Impact of exotic generalist predators on the native fauna of Australia

Author: Dickman, Chris R.

Source: Wildlife Biology, 2(3) : 185-195

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.1996.018

Impact of exotic generalist predators on the native fauna of Australia

Chris R. Dickman

Dickman, C.R. 1996: Impact of exotic generalist predators on the native fauna of Australia. - Wildl. Biol. 2: 185-195.

This paper reviews the impacts of three species of introduced mammalian predators on native fauna in Australia. The feral cat *Felis catus*, introduced over 200 years ago, is linked with early continental extinctions of up to seven species of mammals, regional and insular extinctions of many more species of mammals and birds, and the failure of management programs attempting to reintroduce threatened native species to parts of their former ranges. Evidence for cat-impact is largely historical and circumstantial, but supported by observations that afflicted native species are, or were, small (<200 g) occupants of open habitat and hence likely to be especially vulnerable to cat predation. The red fox *Vulpes vulpes* was released successfully in 1871. Its subsequent spread into all except parts of arid and tropical Australia coincided with local and regional declines of medium-sized (450 - 5,000 g) mammals, birds and chelid tortoises. The fox has also created recent failures of many management attempts to recover threatened native species. Unequivocal demonstration of fox-impact has been obtained in removal experiments, especially on rock-wallabies *Petrogale lateralis*. The dingo *Canis lupus dingo*, introduced 3,500-4,000 years ago, probably caused the extinction of the thylacine *Thylacinus cynocephalus* and Tasmanian devil *Sarcophilus harrisii* on mainland Australia. It effectively suppresses extant populations of large mammals, such as kangaroos, and emus, over large areas. Impacts of all three predators are wrought primarily by direct predation. Negative impacts appear to be increased in spatially fragmented forests where native species are restricted to remnant vegetation, and in arid landscapes when native species become restricted temporarily to scattered oases during drought. Alternative prey, especially rabbits *Oryctolagus cuniculus*, enhance negative impacts on native species by supporting large populations of the predators. It is concluded that feral cats and especially foxes have major negative impacts on certain small and medium-sized native vertebrates in Australia, whereas dingoes have major negative impacts on large species. Dingoes could have positive effects on smaller native species if they significantly suppress populations of foxes and cats. Further quantification of both the direct and indirect impacts of the three predators on native fauna is needed, and should be obtained from experimental field studies.

Key words: feral cat, red fox, dingo, predator, exotic, Australia

Chris R. Dickman, School of Biological Sciences and Institute of Wildlife Research, University of Sydney, New South Wales 2006, Australia

Generalist predators have been introduced by humans to new environments in many parts of the world, often impacting negatively on native species. Impacts have been most conspicuous on species on small islands isolated from continents (Brockie et al. 1988), in part because such species have evolved in the absence of predators and lack effective anti-predator adaptations (Atkinson 1985). However, impacts have occurred also on near-shore islands and even large continental areas (Atkinson 1989, Dickman 1992a). Mammals such as rats *Rattus* spp. and feral domestic cats *Felis catus* have had particularly destructive effects on a broad range of native vertebrate species (Atkinson 1985, Dickman 1996). However, predatory birds, reptiles, amphibians and fish have also been implicated in the demise of native species (Covacevich & Archer 1975, Wiley 1985, Savidge 1987); the impacts of some, such as the Nile perch *Lates niloticus*, have been severe (Baerl et al. 1985).

The most obvious impact of exotic predators is that they cause extinctions or reductions of range and population size of native species. However, impacts may also be subtle. The introduction of feral cats to some Galápagos islands, for example, has apparently selected for increased wariness in lava lizards *Tropidurus* spp.; loss of 'tameness' has been interpreted as a loss of biological diversity although the lizards remain extant (Stone et al. 1994). Amarasekare (1994) showed further that three species of introduced mammalian predators had no obvious effects on endemic birds on Hawaii, while Diamond (1987) presented equivocal evidence for impacts of predators introduced to the Mascarene Islands. Predator-impacts may occasionally even be beneficial. For example, predation by feral cats on ship rats *R. rattus* can reduce the impacts of rats on the eggs and hatchlings of birds (Ebenhard 1988); this has been presumed to benefit native bird faunas on several islands where rat populations would otherwise explode (Disney & Smithers 1972, Fitzgerald et al. 1991, Tidemann et al. 1994).

