jones & Coman, 1982; Langham & Porter, 1991) and could be expected to act as resident generalists. However, in arid regions preliminary evidence shows that cats may be more mobile (Pettigrew, 1993; R. Palmer, pers. comm.; unpub. obs), tracking shifts in prey abundance that are driven by spatially unpredictable rainfall (Dickman et al., 1995). Heavy rain in western Queensland in late 1990 and early 1991 triggered a rapid population increase of native long-haired rats *Rattus villosissimus* (Predavec & Dickman, 1994), which in turn allowed a many-fold increase in cat numbers. This increase, between mid-1991 and mid-1992, was too rapid to have been due solely to reproduction, indicating that some tracking of the food resource had occurred (Pettigrew, 1993). If cats impact on prey in a similar manner to nomadic specialists elsewhere (Korpimäki & Norrdahl, 1991), they could dampen fluctuations in the numbers of irruptive species. More likely, however, cats could be expected to switch to alternative prey when an irruptive species collapses, and have particularly destructive local effects due to their elevated numbers. In the Simpson Desert, all species of small mammals have become scarce since the decline of *R. villosissimus* in late 1992, and one vulnerable species, the mulgara *Dasyercus cristicauda*, has disappeared from one locality of about 25 km² (unpub. obs). Although foxes also moved to the area in mid-1991, analysis of cat faeces confirms a switch from predation on *R. villosissimus* to smaller native species when the rat plague subsided. Similar prey switching has been observed following the end of a rat plague on the Barkly Tableland, NT (G. Edwards, pers. comm.).

5.6 Interactions with other predators

Our understanding of predator-prey systems is reasonably advanced, due both to a long history of development of models (Caughley & Sinclair, 1994) and to the testing of hypotheses derived from them (e.g. Pech et al., 1992). However, addition of other species to the system, especially predators, simultaneously increases the complexity of predator-prey interactions and decreases our

ability to predict outcomes. Indeed, Newsome (1994a) pointed out that the processes producing observed patterns are often far more complex than they might appear, and described attempts to force reality to fit our expectations as Procrustean after the infamous innkeeper of Greek legend. Nevertheless, several conceptual models have been developed to explain some predator-prey webs in Australia (e.g. Lundie-Jenkins et al., 1993; Newsome, 1994b; Corbett, 1995), and some brief comments on interactions and their effects are warranted here.

Taking cats as the focal species, we can consider smaller predators such as rats that may themselves fall prey to cats, and similar-sized or larger predators such as foxes and dingoes that may depredate on or compete with cats.

As described above and in section 4.2.4, rats can facilitate local increases in cat populations or maintain cats during seasons when alternative prey are scarce, and hence have an important subsidising effect on cat impacts. However, *Rattus norvegicus*, *R. rattus* and the Pacific rat *R. exulans* are capable of eating native fauna, and have had particularly deleterious effects on island lizards (Whitaker, 1978; McCallum, 1986) and birds (Atkinson, 1977, 1985). On Lord Howe Island, for example, five species of birds were extirpated following introduction of *R. rattus*; only one extinction has been attributed, in part, to cats (Recher & Clark, 1974). Because of the potential depredatory impact of rats, as well as their effects on vegetation, several authors have concluded that cats may have beneficial effects on island faunas if they suppress rat populations (Disney & Smithers, 1972; Fitzgerald *et al.*, 1991; Tidemann *et al.*, 1994). There is little evidence that cats have generally beneficial effects on native fauna in mainland Australia, although local suppression of introduced rats has been described for rural and suburban rubbish dumps (Wilson *et al.*, 1994).

Canid predators have also been shown to impact on native fauna in Australia, with the impact of foxes being particularly severe on small and medium-sized species such as rock-wallabies (Kinnear *et al.*, 1988). However, their relationships with feral cats are not clear. Cats are eaten consistently but at low frequency by dingoes in all regions of Australia (Corbett, 1995), and may be taken

on occasion also by foxes (Coman, 1973b). Both canid predators probably also compete with feral cats, especially when food is limited, although dingoes focus on larger mammalian prey when these are available. Competition is further suggested in southern NSW, where the abundance of feral cats tends to be correlated negatively with the abundance of both foxes and dingoes (partial correlation coefficients, respectively, of -0.32 and -0.39, were computed from data in Table 2 of Catling and Burt, 1994). Experimental removal of foxes has been shown to cause dramatic increases in cat numbers (Christensen & Burrows, 1995; J. Short, pers. comm.), presumably because this reduces direct interference or exploitative competition for food. Local declines in dingo numbers also appear to allow dramatic increases in the numbers of feral cats (Pettigrew, 1993). Under certain conditions, however, dingoes can have positive effects on feral cats. G. Edwards (pers. comm.) has described how carcasses of kangaroos killed by dingoes kept cats alive during drought near Alice Springs in 1994.

The depressive and occasionally positive effects of canids on feral cats are likely to be modified by season, availability of food and habitat, with potential impact usually being greater in lean periods and in open areas which lack refuges such as trees. Because of the complexity of relationships among these predators, it is difficult to make an a priori assessment of how the impact of feral cats on any susceptible native species is likely to be altered by the additional presence of foxes and dingoes. In the following section, native species that appear most susceptible to cat predation are identified and their distributions mapped. I then consider *a posteriori* whether foxes and dingoes cooccur with these species, using Wilson *et al.* (1992). Although the distributions of foxes and dingoes in Wilson *et al.* (1992) are likely to be accurate, the data on relative abundance of these predators were collected subjectively and may not depict true differences in density between regions. I have therefore been cautious in interpreting whether threatened native species co-occur with low or high densities of foxes and dingoes, and accord these interpretations with little weight.

6. WHICH NATIVE SPECIES ARE SUSCEPTIBLE TO CAT IMPACT?

6.1 Development of a rank-scoring system to predict susceptibility

In this section, I use the findings of sections 4 and 5 to list native species that are most likely to be impacted by feral cats. Listing is achieved by assigning rank scores to attributes of the biology of native fauna and cats that relate to intensity of impact. Such rank-scoring systems have been used successfully to judge the conservation status of vertebrate species in several previous studies (Cogger *et al.*, 1993; Dickman *et al.*, 1993; Lunney *et al.*, 1995) but, with the exception of an unpublished study by Jarman & van der Lee (1993), have not been applied previously to assess the effects of any single threatening process such as cats. In developing a rank-scoring system, I have assumed that the major impact of feral cats on native fauna is from predation, due to uncertainty about the importance of either competitive or amensal effects. However, it is likely that amensal and competitive impacts will co-vary with predatory impacts for at least some attributes (e.g. any effects of cats should increase with cat density), so that scores for predation alone may still be broadly representative of total impact. Because the ranking system developed is generic, it will be simple to modify should future research show that separate ranking of predatory, competitive and amensal impacts is desirable. For the same reason, the system could be extended to investigate impacts of cats on species at local, regional or state levels rather than just at the national level explored here.

Six sets of independent biological attributes of cats and native fauna are listed below, and applied to all non-marine species of mammals, birds and reptiles listed as vulnerable and endangered by ANCA (1994). (For convenience I will refer to all taxa in ANCA (1994) as species, even though ANCA listings include both species and allopatric

subspecies). Each attribute is scored between 0 and 3. Zero indicates no or negligible susceptibility to cat predation, three indicates high susceptibility. Scores were developed from the review above (sections 4 and 5), and awarded according to the following criteria:

Attribute	Score	Criteria for scores	
Cat density*	0	Cats absent	
	1	Low density	
	2	Medium density	
	3	High density	
*(Modified, after Wilson <i>et al.</i> , 1992)			
Body weight		>2000 g	
	mainland	0	1001-2000g
	mammals	1	220-1000 g
		2	<220 g
		3	>3000 g
	island	0	1001-3000 g
	mammals	1	220-1000g
		2	<220 g
		3	>1000 g
	mainland	0	501-1000g
	birds	1	200-500 g
		2	<200 g
3		>3500 g	
island birds	0	1001-3500 g	
	1	200-1000g	
	2	<200 g	
	3	>500 g	
reptiles	0	101-500g	
	1	11-100g	
	2	0-10 g	
	3		
Habitat use	0	Very dense ground-level vegetation (e.g. dense, low coastal heath) or difficult for cats to access (e.g. sea cliffs, rock piles)	
	1	Dense ground-level vegetation with high structural complexity (e.g. closed forest, gullies in tall - open forest, mangrove, riparian or swamp habitats) or difficulty of hunting (caves)	

Attribute	Score	Criteria for scores
Behaviour	2	Moderate to open ground level or understorey vegetation (e.g. open-forest, mallee, scrub, hummock grassland)
	3	Open vegetation (woodland, tussock grassland, gibber plain, some cultivated lands)
	0	Diurnal
	1	Nocturnal
		(0-1 scored if a species is active by day and night or if activity rhythm is not known)
	0	Aquatic, arboreal, fossorial, volant
	1	Scansorial, terrestrial
	0	Yes (e.g. aggressive defence, tail loss or skinning, unpalatable taste)
	1	No behaviours known
		* Scores within this category are additive
Mobility		No coloniality known, individuals usually dispersed and forage and reproduce at most in small groups
	1	Yes, individuals flock or aggregate in large groups for feeding or reproduction
	0	No fidelity shown, all age classes are nomadic or migratory over large areas
	1	Yes, individuals are usually sedentary within small areas
	0	seasonality Individuals show no seasonal tendency to congregate
	1	Individuals congregate seasonally at focal points for feeding, breeding or hibernation
		* Scores within this category are additive
Fecundity	0	>10 young produced per female per year
	1	3-9 young produced per female per year
	2	1-2 young produced per female per year
	3	< 1 young produced per female per year

Cat density scores were awarded by overlaying the distributions of vulnerable and endangered native species on a map of cat densities modified from Wilson *et al.* (1992). For most species the major part of the distribution (>75%) coincided with a particular density of cats, and were thus given the appropriate score. A small number of species had distributions that overlapped relatively large areas with different cat densities (>25% of the overall distribution), and these are shown by a hyphen to indicate the range of cat density scores encompassed. Body weight scores are shown separately for mainland and island species of mammals and birds, and for reptiles, due to the evidently different susceptibilities of these groups to cat predation (section 4). Size categories are for mean adult body weight and reflect likely impacts of cats at the population level. For mainland mammals, for example, there is no convincing evidence that cats regularly kill any life history stages of species weighing more than 2000 g; the score for such species is therefore 0. For species weighing 100 1-2000 g small juveniles are likely to be susceptible to cat predation while adults may be immune (score 1), whereas for species weighing 220-1000 g all juveniles and some adults may be at risk (score 2, e.g. *Perameles gunnii*). For species with a mean adult body weight <220 g, all population components are at risk and so the species receives the highest score of 3. Scores for habitat use were awarded to reflect the degree of difficulty for cats in hunting or gaining access to native species. Information on habitat use was obtained from several reference sources (Table 9), and refers only to the habitat that is currently occupied. For example, the endangered dibbler *Parantechinus apicalis* now occupies mainland localities that provide dense to very dense vegetative cover at ground level, and so receives a habitat use score of 0-1. However, historical records indicate that the species formerly occupied open-forest in parts of its range (Baynes, 1979), and thus could have received a habitat use score as high as 2. For many species scores for habitat fell between categories, either because they are habitat generalists or because different habitats are used for different activities such as foraging and nesting. These are shown by a hyphen to indicate the range of scores encompassed (e.g. 1-3), or by a comma if the scores are not consecutive (e.g. 1,3).

Table 9. Susceptibility of endangered native vertebrates to predation from feral cats *Felis cat* us on the mainland of Australia.

Species	Factors contributing to susceptibility of native species:						Overall risk ⁴
	Cat density ¹	Body weight ²	Habitat use ³	Behaviour ³	Mobili	Fecundity ³	
Mammalia							
<i>Bettongia penicillata</i>	1	1	2	3	1	2	L
<i>B.tropica</i>	2	1	2	3	1	2	L
<i>Dasyuroides byrnei</i>	3	3	3	3	1	0-1	H
<i>Dasyurus geoffroi</i>	1	1	2	3	1	1	L
<i>Gymnobelideus leadbeateri</i>	1	3	1	2	2	2	N
<i>Isoodon ouratus</i>	2	2	2	3	1	0-1	L
<i>Lasiorhinus krefftii</i>	2	0	2	2	2	2	N
<i>Myrmecobius fasciatus</i>	1	2	2	2-3	1	1-2	L
<i>Onychogalea fraenata</i>	2	0	2	2-3	1-2	2	L
<i>Parantechinus apicalis</i>	3	3	0-1	2-3	1	1	H
<i>Petaurus gracilis</i>	2	2	2	2	1	2	N
<i>Phascogale caluro</i>	2-3	3	1-2	2	1	1	H
<i>Potorous longipes</i>	2-3	1	1	3	1	2	L
<i>P. tridactylus gilberti</i>	2	1	1	3	1	2	L
<i>Pseudocheirus occidentalis</i>	2	2	1-2	2-3	2	2	L
<i>Sminthopsis douglasi</i>	3	3	3	3	1	1	H
<i>Notomys fuscus</i>	2	3	2	3	2	0-1	H
<i>Pseudomys oralis</i>	1	3	1	3	1	1	H
<i>P. shortridgei</i>	2	3	2	3	1	1	H
<i>Zyomys pedunculatus</i>	2		0-1	2	1	1	L
Aves							
<i>Coccyzus pectorator pectorator</i>	2	2	2-3	0-1	1	2	L
<i>Collyprohynchus banksii graptogyne</i>	1	0	2-3	0-1	1	2-3	N
<i>Erythrura gouldiae</i>	2	3	2-3	2	2	1	H
<i>Falcunculus frontatus whitei</i>	2	3	2-3	1	1	1-2	H
<i>Geopsittacus occidentalis</i>	2	3	2-3	3	0-1	1	H
<i>Leipoa ocellata</i>	1	0	2	2	1	0	N
<i>Lichenostomus melanops cassidix</i>	2	3	1	1	1	2	L
<i>Manorina melanotis</i>	1	3	2	1-2	2	1	L
<i>Neophema chrysogaster</i>	1	3	1-2	1-2	2	1	L
<i>Pardalotus quadragintus</i>	2	3	1-2	1	1	1	L
<i>Petrophassa smithii blaauwi</i>	1	3	3	2	2	2	H
<i>Pezoporus wallicus flaviventris</i>	2	3	0-1	1-2	1	1	L
<i>Poecilodryas supercilioso cerviniventris</i>	2	3	1	1-2	1	2	L
<i>Psephotus chrysopterygius</i>	1	3	1,3	2	1	1	H
<i>Psittaculirostris diopthalma coxeni</i>	1	3	1	1	1	2	L
<i>Sterna albifrons</i>	1	3	3	2	2	2	H
<i>Stipiturus malachurus intermedius</i>	1	3	0-1	1-2	1	1	L
<i>Xanthomyza phrygia</i>	2	3	2-3	1	2	1-2	L
Reptilia							
<i>Aprasio ourita</i>	3	3	2	1-2	1	2	H
<i>A. parapulchella</i>	2	3	2	1-2	1	2	L
<i>Tiliqua adelaidensis</i>	1	2	2	1	1	1-2	L
<i>Hoplocephalus bungaroides</i>	3	2	0,2	2	1	1	L
<i>Pseudemidura umbrina</i>	1	0-	0	0	1	1	N

Notes. Endangered marine mammals and reptiles have been omitted, as they are unlikely to contact feral cats, while species endemic to Tasmania are included. Numerical scores are as defined in text. Species names are as listed in ANCA (1994), except that *Pseudocheirus peregrinus occidentalis* is given here as *P. occidentalis* and *Pseudomys praeconis* is synonymised with *P. fieldi*. Gilbert's potoroo *Potorous tridactylus gilberti* is included here as endangered rather than extinct (ANCA, 1994) following its rediscovery in late 1994.

Sources: ¹ Wilson *et al.* (1992), as modified (see text).

² Strahan (1983), Blakers *et al.* (1984), Burbidge & McKenzie (1989), Kennedy (1990), Shine (1991), Cogger (1992), Cogger *et al.* (1993). ³ As for 2, but including Wilson & Knowles (1988). ⁴ H = high risk, L = low risk, N = no risk of cat impact.

Unlike the continuous scores established for other attributes, scores for behaviour and mobility were awarded to three independent sub-attributes that could sum to between 0 and 3. These sub-attributes probably vary in importance with respect to cat impact, and hence are unlikely to be strictly additive. However, higher summed scores for both behaviour and mobility may still be taken as representing greater likelihood of cat impact; any potentially anomalous scores are flagged and discussed separately.

The attribute categories are listed in order of their likely importance in evaluating susceptibility of native fauna to cat predation. For example, cat density is listed first because a species with a score of 0 for cat density cannot be at any immediate risk from cats if none is present, even if all remaining scores are awarded maximum values of 3. In contrast, another species may score 0 for fecundity but sustain heavy impact from cats. Because the attributes are not equal in importance, scores among the attribute categories cannot be seen as additive or strictly comparable. Thus, scores for each attribute should be seen as indicative of the degree of susceptibility to cat predation for that attribute, and attempts to equate scores among attributes resisted.

6.2 Zero, low and high risk species

Rank-scores for endangered and vulnerable mammals, birds and reptiles with predominantly mainland distributions are shown in Tables 9 and 10, scores for species occurring wholly or mostly on islands in Table 11. Scores for the first four attribute categories ranged from 0 to 3, suggesting that their power to predict susceptibility to cat predation is good. In contrast, scores for mobility and fecundity showed less variation and hence less power to distinguish susceptibility between species, justifying their listing as less important attributes.

On the basis of the scores, species were split into three groups according to their likely susceptibility to cat predation. Species at *no risk* were defined as those where cat density is zero (as on some islands, Table 11a) and, generally, where cats are present, as those with at least one score of zero for the important categories of body weight, habitat

use and behaviour. Fourteen species on islands are considered to be at no risk to cats (Table 11). However, because these species have high scores for several attributes, they would probably be very susceptible to predation should cats ever be introduced. Twelve further species in mainland Australia are considered to be at no risk to cats, due to zero scores, with at least nine of these being too large to be taken (Tables 9 and 10). In addition to these species, two species of mammals (*Gymnobelideus leadbeateri* and *Petaurus gracilis*) and one species of bird (*Electus roratus*) probably face no risk of cat predation because their activities are confined to the tops of tall trees where cats have no access. *Onychogalea fraenata* scores 0 for body weight, and could also be listed as being at no risk of cat depredation. However, this species is apparently exceptional in being relatively large (mean adult weight 4.5 kg) but vulnerable to cats (Horsup & Evans, 1993; D.O. Fisher, pers. comm.), and hence is considered to be at some risk here (Table 9).

In addition to the 14 species on cat-free islands, six endangered and nine vulnerable species of mainland Australia and Tasmania are judged unlikely to suffer any cat-impacts (Tables 9 and 10), and are excluded from further consideration. Independent studies on several of these species have not listed cats as a threatening factor, hence supporting the conclusions reached here (Burbidge, 1981; Gordon *et al.*, 1985; Short & Milkovits, 1990). Only the malleefowl *Leipoa ocellata* has been recorded as falling prey to feral cats (Priddel & Wheeler, 1994), but victims were young captive-bred birds and losses to cats alone were negligible.

Species at low *risk* of predation by cats were defined differently according to whether they occur on islands or on mainland Australia. On the mainland, species were placed in the low-risk category if a score of three was awarded for any one of the attributes cat density, body weight, habitat use and behaviour, with a non-zero score less than three for all remaining attributes. Island species, because of their generally tiny population sizes, very restricted distributions and lack of appropriate behavioural responses to predators (Bunin & Jamieson, 1995), were considered to be at low risk to cats with scores of 1-2 for the first four attributes. Two species, *Delma mitella* and *Tiliqua adelaidensis*, were not awarded a

score of three for any attribute, but were nevertheless considered to be at low risk of cat predation because several attributes scored a moderately high value of two (Tables 9 and 10). Three further species were judged to be at low risk of cat predation despite exceeding the definition advanced above for this category. On the mainland, both *Xanthomyza phrygia* and *Falcunculus frontatus leucogaster* scored up to three for body weight and habitat use, but are likely to experience low risk of predation because most activity occurs in trees (Blakers *et al.*, 1984). On Christmas Island, *Crocidura tenuata* is in the range of preferred body weights for cats, but its unpalatability suggests that it should be at low risk (Tidemann *et al.*, 1994). In total, 23 endangered mainland species are considered to be at low risk of predatory impact from feral cats, as are a further 12 vulnerable species (Tables 9 and 10). For insular taxa, one species of mammal and seven species of birds are judged to be at low risk (Table 11).

Species at *high risk* of predation from cats were defined as those awarded two or more attribute-scores of three if extant on the mainland, and a single score of three for any of the first four attributes if present on an island. *Turnix melanogaster* was added to the list of high-risk species despite only a single score of three for body weight (Table 10). Its use of dry litter for foraging and nesting and slow conspicuous movement under overhead cover (Blakers *et al.*, 1984) probably combine to place it at greater risk of cat predation

than the attribute scores alone would suggest. Fourteen endangered species and 20 vulnerable species are judged to be at high risk of predatory impact from feral cats on the mainland of Australia (Tables 9 and 10), as are a further four species offshore (Table 11). Among the high risk species, there are several that have scores of three for three or more attributes. These species are confined largely to arid inland areas and are probably critically susceptible to predatory impact from feral cats (Table 9 and 10).