In Australia, three major species of generalist mammalian predators have been introduced: the feral cat, the red fox *Vulpes vulpes*, and the dingo *Canis lupus dingo*. All three have been implicated in the past demise of native animals, and all three are subject to current management to mitigate further impact. Although other generalist predators have also been introduced to Australia, they have either established less successfully than the carnivores and have had little evident impact (ship rats, Norway rats *R. norvegicus*), are restricted to specific environments (carp *Cyprinus carpio*, gambusia *Gambusia holbrooki*; Pollard 1989, Faragher & Harris 1994), or eat flesh only infrequently (pig *Sus scrofa*; Pavlov 1995).

In the present paper, I describe briefly the introduction, spread, and distribution of the feral cat, the red fox, and the dingo in Australia, and review the impact of each species on native animals. Impact is discussed also in relation to human modification of the environment at local and regional scales.

Definition of 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. Neutral and positive impacts have not been recorded for the three predator species discussed here; except for a possible facilitatory effect involving dingoes these are not further considered. Negative impacts could be caused directly by three processes: predation, competition, and via transmission of disease, parasites or pathogens to native species (Dickman 1992b). In addition, indirect impacts could occur at the community level via effects on keystone species (e.g. Spiller & Schoener 1994). Such impacts have long been suspected for certain mammalian predators, such as cats (Darwin 1859), but remain poorly studied.

It is important to note that, while these processes affect individuals, population or community effects do not follow automatically. Here, I limit discussion to influences detectable at the population level at a local or regional scale. Following Dickman (1996), I define a *minor impact* of a predator as one that produces a decrease of 25% or less in the population size or geographical area occupied by a native species, and a *major impact* as one that produces a decrease of 75% or more in the population size or geographical area occupied by a native species. The latter definition includes predator-induced extinction. Initial review of relevant literature indicated that impacts were either minor or major with little in between, hence justifying the dichotomy. These definitions of impact are relevant only on an ecological time scale of days to years. Due to the relatively recent arrival of the three species of carnivores in Australia, evolutionary impacts on native species are probably still minor.

Feral cat *Felis catus*

Introduction and establishment

Cats were certainly brought to the east coast of Australia in the late eighteenth and early nineteenth centuries (Rolls 1969), and feral populations were established shortly after settlement. Some evidence suggests that cats were introduced earlier, in the seventeenth century, to the northwestern coast from the wrecks of Dutch ships; arrivals as early as the fifteenth century have been postulated via mariners from Indonesia (Baldwin 1980). Aboriginal people of the central and western deserts think that cats have always been present (Finlayson 1943, Burbidge et al. 1988), providing further support for the notion that introduction preceded European settlement.

The pattern of spread of feral cats is obscure. Cats are not mentioned in the journals or diaries of most early European colonists and explorers in Australia (e.g. Sturt 1833, Grey 1841), perhaps suggesting that populations were small or localised. Reports of cats became much more frequent toward the end of the nineteenth century, coinciding with releases of cats in southeastern and western Australia to control plagues of mice, native rats and rabbits *Oryctolagus cuniculus* (Rolls 1969, Long 1988). Cats now occupy all terrestrial environments in Australia (Fig. 1A) as well as some 40 offshore islands (Dickman 1992a, 1996). Densities on the mainland usually are in the order of 1-2 cats/km^2, or less, although higher densities of >6/km^2 have been recorded (G. Edwards, pers. comm.). Densities of up to 100/km^2 have been reported on small islands.