In evaluating the attribute scores and assigning categories of risk, I used the precautionary principle by placing greatest weight on the higher score for any attribute when a range of scores had been assigned. Several species were also moved between categories of risk following an *a posteriori* evaluation of rank scores, suggesting that the listing procedure adopted was not entirely objective. However, assignments of low and high risk in Tables 9-11 accord well with conclusions about cat impacts derived independently in studies on several of the listed species (e.g. low risk: *Pardalotus quadragintus*, Rounsevell and Woinarski, 1983; *Myrmecobius fasciatus*, Friend, 1990; *Dasyurus geoffroii*, Serena *et al.*, 1991; high risk: *Parantechinus apicalis*, Baynes, 1979; *Perameles gunnii*, Maguire *et al.*, 1990; *Sterna albifrons*, Smith, 1990). Hence, I believe that some confidence may be placed in the ranking system developed here, as well as in the listings of species produced.

Table 10. Susceptibility of vulnerable native vertebrates to predation from feral cats *Felis catus* on the mainland of Australia.

Species	Factors contributing to susceptibility of native species:						Overall risk ⁴
	Cat density ¹	Body weight ²	Habitat use ³	Behaviour ³	Mobility ³	Fecundity ³	
Mammalia							
<i>Burramys parvus</i>	1	3	0-1	3	2	1	H
<i>Dasyercus cristicauda</i>	2	3	2-3	3	2	1	H
<i>Dasyurus viverrinus</i>	2	1-2	2-3	3	1	1	H
<i>Mocrotis lagotis</i>	2	1	3	3	2	1	H
<i>Perameles gunnii</i>	2-3	2	3	3	1	0-1	H
<i>Petrogale lateralis</i>	1	0	0	2	2	2	N
<i>P. penicillata</i>	1	0	0	2	2	2	N
<i>P. persephone</i>	2	0	0	2	2	2	N
<i>Sminthopsis psammophila</i>	2	3	2	3	1	1	H
<i>Mesembriomys macrurus</i>	2	3	1-3	2-3	1	1-2	H
<i>Notomys aquilo</i>	1	3	2	3	1	1	H
<i>Pseudomys australis</i>	1-2	3	3	3	2	0-1	H
<i>P. chapmani</i>	1	3	2	3	2	1	H
<i>P. occidentalis</i>	2	3	1-2	3	1	1	H
<i>PP pilligaensis</i>	2	3	2	3	1	1	H
<i>Xeromys myoides</i>	2	3	0-1	2-3	1	1	H
<i>Macroderma gigas</i>	2	3	1	2		2	L
Aves							
<i>Amytornis dorotheae</i>	1	3	1-2	2		1-2	L
<i>A. textilis textilis</i>	1	3	2-3	2	1	1-2	H
<i>Atrichornis clamosus</i>	2	3	1	2	1	2	L
<i>Casuaris casuaris</i>	1	0	1	- 1	1	1	N
<i>Cereopsis novaehollandiae grisea</i>	1	0	2	1-2	2	1	N
<i>Charadrius rubicollis</i>	2	3	3	2	2	1-2	H
<i>Dasyornis brachypterus</i>	2	3	1	2	1	2	L
<i>D. longirostris</i>	2	3	0-1	2	1	2	
<i>Eclectus roratus</i>	1	2-3	1	1	2	2	
<i>Erythrorichis radiatus</i>	1	1	2	0	0	1-2	N
<i>Falcunculus frontatus leucogaster</i>	2	3	2-3	1	1	1-2	L
<i>Lathamus discolor</i>	2	3	2	1-2	2	1	L
<i>Pachycephala rufogularis</i>	1	3	2-3	1-2	1	1-2	H
<i>Pedionomus torquatus</i>	2	3	3	2	1	1	H
<i>Polytelis alexandrae</i>	2	3	2-3	1-2	1	1	H
<i>Stipiturus malachurus parimeda</i>	1	3	0-1	1-2	1	1	L
<i>Tum ix melanogaster</i>	2	3	1-2	2		1-2	H
Reptilia							
<i>Ctenophores yinnietharra</i>	1	2	3	2	1	1	L
<i>Delma impar</i>	2	2	3	1-2	1	2	L
<i>D. mitella</i>	2	2	2	1-2	1	2	L
<i>D. torquaua</i>	2	2	2-3	1-2	1	2	L
<i>Morelia carinata</i>	2	0	2-3	0-2	1	0	N
<i>Ophidiocephalus taeniatus</i>	2	2-3	3	1-2	1	2	H
<i>Rheodytes leukops</i>	1	1	0	0-1	1	?	N

Notes. Vulnerable marine reptiles have been omitted, as they are unlikely to contact feral cats, while species endemic to Tasmania are included. Numerical scores are as defined in text. Species names are as listed in ANCA (1994). Sources 1-3 as in Table 9. ⁴ H = high risk, L = low risk, N = no risk of cat impact.

Table 11. Susceptibility of endangered and vulnerable native vertebrates to predation from feral cats *Felis catus* on Australian offshore islands and island territories.

Species ¹	Factors contributing to susceptibility of native species:						Overall risks
	Cat density ²	Body weight ³	Habitat use ⁴	Behaviour ⁴	Mobility ⁴	Fecundity	
<i>(a) Islands with no feral cats</i>							
Mammalia							
<i>Bettongia lesueur</i> (E)	0	1	2	3	2	1-2	N
<i>Lagorchestes hirsutus</i> (E)	0	1	2	3	1	2	N
<i>Lagostrophus fasciatus</i> (E)	0	1	1	3	1	2	N
<i>Macropus robustus isabellinus</i> (V)	0	0	2	2	2	2	N
<i>Perameles bougainville</i> (E)	0	2-3	1-2	3	1	1	N
<i>Leporillus conditor</i> (E)	0	2	1-2	2	2	1	N
<i>Pseudomys fieldi</i> (E)	0	3	1-2	3	1	1	N
Aves							
<i>Anous tenuirostris melanops</i> (V)	0	2	2	1	2	2-3	
<i>Malurus leucopterus edouardi</i> (V)	0	3	2	2	1	1	N
<i>Pterodroma leucoptera leucoptera</i> (E)	0	2	1	1-2	2	2-3	N
<i>Turnix varia scintillans</i> (V)	0	3	1-2	2	1	1	N
Reptilia							
<i>Ctenotus angusticeps</i> (V)	0	3	2	1	1	1	N
<i>C. lanceolini</i> (V)	0	3	2	1	1	1	N
<i>Egernia stokesii aethiops</i> (V)	0	2	2	2	1	1	N
<i>Pseudemoia palfreymani</i> (V)	0	2-3	3?	1	1	1-2	N
<i>(b) Islands with feral cats</i>							
Mammalia							
<i>Crocidura tenuata</i> var. <i>trichura</i> (E)	1	3	1	1-2	1	0?	L
Aves							
<i>Coracina tenuirostris melvillensis</i> (E)	1	2	1-2	1	1	2-3	L
<i>Cyanoramphus novaezelandiae cookii</i> (E)	2	1	1	1-2	1-2	L	
<i>Diomedea exulans chionoptera</i> (E)	1	0	1	1	0	3	N
<i>Fregata andrewsi</i> (V)	2	0-1	1	0-1	1	3	L
<i>Malurus leucopterus leucopterus</i> (V)	1?	3	2	2	1	1	H
<i>Ninox novaeseelandiae undulata</i> (E)	1?	2	1	1	1	1-2	L
<i>N. squamipila natalis</i> (V)	1?	1	1	1	1	1-2	L
<i>Strepera graculina crissalis</i> (V)	1?	2	1-3	1-2	2	1	H
<i>Sula obbotti</i> (E)	1	1	1	0-1	1	3	L
<i>Tricholimnas sylvestris</i> (V)	1?	2	0-1	2	1	2	L
<i>Turdus poliocephalus poliocephalus</i> (E)	1?	3	1	1-2	1	1?	H
<i>Zosterops albogularis</i> (E)	1?	3	1	1-2	2	1-2	H

Notes. 1 Species are listed if the major part or whole of the distribution occurs on islands; species endemic to or occurring mostly in Tasmania are shown in Tables 9 and 10. E = endangered, V = vulnerable.

²Wilson et al. (1992), Tidemann et al. (1994); ? = best guess, estimated from data in Table 8.

³Hindwood (1940), Schodde et al. (1983), Strahan (1983), Blakers et al. (1984), Stokes (1988), Kennedy (1990), Cogger (1992), Cogger et al. (1993).

⁴As for 3, but including Wilson & Knowles (1988).

⁵H = high risk, L = low risk, N = no risk of cat impact.

7. WHERE DO NATIVE SPECIES SUSCEPTIBLE TO CAT IMPACT OCCUR?

Sixty-nine of the 81 endangered and vulnerable species at risk of being impacted by feral cats occur in Tasmania or on the mainland of Australia, whereas 12 species occur in specific localities on islands. Norfolk and Christmas Islands each contain four susceptible species, with all those on Norfolk being endangered (Table 11). Two further species occur on Lord Howe Island, with one each on Melville and Dirk Hartog Islands. On the mainland, preliminary inspection of species distributions indicated some overlaps in where susceptible species occur, but also large areas where they do not. To identify more precisely the localities where susceptible native species co-occur, and hence where cat impacts may be greatest, I compiled a series of species density maps (Figs 1 and 2).

For ease of plotting distributional data, I divided a map of Australia into $1^\circ \times 1^\circ$ blocks. This provided resolution sufficient both for accurate plotting of species distributions, and for subsequent identification of specific localities and broader regions where susceptible native species co-occur. Distributional data for birds were taken from the field atlas maps of Blakers *et al.* (1984). Data for these maps were compiled only between 1977 and 1981, and hence may under-represent the true distributions of some species. However, the maps provided the required spatial accuracy of 1° squares, and were based on species records from all 1° squares covering continental Australia, Tasmania and offshore islands. Preliminary inspection of raw distribution maps for birds suggested that little improvement of resolution would be obtained by plotting breeding and non-breeding records separately, so all records for each species were combined. Distributional data for reptiles were obtained from Cogger *et al.* (1993). Accurate distribution data were not readily available for mammals. Generalised distribution maps in standard reference works (e.g. Strahan, 1983) were too small to transcribe reliably to a base map of 1° square resolution; moreover, many of the

distribution maps in these works are inaccurate. Thus, locality records for mammals were taken directly from museum records, published sources (Kitchener & Vicker, 1981; Churchill & Holman, 1990; Southgate, 1990; Ingram & Raven, 1991; Rounsevell *et al.*, 1991; Read, 1993; Jones *et al.*, 1994) and, for rodents and dasyurids, from monographs in preparation (C.R. Dickman & M. Predavec, unpub.). I used records obtained only since 1950, deleting those for localities at which species have been shown subsequently to have gone extinct (e.g. Jones *et al.*, 1994). Species density maps were then compiled for all endangered and vulnerable species categorised in section 6 as being at low and high risk of impact from cats by tallying the numbers of species recorded from all 1° squares.

Species at high risk of cat impact are distributed patchily throughout mainland Australia (Fig. 1). Both endangered and vulnerable species (ANCA, 1994) occur predominantly in the south-west, the Top End, the Channel Country, and parts of Victoria and Tasmania. Other regions with localised distributions of high-risk endangered species include Cape York and the coasts of northern NSW and southern Queensland (Fig. 1a), while other regions with aggregations of high-risk vulnerable species include the central and western deserts (Fig. 1 b). A summarised species density map of all ANCA-listed species at high risk of cat impact (Fig. 1c) identifies five regions of outstanding importance. These are the south-west, Tasmania, the Channel Country and parts of the Kimberley and the Top End. These regions have one or more 1° squares containing at least four endangered and vulnerable species at high risk of cat impact. Although not shown separately on the figures, high-risk endangered mammals are represented exclusively in the south-west and almost exclusively in the Channel Country. With the exception of the arid-distributed night parrot *Geopsittacus occidentalis*, high

risk endangered birds are represented only parts of the Top End (Figs 2a, 2b). Overall, across northern Australia and along the low-risk species are represented poorly in the eastern seaboard. High-risk vulnerable and zone and clustered most conspicuously mammals are distributed extensively in

inland Australia, the Top End and in Tasmania, while high-risk vulnerable birds occur primarily in coastal and sub-coastal regions at latitudes above 20°S. Alexandra's parrot *Polytelis alexandrae* is exceptional in this group in having an extensive inland distribution. Only two species of reptiles are judged as being at high risk of cat impact, *Aprasia aurita* and *Ophidiocephalus taeniatus*, and occur respectively in Victoria and central Australia.

The distributions of species at lower risk of cat impact are similar for endangered and vulnerable taxa, but different from the patterns shown by high-risk species (Fig. 2). Both endangered and vulnerable species occur predominantly in the south-west, the south-east, especially Victoria, and in some

in southern temperate regions (Fig. 2c). With some scattered exceptions, low-risk endangered mammals are concentrated in south-western Australia, whereas low-risk endangered birds are distributed more broadly in the south-east, south-west and across the Top End. Low-risk vulnerable birds occur almost exclusively in the south east and south-west above 30°S, whereas the sole low-risk vulnerable mammal (the ghost bat *Macroderma gigas*) occurs patchily in inland and coastal localities at latitudes less than 27°S. Except for the Yinnietharra rock dragon *Ctenophorus yinnietharra* in the north-west and the legless lizard *Delma mitella* in the north-east, all low-risk species - of reptiles are restricted to localities in south eastern Australia.

Figure 1. Species density maps of endangered and vulnerable species of native vertebrates (mammals, birds and reptiles) at high risk of impact from feral cats *Felis cat us* in Australia. a) endangered species, b) vulnerable species, c) endangered and vulnerable species combined. Species densities are shown in 1° x 1° grid squares. No, shading = no at-risk species occur, light stippling = 1 at-risk species occurs, medium stippling = 2 at-risk species occur, heavy stippling = 3 at-risk species occur, black shading = 4 or more at-risk species occur.

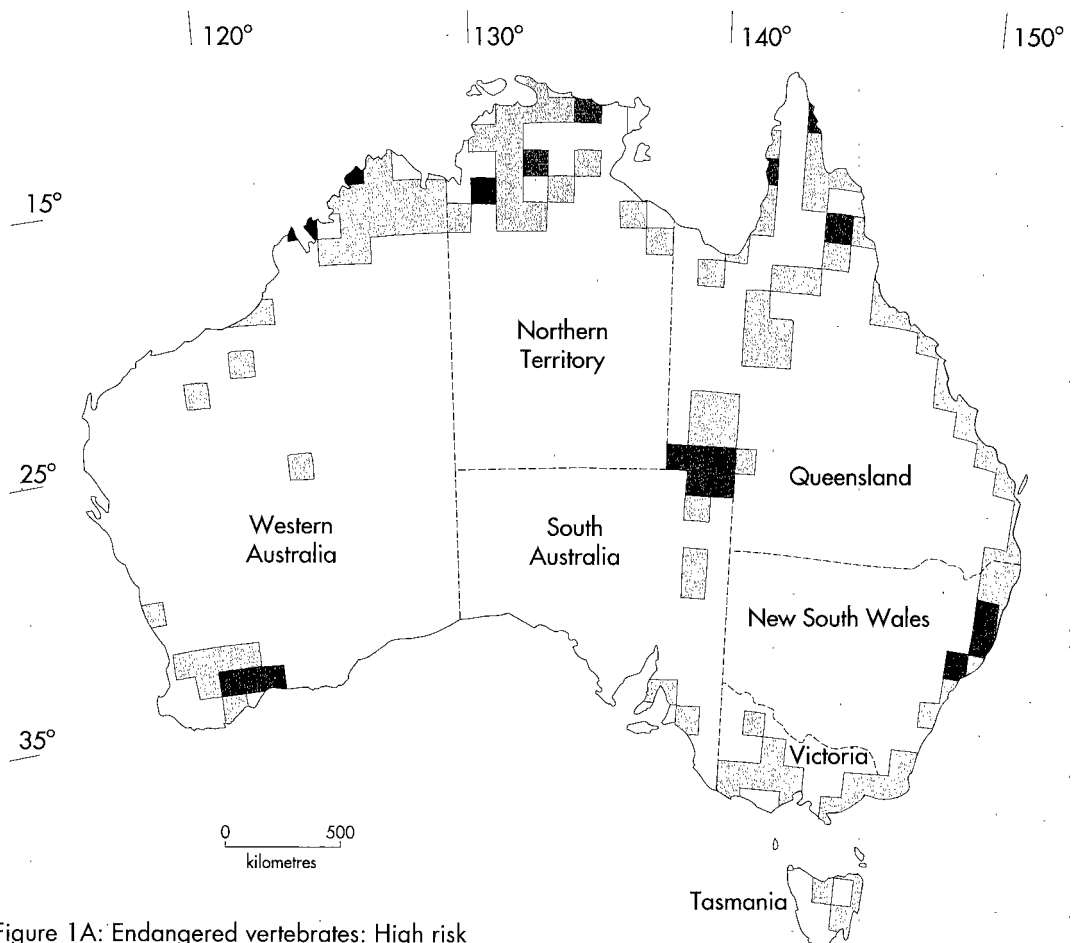


Figure 1A: Endangered vertebrates: High risk

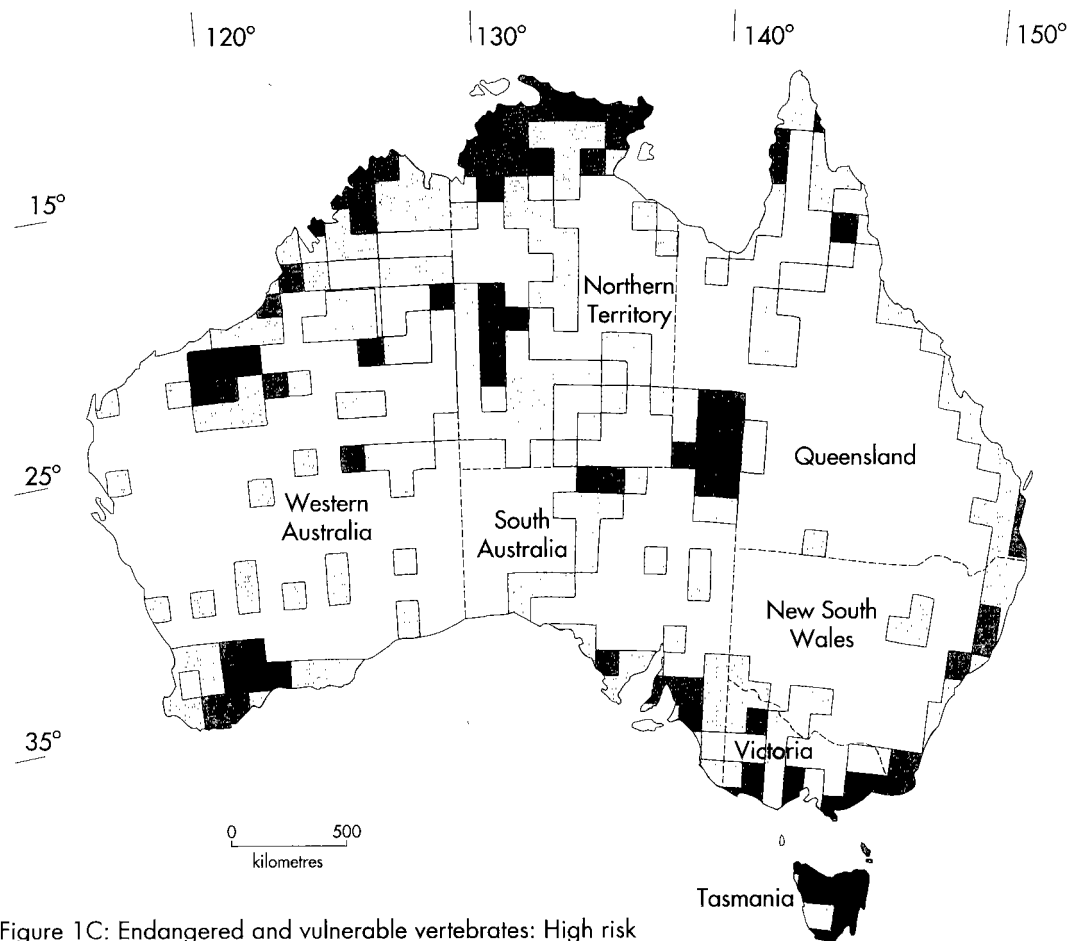
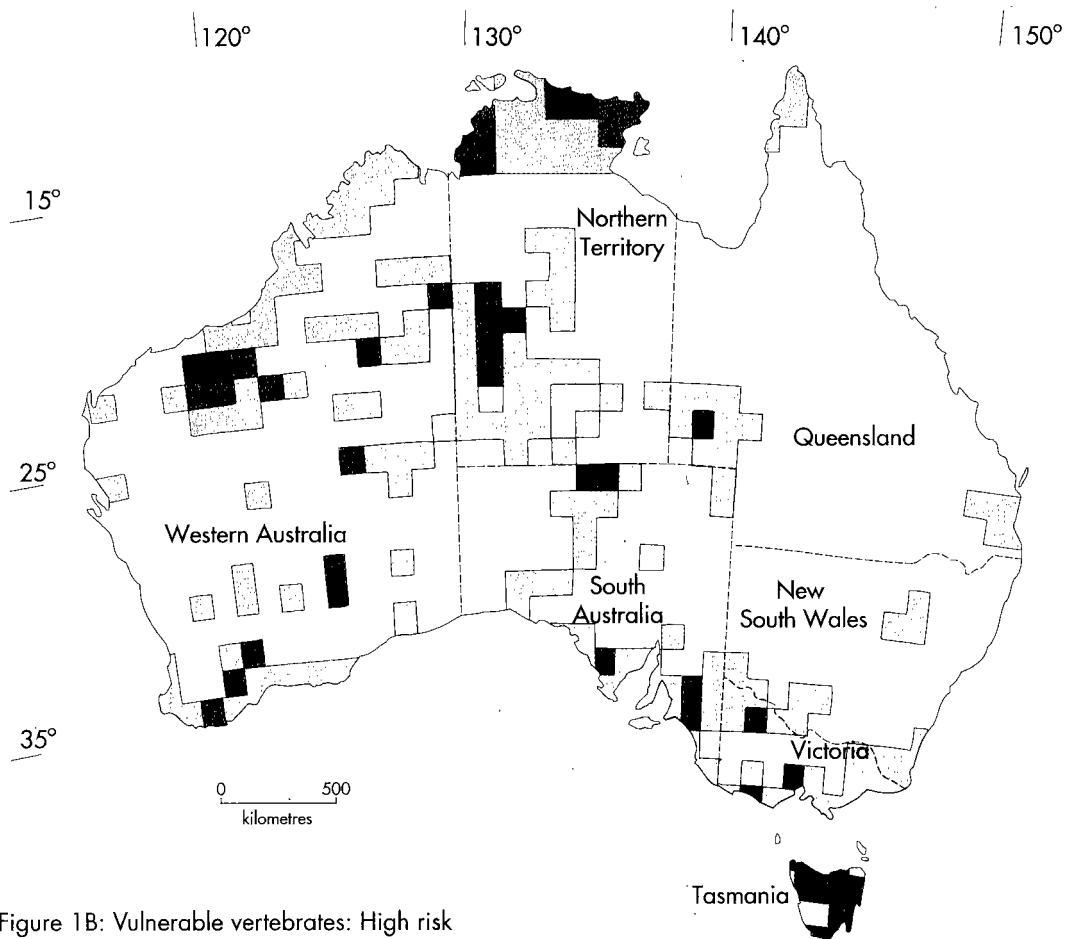