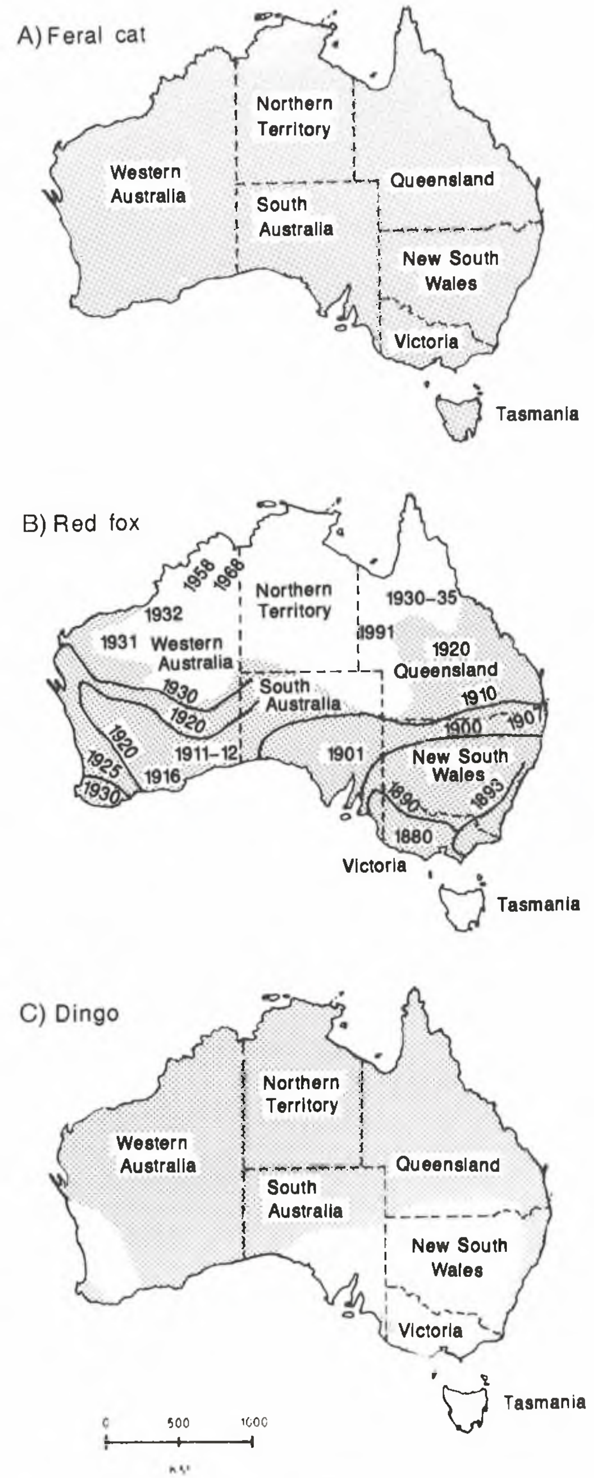

Figure 1. Geographical distribution in Australia of (A) the feral cat *Felis catus*, (B) the red fox *Vulpes vulpes*, and (C) the dingo *Canis lupus dingo*. Contours and dates in (B) indicate the spread of the fox following introduction to southern Victoria in 1871. Redrawn from Jarman (1986) and Saunders et al. (1995).

Diet

In Australia, as in other parts of the world, feral cats take a wide range of vertebrate and occasionally invertebrate prey, but prefer mammals where available. Rabbits and house mice *Mus domesticus* are major prey in semi-arid and some arid habitats, whereas marsupials predominate in the diet in forest and suburban areas (Dickman 1996). Birds are a consistent but minor component of cat diets on mainland Australia, but may predominate in the diet on islands (e.g. Hayde 1992); reptiles feature most prominently in the diet in arid areas. Vertebrates up to about 2,000 g can be taken (exceptionally, 3,500 g on islands), but prey <200 g are usually preferred (Dickman 1996).

Impact

Evidence for cat-impacts on Australian native fauna is based mostly on historical and comparative studies rather than experimental inference, but is nonetheless quite compelling (see reviews in Dickman 1993a, 1996). Major impacts most likely stem from direct predation.