Figure 2. Species density maps of endangered and vulnerable species of native vertebrates (mammals, birds and reptiles) at low risk of impact from feral cats *Felis cat us* in Australia. a) endangered species, b) vulnerable species, c) endangered and vulnerable species combined. Species density shading code as in Figure 1.

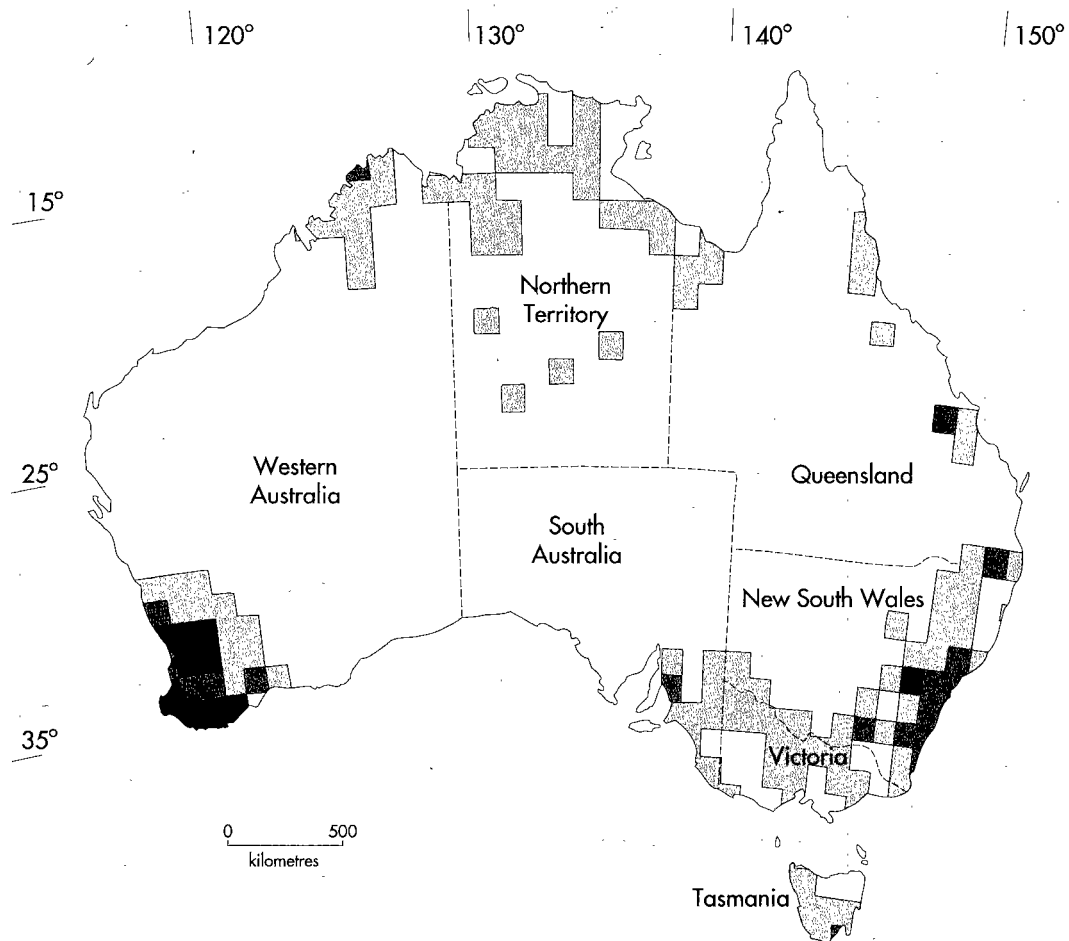


Figure 2A: Endangered vertebrates: Low risk

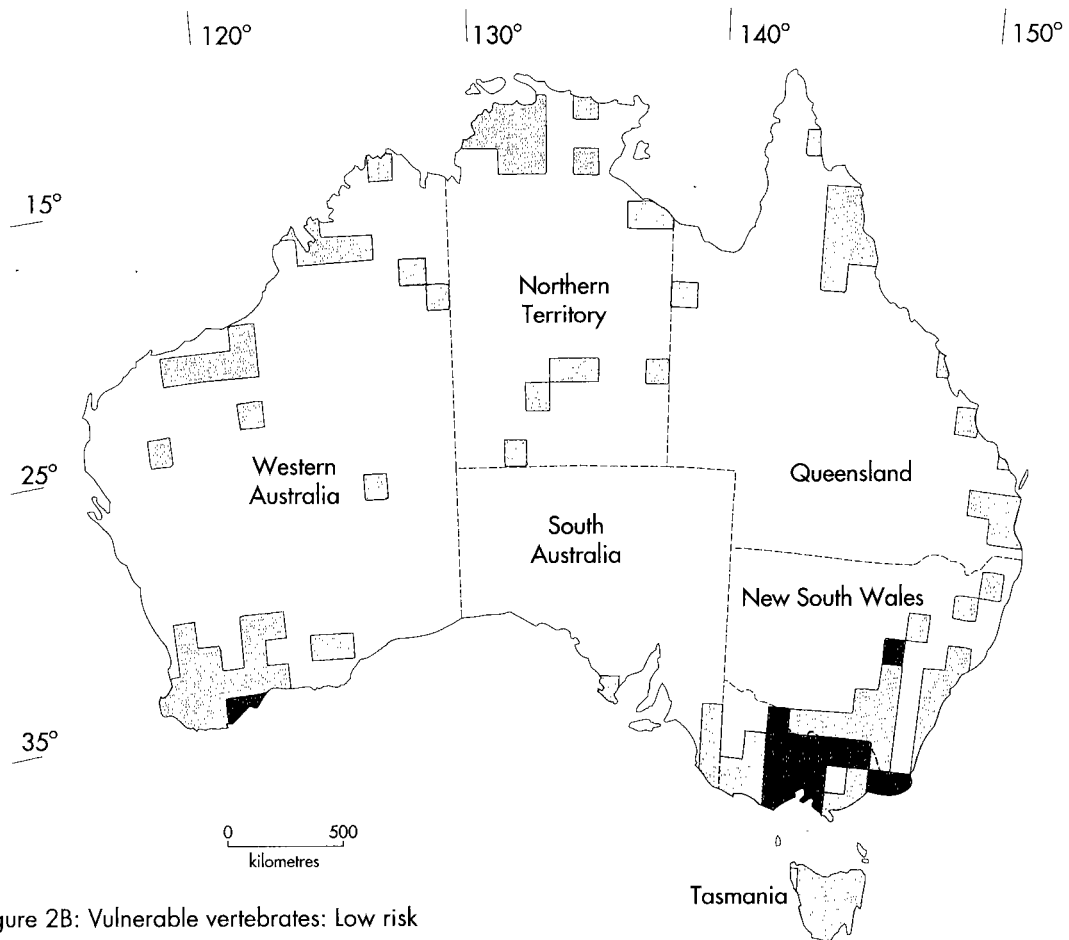


Figure 2B: Vulnerable vertebrates: Low risk

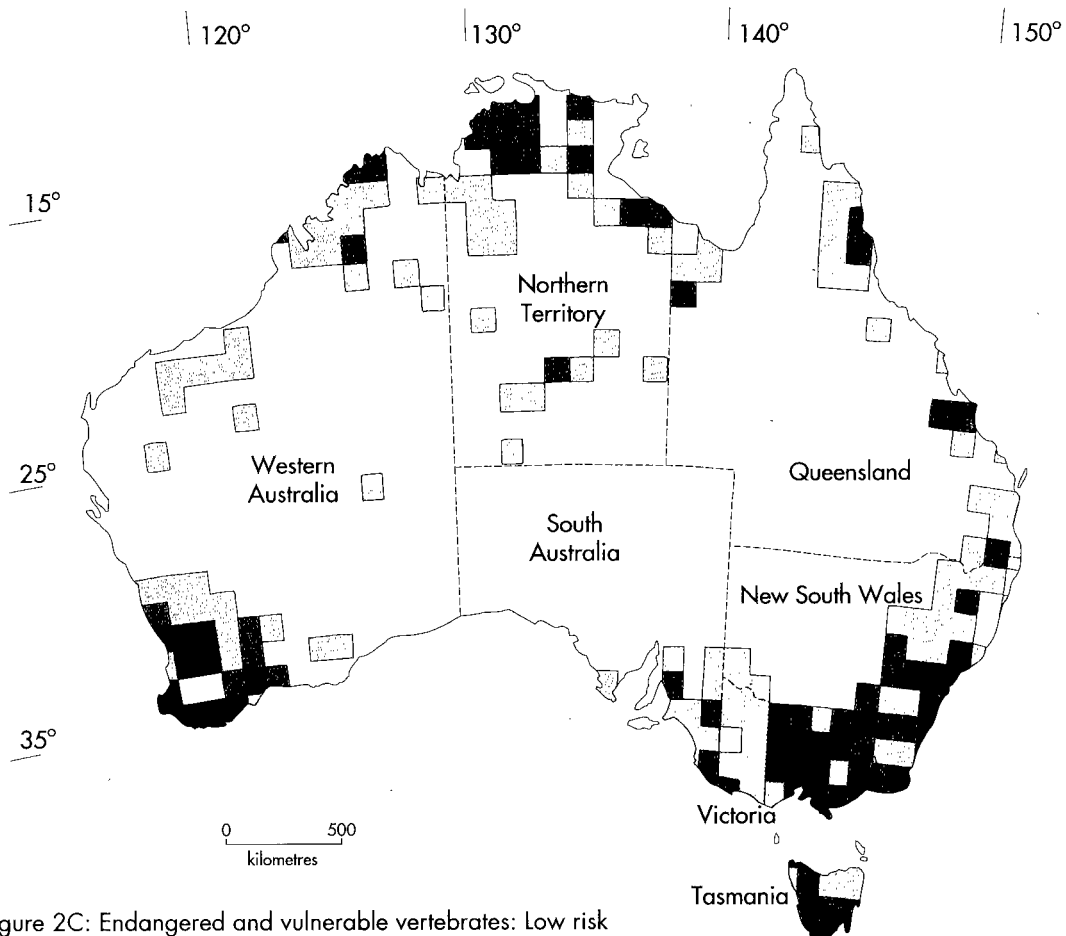


Figure 2C: Endangered and vulnerable vertebrates: Low risk

8. CRITICAL DETERMINATION OF CAT IMPACTS: PRIORITIES FOR RESEARCH

In combination, the results of Tables 9-11 and Figures 1 and 2 show that cats can be expected to have impacts on native fauna throughout Australia and its offshore islands and territories. However, as emphasised in section 4 and elsewhere, inferences and expectations about magnitudes of impact can be critically tested only by controlled removal (or addition) experiments with cats and by concomitant monitoring of responses of prey species. The objective of this final section is to first prioritise species and localities that should be targeted for such experimental work, and to then recommend experimental designs that will precisely clarify cat impacts.

8.1 Priority species and localities for research

In decreasing order of importance, the criteria I have used for prioritising localities for research are the:

1. numbers of endangered species at high risk of cat impact that co-occur (at the scale of Y grid squares, Fig. 1 a);
2. numbers of vulnerable species at high risk of cat impact that co-occur (Fig. 1 b);
3. numbers of endangered species at low risk of cat impact that co-occur (Fig. 2a);
4. numbers of vulnerable species at low risk of cat impact that co-occur (Fig. 2b);
5. density of cats, and effects of alternative prey (e.g. rabbits) and other predators on cat density; and
6. ease of carrying out effective field experiments, including consideration of habitat types and the native species putatively impacted by cats.

Further factors, considered *ad hoc* in the prioritisation process, were the degree of risk of cat impact to native species within the low risk and high risk categories, and whether species co-occurring in the same 1° grid squares co-occur in the same habitat.

Priority 1: South-west Western Australia

This region contains 15 ANCA-listed species judged to be at risk from cat impact, with up to six species occurring in eight 1° squares and seven species in one. Parts of this region have medium to high densities of cats, as well as foxes and rabbits (Wilson *et al.*, 1992), thus ensuring that overall intensity of predation is likely to be high.

Because of differences in habitat preferences, between 1 and 5-6 species could be expected to occur locally in the south-west. Thus the hooded plover *Charadrius rubricollis* would be the sole ANCA-listed species using beaches and salt lakes in this region, while up to six species may occur in coastal heath and woodland. The most important area for future investigation is the coastal and sub-coastal strip between 118° and 120°E, roughly between Albany and Ravensthorpe. This area encompasses the Fitzgerald River National Park, and contains extensive areas of undisturbed coastal heath and woodland. The following species have been recorded there: *Parantechinus apicaiis*, *Dasyurus geoffroii*, *Pseudocheirus occidentalis*, *Pseudomys shortridgei*, *Dasyornis longirostris* and *Falcunculus frontatus leucogaster*. In addition, the noisy scrub-bird *Atrichornis clamosus* and Gilbert's potoroo *Potorous tridactylus gilberti* occur in one small coastal locality at Two Peoples Bay, while records of the western ground parrot *Pezoporus wallicus flauiventris* to the immediate west, north and east suggest that it may occur also in the Albany-Ravensthorpe area. Several of these species once occurred more extensively outside the south-west (*P. shortridgei* still does) in more open habitats, suggesting that the dense coastal heaths and adjoining woodland may provide some buffer against cat impact and other threatening processes.

Priority 2: Channel Country

This region occupies a large area of western Queensland and north-eastern South Australia. It is bounded in the east by the Thompson River, and in the west by the

Mulligan, and encompasses the Cooper Creek, Diamantina River, Georgina River and numerous smaller tributaries and braided channels. The region contains only eight ANCA-listed species, but all are considered to be at high risk of cat impact. Two endangered species, the kowari *Dasyuroides byrnei* and Julia Creek dunnart *Sminthopsis douglasi* received scores of 3 for the four most important predictors of susceptibility to cat impact (Table 9), while three others received three scores of 3 (Tables 9 and 10). Productivity in the region is governed both by on-site rainfall and by rainfall in catchments to the north which may lead to flooding of the channels downstream. Flushes of vegetative growth that punctuate droughts allow local or regional plagues of rabbits or long-haired rats, and also fluctuations in the numbers of cats, foxes and dingoes. Elevated predator numbers following flush conditions may lead to brief but severe 'crunch' periods for susceptible native species, thus helping to make this region the second priority for further investigation. Localities with gibber plain and sand ridges between 24° and 26°S and between 139° and 141°E contain the highest numbers of susceptible species in the Channel Country. Species associated with gibber include *D. byrnei*, *Macrotis lagotis*, *Pseudomys australis* and *Pedionormus torquatus*, those associated more with dunes include *Dasyercus cristicauda*, *Notomys fuscus* and perhaps *Geopsittacus occidentalis*. All of these species have declined dramatically in range since European settlement, and there is no clear indication that populations are stabilising. The high potential susceptibility of all species to impact from cats and the apparent insecurity of remaining populations combine to make the Channel Country the second most important area for future investigation.