Predation

Several species of small mammals and birds declined or became extinct on the mainland of Australia in the first half of the nineteenth century, or earlier, coinciding with the introduction and establishment of cats. Two species of native rodents and a potoroid marsupial are known only from very recent sub-fossil deposits (Watts & Aslin 1981, Baynes 1987), and may represent the first cat-induced extinctions on the continent. Four other species of native rodents were last recorded on the mainland in the 1840s and 1850s (Table 1). In New South Wales 13 species of mammals and four species of birds had disappeared by 1857 from the Western Division, an area of 325,000 km^2; similar regional declines were evident in other states (Dickman et al. 1993, Smith et al. 1994).

Although cats were present when the extinctions of last

Table 1. Early extinctions of native Australian mammals, showing dates of last records and estimated body weights.

Species	Last record	Weight (g)
Unnamed potoroid	pre-1850	>200
White-footed rabbit-rat *Conilurus albipes*	1846	200
Darling Downs hopping-mouse *Notomys mordax*	~ 1840	50
Big-eared hopping-mouse *Notomys macrotis*	1844	60
Great hopping-mouse *Notomys* sp.	pre-1850	<200
Gould's mouse *Pseudomys gouldii*	1857	50
Basalt Plains mouse *Pseudomys* sp.	pre-1850	<100

Sources: Baynes (1987), Burbidge & McKenzie (1989), Dickman (1993b). The white-footed rabbit-rat possibly persisted until 1875 or even later, but evidence is circumstantial (Dickman et al. 1993).

century occurred, several lines of evidence further implicate cats as the causal factor. First, with the likely exception of the unnamed potoroid, all species that had disappeared from the Australian mainland by the 1850s weighed 200 g or less (see Table 1), and hence fell within the size range of prey most preferred by feral cats. Regional declines also were mostly of small species (Dickman et al. 1993). Second, the habitats occupied by most of the now-extinct species were open plains, grasslands or woodlands, which would have provided little shelter from visually-hunting predators. Third, several species probably had behaviours that would have rendered them conspicuous to foraging cats, such as saltatory locomotion (hopping-mice) and ground foraging and nesting (passerines and other small birds). Finally, because extinctions occurring in the first half of the nineteenth century preceded the introduction of other exotic species such as foxes and rabbits, as well as broadscale changes in land use, cats remain the most obvious causative agents for the demise of many native species (Dickman 1993a, Smith & Quin 1996). Counter evidence for an early impact of cats is that cat populations early last century may have been small or localised; this prevents unequivocal conclusions from being drawn.

Further evidence for major cat-impacts in Australia derives from changes in the composition of island faunas after the introduction of cats. Three case studies, in particular, deserve attention. The first case study involves the loss of brush-tailed bettongs *Bettongia penicillata* from St Francis Island (809 ha), South Australia. When this island was first settled in the 1860s bettongs were reported to be 'swarming' (Jones 1924), and cats were introduced to control bettong damage to the settlers' gardens. Along with clearance of much of the original vegetation (Robinson & Smyth 1976), cats almost certainly contributed to the demise of the bettongs in the early 1900s. In the second case study, Burbidge (1971) implicated cats in the losses of two species of marsupials and up to six species of birds from Hermite Island (1,010 ha), Western Australia. Cats were introduced sometime prior to 1912. One of the marsupials and four of the bird species were last recorded in this year or slightly earlier, the second marsupial survived beyond 1912, and the remaining two species of birds until 1950 (Burbidge 1971). Finally, at least nine species of native mammals have disappeared from Dirk Hartog Island (54,360 ha), Western Australia, probably following liberation of cats there around the turn of the century (Burbidge & George 1978). Impacts on other native animals on this island are unclear.