Priority 3: Top End, and

Priority 4: Kimberley

These two regions are considered together because of the large overlap in their faunas. However, the Top End is ranked above the Kimberley because of the presence of two vulnerable species at high risk of cat impact, the northern hopping-mouse *Notomys aquilo* and false water-rat *Xeromys myoides*, that are not present in the Kimberley region. Nine at-risk species on the ANCA listing occur in

the Top End, seven in the Kimberley, with up to seven and six respectively occurring in any one 1° square.

The at-risk species in these northern regions occupy a wide range of habitats, from coastal flats (little tern, *Sterna albifrons*) through tidal mangroves and grassy swamps (*X. myoides*) to hummock grassland (*N. aquilo*). However, at least six species use woodland as their preferred or secondary habitat, and localities with woodland should be targeted in future investigations. In the Top End woodland localities north of Katherine appear optimal, with records of *Mesembriomys macrurus*, *Erythrura gouldiae*, *Falcunculus frontatus whitei* and *Poecilodryas superciliosa cerviniventris* having been obtained. Except for *F. whitei*, which is known from only a handful of localities, the three other species are distributed widely in wooded habitats across the Top End so that a range of localities could prove useful for research on cat impacts. In the Kimberley, woodland habitats in the Mitchell River area should be targeted. This locality has records for the same suite of species as near Katherine except for *F. whitei*. However, the endangered golden bandicoot *Isodon auratus* and western partridge pigeon *Petrophassa smithii blaaui* have been recorded from woodland near Mitchell River, so that a potentially high number of species at risk of cat impact might be expected. Cats occur at medium density over much of northern Australia; rabbits and foxes are absent, and dingoes are apparently at low density in the Top End but at high density over much of the Kimberley (Wilson *et al.*; 1992). In this simplified predator-prey environment, the task of unravelling impacts of cats alone on native species may be relatively tractable.

Priority 5: Tasmania

Seven species at risk of impact from feral cats occur in Tasmania and on adjacent islands. It does not rank more highly because; while three vulnerable species are at high risk of impact from cats, only one endangered species (*Sterna albifrons*) is in the high risk category. Except for the little tern and hooded plover *C. rubricollis*, all other species at risk in Tasmania occupy forest, woodland' or buttongrass habitats.

The most effective locality for research on cat impact is probably in the vicinity of Hobart, Orford and Oatlands in south-eastern

Tasmania. Woodland habitats here have been recorded to contain *Dasyurus viverrinus*, *Perameles gunnii*, swift parrot *Lathamus discolor* and occasional orange-bellied parrot *Neophema chrysogaster*. Forty-spotted pardalote *Pardalotus quadragintus* have also been recorded, but the major population is offshore on Maria Island (Rounsevell & Woinarski, 1983). Because both species of parrots migrate seasonally, impacts of cats are most likely to be detected on the highly susceptible *D. viverrinus* and *P. gunnii*. Localities in eastern Tasmania have medium densities of feral cats and few rabbits; foxes and dingoes are absent from the state (Wilson *et al.*, 1992). Hence, removal experiments involving feral cats could be expected to yield unusually clear insight into their impact on native fauna, including species such as the spotted-tail quoll *Dasyurus maculatus* and Tasmanian devil *Sarcophilus harrisii* that are not listed in ANCA (1994).

Priority 6: Norfolk Island

Two of the four endangered species of birds on Norfolk are considered to be at high risk of cat predation, the other two at low risk (Table 11). Because of the small size of the island and evident restriction of listed species to the few remaining fragments of forest (Smithers & Disney, 1969), localities to investigate cat impacts are quite clearly delimited.

Priority 7: Coastal Victoria

Eleven ANCA-listed species at risk of cat impact occur along the coast of Victoria, with up to six occurring in any one 1° square. Despite these numbers, the region is not ranked more highly because only two endangered species are at high risk of cat impact and these do not co-occur. Localities with the highest numbers of co-occurring species lie within 50 km of Melbourne, with disparate forest and beach habitats each containing up to three species at risk of cat impact. Beaches on the western side of Port Phillip Bay have records of the endangered *Sterna albifrons* as well as the vulnerable *Pedionomus torquatus* and *Charadrius rubricollis*, all of which face high potential risk of cat impact. Forested localities in the hills north-east of Melbourne contain three low-risk species, *Xanthomyza phrygia*, *Lathamus discolor* (during heavy local flowering of eucalypts) and, in the Yellingbo State Nature Reserve only, the helmeted

honeyeater *Lichenostomus melanops cassidix*. *Delma impar* could also be expected to occur in lightly-wooded situations in this region, although there are no actual records. Forested and littoral localities near Melbourne contain medium densities of feral cats and high densities of foxes (Wilson *et al.*, 1992), so that predation on native species could be relatively intense.