As with the historical evidence for cat-impacts on the mainland of Australia, evidence for impacts on islands is strong but not certain. In the case studies described above and in further examples noted elsewhere (Dickman 1996), other factors that could decimate native faunas were introduced to islands along with cats. Vegetation changes accompanied settlement on Dirk Hartog and St Francis Islands, presumably reducing the availability of suitable habitat and perhaps also providing more open hunting areas for cats. Ship rats were introduced to both St Francis and Hermite Islands, sheep, goats and house mice to Dirk Hartog. Despite these complications, feral cats remain implicated in the island extinctions. Small species disappeared quickly after the introduction of cats, and islands that have been subjected to human disturbance but not invasion by cats have usually maintained their original faunas (e.g. Ride et al. 1962). The persistence of some apparently susceptible native species on other islands with cats, such as Tasmania, is ostensibly surprising. However, coexistence may be possible if refuge habitats are available, such as rock piles or dense vegetation (Burbidge & McKenzie 1989, Dickman 1993a, 1996).

The final category of evidence for cat-impacts is provided by local management attempts to recover native species. These attempts can be divided into two types. First, many native species have been reintroduced to parts of their geographical ranges from which they had become locally extinct. Many of these programs have failed because translocation sites have not been cleared of predators, and reintroduced individuals have fallen prey to cats (see Serena 1995 and Dickman 1996 for reviews). In a reintroduction involving the rufous hare-wallaby *Lagorchestes hirsutus*, hare-wallabies persisted in the presence of cats for several weeks to many months before being killed, probably by one or two cats that achieved a first kill by chance and then hunted hare-wallabies in an efficient, selective manner (Gibson et al. 1994). Second, recovery of native species has been attempted by controlling or excluding cats from fenced areas. In four studies where effective control was achieved, seven native species of birds increased in population size and none declined (Dickman 1996). Problems with interpreting the results of most of the management programs include lack of controls and replication, as well as simultaneous control of cats and other threat factors. Nonetheless, taken in their entirety, these studies provide some of the strongest direct evidence for cat-impact that is available.

Competition

Competitive interactions between feral cats and native animals have not been demonstrated, although several studies have proposed that they should occur (e.g. Caughley 1980, Cross 1990). Among native mammals, only the larger quolls *Dasyurus geoffroii* and *D. maculatus* are potential competitors. Both eat vertebrates of similar size to those taken by feral cats, probably have similar den requirements, and occur with cats throughout their geographical ranges (Serena et al. 1991, Dickman & Read

1992). Among native birds, owls and letter-winged kites *Elanus scriptus* could potentially compete for food. Such competition has been suggested to occur between boobook owls *Ninox novaeseelandiae undulata* and cats on Norfolk Island (Smithers & Disney 1969), but this remains speculative. Clearly, much potential exists for feral cats to impact competitively on native fauna, most likely in a minor way, but critical evidence is wanting.

Disease

Coincidence of disease and parasitic organisms in cats and native fauna is relatively small (Moodie 1995, Dickman 1996), but minor impact on native species remains a possibility. The cat and related felids are the only definitive hosts for the protozoan parasite *Toxoplasma gondii*, which causes the disease toxoplasmosis. This disease can cause blindness, poor coordination and often sudden death in native mammals and birds, and has contributed to the decline of a remnant, urban population of the eastern barred bandicoot *Perameles gunnii* in Victoria (Lenghaus et al. 1990). A second parasite, the pseudophyllidean tapeworm *Spirometra erinacei*, is carried by all species of introduced carnivores in Australia but is especially prevalent in feral cats. The second intermediate stage of the parasite, the plerocercoid, causes the condition sparganosis in a wide range of vertebrates, and may result in muscular haemorrhage, damage to soft tissues, and eventually death. The impact of sparganosis, at the population level, is not known for any native species.