Priority 8: Pilbara

Eight ANCA-listed species occur in the Pilbara region. Six of these are at high risk of cat impact. Solitary records for three species, *Geopsittacus occidentalis*, *Sterna albifrons* and *Polytelis alexandte*, appear to represent scattered outliers from the species' main distributions, while *Ctenophorus yinnietharra* is known from only a single locality on the western edge of the Pilbara. However, three vulnerable species at high risk of cat impact do co-occur in hummock grass habitats of the northern Pilbara, and should be targeted in future investigations. These species, *Dasycercus cristicauda*, *Macrotis lagotis* and *Pseudomys chapmani*, co-occur in two 1° squares between 21° and 22°S and 118° and 120°E. Recent records of these species have been made in the Abydos-Woodstock Reserve in the centre of this area (How *et al.*, 1991), making it a useful location for further research. A single vulnerable species, the ghost bat *Macroderma gigas* occurs also in the Abydos region. Although at low risk of cat impact, it is uncommon and restricted to isolated rock-piles (How *et al.*, 1991).

Other priorities

Several other regions within Australia, such as the coasts of New South Wales and Queensland, Cape York and southern South Australia, contain species at risk of cat predation (Figs 1 and 2). So do four islands (Christmas, Dirk Hartog, Lord Howe and Melville) not considered in the above list of priorities (Table 11). However, these areas generally contain only 1-2 species at high risk from cats in 1° squares and 1-2 species that co-occur, and so have not been placed in the priority listing.

In prioritising areas for further research, the primary criteria were the numbers of ANCA-listed species that could be considered at high risk and then at low risk from feral cats. This approach was adopted to maximise the number of native species that could be

surveyed locally in subsequent cat-removal experiments, and to maximise the chance that the species selected would show strong responses. No consideration has been given to native prey species not listed by ANCA (1994), nor have considerations of the taxonomic uniqueness or biological role of impacted species been addressed. However, alternative approaches based on these or other considerations could still be directed using the scoring system for biological attributes in section 7. For example, if any one species were to be picked for very high susceptibility to cat impact it would be the Julia Creek dunnart *Sminthopsis douglasi*, which scored 3 for the four most important attributes associated with risk (Table 9). This species occurs alone, and hence is not included in the priority list above. Thus, alternative lists of priority species and localities could be developed according to need.

8.2 Experiments to clarify cat impacts

In mainland Australia, the most effective way to quantify cat impacts will be to remove cats from specified areas and monitor the responses of native species assumed to be at risk. Impacted species should show increases in numbers or expansions of area occupied following cat removal, and the degree of increase will provide a measure of the degree of cat impact. Such experiments must be seen as constituting a very important scientific and conservation goal, and as the only means of reliably guiding management on the level of cat control that will achieve recovery objectives. For experiments to be interpretable, cats should be removed from at least two replicate areas, and responses of native species evaluated with respect to those in two or more control areas from which cats have not been removed. Experimental power, and hence ability to identify responses correctly, should increase with more replicate study areas and also if responses to cat removal are relatively great. The most appropriate statistical designs to identify responses to cat removal are based on analysis of variance, with units of replication being study areas rather than individual animals. Recent advances in methodology have provided asymmetrical designs that will allow reliable detection of species responses

to cat removal in a single area, provided that several control areas are available and species responses are monitored before and after cat removal (Underwood, 1994). Because of the very high cost and logistical difficulty of removing cats from specified areas, such designs may be particularly attractive for future research.

Although designs for cat removal experiments are conceptually simple, several practical considerations are likely to affect their success. First, cats must be known or suspected to affect particular native species prior to experimentation so that appropriate monitoring methods for these species can be established. Evidence of cat predation or incidence of cat-transmitted parasites would provide direct evidence, but high scores on the attributes of susceptibility to cat impact (section 7) might also be used. In New Zealand, increasing use is being made of video-surveillance to quantify cat predation at nests of endangered species of birds (E.C. Murphy, pers. coram.); greater use of this technique could be made with profit in Australia. Ideally, all species potentially impacted by cats should be monitored, including endangered, vulnerable and "common" species not listed by ANCA (1994), to maximise returns from field experiments and to provide more information by which to judge magnitudes of cat impact. Second, effective removal of cats from one or more study areas may require intensive shooting, trapping and baiting for the duration of any experiment. It would be premature here to recommend baits because bait type and delivery for feral cats are being actively researched in several areas (D. Algar, M. Anderson, G. Edwards, J.A. Friend, J. Lee, A. Rathore, D. Risbey, J. Short, pers. comms.). However, the effectiveness of any control program would need to be evaluated continuously by census of cats (by spotlighting or track counts) and modified if necessary. For proper experimental procedure, control measures carried out in cat-removal areas should be duplicated to a degree in trial areas. Thus, some shooting with blanks would minimise any differences in treatment between all study areas except for the removal of cats. Third, study areas should be large enough for putatively impacted species to show a response to cat removal, and far enough apart that control and removal site effects are not confounded.

The minimum effective size for study areas would depend on the native species being studied, and be larger for large, mobile species than for small sedentary ones. However, because of the continuous possibility of cat incursions into removal sites, study areas should be a minimum of several km² and be separated by distances of 20-25 km. To counter any confounding effects arising from variable climate or different habitats in distantly-spaced study areas, control and removal areas should be interspersed if replication is low ($n = 2$ for each of the control and removal areas) and assigned randomly to treatment if replication is greater ($n > 2$ for each of the control and removal areas). Fourth, any experimental study of cat removal must run for long enough for any impacts to be detected. For native species at low population densities, numerical increases may not be evident for several years after cat removal, especially if fecundity is low. A reasonable minimum time to allow for detection of impact might be at least two effective breeding seasons for targeted native species, excluding seasons in which breeding and recruitment are poor due to external factors such as weather. Finally, as described in section 5, interactions between cats and native prey species may be clouded if non-native prey and predators are present. Census of these species, especially rabbits and foxes, should be carried out throughout any cat-removal experiments to

evaluate any indirect effects that may be introduced. Experimental work carried out in Tasmania, on Kangaroo Island, in northern Australia or inland areas of gibber plain may yield particularly clear insight into cat impacts as either rabbits, foxes or both are absent. Finally, a more cautious approach to removal of cats is required on islands with large populations of introduced rats. On Christmas, Lord Howe and Norfolk Islands rats may prey directly upon native fauna, and removal of cats could allow a deleterious release of rat populations. Preliminary research should establish diets and likely impacts of both cats and rats, and compare the spatial and temporal distributions of the predators on the islands. Cat removals alone should take place only if the overall impact of rats on native fauna appears to be small, and if cats and rats occur independently with no evidence of either an inverse numerical or spatial relationship between them. With these caveats satisfied, removal of feral cats from the three oceanic islands could be attempted using a combination of shooting, trapping and carefully targeted baiting, and responses of the 10 at-risk species (Table 11) monitored. If rats appear likely to increase following the removal of cats, cat removals should be carried out as part of an integrated control program which includes rats and which again monitors the responses of native species.

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APPENDIX I

Diet of the feral cat *Felis catus* in different habitats in Australia. Data are taken from 22 published and unpublished studies, and represent diet as % volume of occurrence of food categories (Roman type) or frequency of occurrence of food categories (bold). Samples (n) were obtained from stomachs (s), faeces (f), or both sources combined (b).

Food Category	ARID HABITATS				
	1. Southern NT (Strong & Low, 1983)	2. Western NSW (Jones & Coman, 1981)	3. Purple Downs SA (Bayly, 1976)	4. Lyndhurst SA (Bayly, 1978)	5. Nullarbor WA (Brookes, 1977)
	n = 20 (s)	n = 65 (s)	n = 14 (s)	n = 20 (s)	n = 8 (s)
Rabbit	50.0	56.0	1		
House Mouse	20.0	2.0			
Other rodent < 50g	20.0				
Other rodent > 50g					
Bats		<1.0			
Polyprotodont marsupial < 100g		<1.0			
Polyprotodont marsupial > 100g					
Diprotodont marsupial < 100g					
Diprotodont marsupial > 100g		3.0			
Monotreme					
All mammals	70.0	62.0	43.2	87.6	
Passerines	5.0				
Non-passerines	15.0		0.8	1	1.3
All birds	15.0	18.0	0.8	6.4	1.3
Lizards <100g	75.0				61.0
Lizards > 100g					
Snakes < 100g	10.0				2.5
Snakes > 100g		?	?		
All reptiles	60.0	2.0	31.9	4.6	63.5
Amphibians					
Fish		9.0			
Invertebrates	55.0	1.0	13.6	0.4	35.2
Scavenge and callion		1.0			
Other	15.0	6.0	10.5	1.0	

Appendix 1 (cont.)

<i>Food Category</i>	<i>ARID HABITATS continued</i>	
	<i>6. Birdsville, Old (C.R. Dickman, unpub.)</i>	<i>7. Ethabuka, Old (C.R. Dickman, unpub.)</i>
	n = 15 (f)	n = 25 (f)
Rabbit		58.5
House mouse	3.0	
Other rodent < 50g	8.3	44.5
Other rodent >_ 50g		8.0
Bats		
Polyprotodont marsupial < 100g	2.0	12.8
Polyprotodont marsupial >_ 100g		
Diprotodont marsupial < 100g		
Diprotodont marsupial >_ 100g		
Monotreme		
All mammals	71.8	65.3
Passerines	1.4	12.4
Non-Passerines	3.8	6.5
All birds	5.2	18.9
Lizards < 100g	6.3	3.1
Lizards >_ 100g		
Snakes < 100g	2.5	
Snakes >_ 100g		
All reptiles	8.8	5.1
Amphibians		
Fish		
Invertebrates		
	12.3	7.6
Scavenge + carrion	1.5	
Other	0.5	3.1

Appendix 1 (cont.)

<i>SEMI-ARID HABITATS</i>				
<i>Food Category</i>	<i>8. Western Vic. (Coman & Brunner, 1972)</i>	<i>9. Western Vic. (Jones & Coman, 1981)</i>	<i>10. Western NSW (Catling, 1988)</i>	<i>11. Wheatbelt, WA. (C.R. Dickman, unpub.)</i>
	n = 27(s)	n = 131 (s)	n = 103 (s)	n = 48 (b)
Rabbit	62.0	74.0	54.0	60.0
House mouse	27.0	9.0	8.8	12.2
Other rodent < 50g				0.3
Other rodent >_ 50g		< 1.0		
Bats		< 1.0	2.7	
Polyprotodont marsupial < 100g			4.4	4.6
Polyprotodont marsupial >_ 100g				
Diprotodont marsupial < 100g				
Diprotodont marsupial >_ 100g		2.0	0.9	
Monotreme			0.2	
All mammals	90.0	86.0	80.5	77.3
Passerines			>5.3	2.3
Non-passerines			> 13.2	1.0
All birds	<1.0	9.0	21.2	3.3
Lizards < 100g		<1.0	55.9	2.0
Lizards >_ 100g			?	
Snakes < 100g		<1.0	2.7	
Snakes >_ 100g				
All reptiles	<1.0	<1.0	30.1	2.0
Amphibians	1.0	<1.0		
Fish		1.0		
Invertebrates	< 1.0	<1.0	42.5	3.5
Scavenge + carrion	4.5	2.0	7.9	10.4
Other	3.0	<1.0	2.6	3.5

Appendix 1 (cont.)

Food Category	TEMPERATE FOREST HABITATS		
	12. <i>Eastern Highlands, Vic.</i> (Coman & Brunner, 1972)	13. <i>Eastern Highlands, Vic.</i> (Jones & Coman, 1981)	14. <i>Mallacoota,</i> (Triggs et al., 1984)
	n = 53 (s)	n = 117 (s)	n = 48 (f)
Rabbit	20.5	43.0	
House mouse	11.8		
Other rodent <50g			
Other rodent >_50g	13.4	5.3	18.8
Bats		<1.0	2.0
Polyprotodont marsupial <100g	1.1	1.6	14.6
Polyprotodont marsupial >_100g	<1.0	0.8	10.4
Diprotodont marsupial < 100g		<1.0	
Diprotodont marsupial >_100g	22.0	32.4	56.3
Monotreme			2.1
All mammals	76.0	84.0	
Passerines			
Non-passerines			
All birds	5.8	13.0	27.1
Lizards < 100g	1.1	<1.0	
Lizards >_100g			
Snakes < 100g			
Snakes >_100g			
All reptiles	1.1	<1.0	22.9
Amphibians		<1.0	
Fish			4.2
Invertebrates	0.8	<1.0	22.9
Scavenge + carrion	9.7	1.0	?
Other	6.4	1.0	20.8

Appendix 1 (cont.)

<i>TEMPERATE FOREST HABITATS</i>				
<i>Food, category</i>	<i>15. Olney SF, NSW (C. R. Dickman, unpub.)</i>	<i>16. Kuringal NP, NSW (C.R.Dickman, unpub.)</i>	<i>17. Brindabellas, A.C.T.(C.R. Dickman, unpub.)</i>	<i>18. Dwellingup, WA. (C. R. Dickman, unpub.)</i>
	n = 12 (b)	n = 17 (f)	n = 20 (f)	n = 14 (f)
Rabbit	1.3	8.5	5.2	5.5
House mouse	1.0	2.6		5.0
Other rodent <50g				
Other rodent >_50g	15.8	17.0	26.6	15.4
Bats		1.0	1.3	
Polyprotodont marsupial <100g	7.3	8.5	9.0	2.1
Polyprotodont marsupial >_100g		2.0		7.8
Diprotodont marsupial < 100g				
Diprotodont marsupial >100g	25.5	29.7	10.8	15.6
Monotreme			<1.0,	
All mammals	50.9	69.3	53.0	51.4
Passerines	11.1	2.4	23.0	7.0
Non-passerines	16.5	10.8	7.2	3.0
All birds	27.6	13.2	30.2	10.0
Lizards < 100g	2.7	3.1	9.4	<1.0
Lizards >_100g		1.0		
Snakes < 100g	1.5			
Snakes >_100g				
All reptiles	4.2	4.1	9.4	<1.0
Amphibians			1.1	
Fish				
Invertebrates	3.0	1.5	4.3	2.2
Scavenge + carrion	7.6	3.4	2.0	16.4
Other	6.6	8.5	<1.0	19.9

Food category	WET DRY TROPICAL HABITATS		URBAN AND SUBURBAN HABITATS	
	19. Coastal flood plains NT (Cameron, 1994)	20. Woodland, NT (Cameron, 1994)	21. Dandenong, Melbourne (Brunner et al., 1991)	22. North Head, Sydney (C. R. Dickman, unpub.)
	n = 25(s)	n = 23(s)	n = 85 (f)	n = 20 (b)'
Rabbit			2.4	21.0
House mouse	4.3		18.8	1.5
Other rodent <50g		5.8		
Other rodent >_50g	74.9	85.7	17.7	19.2
Bats				
Polyprotodont marsupial <1 OOg				
Polyprotodont marsupial >1 OOg	6.8			28.2
Diprotodont marsupial < I OOg				
Diprotodont marsupial _II 009			27.1	14.3
Monotreme				
All mammals	86.0	91.5	54.1	84.2
Passerines		?		
Non-passerines	2.9	6.9		
All birds	2.9	7.3	16.5	8.6
Lizards < 1 OOg	7.7	0.1		
Lizards >_1 OOg				
Snakes <100g	1.2	0.7		
Snakes _100g				
All reptiles	8.9	0.8		3.9
Amphibian	0.1			
Fish				
Invertebrates	2.2	0.3		3.3
Scavenge + carrion			5.6	
Other .			72.9	

General Notes.

Where a study provided both % volume and % frequency of occurrence data, only the % volume results are shown. Percentage frequency data sum to > 100 when more than one food category occurs in any stomach or faecal sample. Over-representation in % frequency data has been compounded in the table due to the need to compact food categories. For example, if raw data in a study showed that four small species of lizards had been eaten in a sample of 20 stomachs, the frequency of occurrence for the compacted category "lizards <100g" could be 5% (1/20) if all lizards occurred in one stomach but 20% (4/20) if each species was recovered from a different stomach. For consistency I have added % frequency data within food categories, hence leading to over-representation of that category in some cases. Totals for mammals (all mammals), birds (all birds) and reptiles (all reptiles) are shown where these were provided or could be calculated from the original data. Sample sizes shown for studies using stomach contents exclude animals with empty stomachs. Weights of species within food categories were taken from the original sources where provided, but were otherwise estimated from field data (C.R. Dickman, unpublished) and literature sources (Strahan 1983; Blakers et al., Shine 1991; Cogger 1992).

Large mammals (sheep, cattle, wombats, kangaroos) are included within the scavenge and carrion category; cat fur, plant material, nonorganic and unidentified materials under "other". Mammal, bird or reptile remains that could not be classified more finely are included within the totals for each group. Hence, % volumes for "all mammals", "all birds" and "all reptiles" exceed the sums of volumes for the identified food categories if unidentified remains were included. A "i" is given if an item was identified but not quantified, a "?" is given if an item could not be certainly allocated to a category.

Notes on particular studies.

- Jones & Conran (1981). Data are expressed as the weight contribution of each food category as a percentage of the weight of all food items. One record of a long-necked tortoise is not shown.
- Brooker (1977). Data are expressed as the percentage of all prey identified, rather than as % frequency of occurrence in stomachs.
- Coman & Brunner (1972). Data are pooled for south-western Victoria as well as the semi-arid mallee.
19. & 20. Cameron (1994). Data are expressed as the % weight contribution of each food category, as in Jones & Conran (1981).
- Brunner et al. (1991). The very large category "Other" includes invertebrates, vegetation, lizards and additional scavenged material, but was not presented separately in the paper.

APPENDIX 2

Diet of the feral cat *Felis catus* on Australian, New Zealand and Pacific region islands.

Data are taken from 12 published and unpublished studies and represent diet as % volume of occurrence of food categories (Roman type) or % frequency of occurrence of food categories (bold). Samples (n) were obtained from stomachs (s), faeces (f), or both sources combined (b).

Food category	(1) Rottneest Island, Gt. Dog Is, WA (C.R. Dickman, unpub.)	(2) Tos (Hayde, 1992)	(3) Christmas Is, Indian Ocean sub- (Tidemann et al. 1994)	(4) Macquarie Is, Stewart Is, New Zealand (Jones, 1977)	(5) New Zealand (Karl & Best, 1982)	(6) Herekopare Is, New Zealand (Fitzgerald & Veitch, 1985)
	n=32(f)	n=75(s)	n=93 (b)	n=756(f)	n=229(f)	n=30(s)
Rabbit				81.9		
House mouse	20.1	8.0		4.4		
Other rodent <50g			2.0			
Other rodent >_50g	7.7		31.0	2.6	79.7	
Bats			21.0			
Diprotodont						
marsupial >_100g	10.5				3.4	
All mammals	38.3		54.0		83.1	
Passerines	15.4		<1.0	0.5	.2.0	3.3
Non-passerines	28.0	90.7	30.0	49.3	-13.5	90.0
All birds	43.4	90.7	30.0		15.5	
Lizards < 100g	6.8	45.3	3.0		1.1	
Lizards >_100g						
Snakes <100g		2.7				
Snakes >_100g	3.0	1.3				
All reptiles	9.8	49.3	3.0	0	1.1	
Amphibians	1.0					
Fish						
Invertebrates	6.3	100.0	12.0	2.3	0.2	50.0
Scavenge+carriion	1.2	?		0.3		
Other				12.5	<1.0	20.0

Appendix 2 (cont.)

Diet of the feral cat *Felis catus* on Australian, New Zealand and Pacific region islands.

Data are taken from 12 published and unpublished studies and represent diet as % volume of occurrence of food categories (Roman type) or % frequency of occurrence of food categories (bold). Samples (n) were obtained from stomachs (s), faeces (f), or both sources combined (b).

<i>Food category</i>	(7) <i>Little Barrier Is, New Zealand (Marshall, 1961)</i>	(8) <i>Campbell Is, New Zealand (bilks, 1979)</i>	(9) <i>Raoul Is, New Zealand (Fitzgerald et al., 1991)</i>	(10) <i>Lord Howe Is south-west Pacific (Miller & Mullette, 1985)</i>	(11) <i>Jarvis Is, central Pacific (Kirkpatrick & Rauzon, 1986)</i>	(12) <i>Howland Is, central Pacific (Kirkpatrick & Rauzon, 1986)</i>
	n=94(f)	n=20(f)	n=57(s)	n=(14(b)	n=73(s)	n=5(s)
Rabbit						
House mouse				3.0	2.0	
Other rodent <50g						
Other rodent >_50g	39.4	95.0	86.0	14.0		
Bats						
Diprotodont marsupial (1008						
All mammals	39.4		88.0			
Passerines	24.5					
Non-passerines	50.0			35.0	97.0	92.0
All birds		35.0	35.0	35.0	97.0	92.0
Lizards < 100g					<1.0	8.0
Lizards >_100g						
Snakes <100g						
Snakes >_100g						
All reptiles					<1.0	
Amphibians						
Fish						
Invertebrates	31.9	60.0	-20.0		<1.0	
Scavenge+carrion			16.0			
Other			23.0	<1.0	<1.0	<1.0

General Notes.

Data in Appendix 2 have been compiled in the same way as Appendix 1. Monotremes, polyprotodont marsupials and diprotodont marsupials <100g are omitted from food category listings in Appendix 2 because these taxa were, not found in the diets of cats on any islands. **Notes on particular studies**

2. Hayde (1992). Autumn data only are presented.
3. & 5 Tidemann *et al.* (1994) and Karl & Best (1982) express data as the weight contribution of each food category as a percentage of the weight of all food items.
9. Fitzgerald *et al.* (1991). Data from samples collected between August and October 1972 are shown. This study also presented results from other periods, but the food categories and their percentage frequencies of occurrence are very similar to those shown in Appendix 2.
10. Miller & Mullette (1985). This study did not provide a sample size. Hence data are presented simply as frequencies of items recorded.