Red fox *Vulpes vulpes*

Introduction and establishment

The first successful releases of the red fox were made in southern Victoria, probably in 1871 (Rolls 1969). The species reached South Australia by 1888, New South Wales by 1893, and Queensland and Western Australia in the early twentieth century (see Fig. 1B). Spread was particularly rapid, up to 160 km per year, in southern coastal and subcoastal areas, but slower in arid Australia and in the tropical north. The early spread and establishment of foxes followed the spread of rabbits, but after a lag of several years (Long 1988). There is some evidence that the rate of spread of foxes was increased by human assistance, especially in southern parts of the present range (Saunders et al. 1995). Occasional new records have been obtained in northwestern Australia as recently as the 1960s and in parts of central Australia in the early 1990s (Long 1988, pers. obs.). These may indicate that invasion is still continuing slowly, or that occupation of arid and northern regions is ephemeral and dependent on seasonal conditions. Foxes have not established in Tasmania, although they occur on at least 18 other islands offshore (Dickman 1992a). Population densities range from 0.2 - 7.2/km^2 in timbered and temperate grazing country, and up to 12/km^2 in suburban Melbourne (Saunders et al. 1995).

Diet

Foxes are capable of taking a very broad range of prey, from carrion and other scavenged material to vertebrates ranging in size from tiny skinks (<2 g) to wallabies (15,000 g). Invertebrates, berries and other vegetative material may be taken predominantly during summer, and mammals, especially rabbits, at other times (Croft & Hone 1978, *cf.* Catling 1988). The fox is usually considered to be an opportunistic predator and scavenger, but selectivity for particular species or components of prey populations has also been demonstrated (Green & Osborne 1981, Dickman 1988a). Sheep make up a consistent and often large proportion of the diet in pastoral areas; predation on lambs may be serious, but much flesh probably is taken as carrion (Saunders et al. 1995).

Impact

Foxes have been linked to major regional declines of medium-sized mammals and birds in Australia, and to major local declines of chelid tortoises (Thompson 1983), with virtually all evidence pointing to impact from direct predation. There is little evidence of significant competitive or disease impacts on any native species (*cf.* Morris 1992), although foxes carry *Spirometra erinacei* (Ryan 1976) and hence may contribute to the maintenance of sparganosis in native populations. Foxes are also vectors of mites *Sarcoptes scabei* that cause sarcoptic mange. This disease has the potential to impact on native species such as wombats (Cross 1990). Unlike feral cats, foxes have some resource value. In the early-mid 1980s over 100,000 pelts were exported each year, with unit values ranging from Aust$10 to over $20 (Ramsay 1994). In the late 1980s and early 1990s, however, exports and unit values have fallen dramatically.

Predation

Because of the relatively recent introduction of foxes to Australia, immediate apparent impacts were chronicled extensively by naturalists, newspaper correspondents and others. In southwest Western Australia, for example, major regional declines of the brush-tailed bettong, quokka *Setonix brachyurus*, numbat *Myrmecobius fasciatus*, and the possums *Pseudocheirus occidentalis* and *Trichosurus vulpecula* occurred in the 1930s to the mid 1940s, some years after the first appearance of rabbits but coinciding with the arrival and establishment of fox populations

(White 1952, Christensen 1980, Dickman 1988b, Stodart & Parer 1988). Losses of other species have occurred more recently in south and east Kimberley following invasion by foxes, but not in northwest Kimberley where foxes have not yet penetrated (King & Smith 1985). In central Australia, losses of small and medium-sized mammals occurred over a period of 25 years as fox populations became established (Finlayson 1961). Dramatic further declines of medium-sized mammals (450 - 5,000 g) occurred in the southwest of Western Australia as recently as the 1970s, following sharp increases in fox abundance (Christensen 1980). Prior to this, fox populations had apparently been suppressed by ingesting the carcasses of poisoned rabbits; rabbit control, using large quantities of 1080 poison, was phased out from the late 1960s following successful establishment of myxomatosis as a mortality agent (King et al. 1981). According to Christensen (1980), losses of native species occurred only in areas with an open understorey, with survivors persisting in patches of dense vegetation.

More critical insight into fox impacts on native fauna has been obtained from reintroduction programs and removal experiments. In a review of attempts to reintroduce medium-sized macropods, Short et al. (1992) noted that only 8% of attempts succeeded where predators, especially foxes, were present, whereas 82% succeeded where they were absent. Foxes were implicated in the demise of macropods reintroduced to 7 of 10 mainland sites, with translocated individuals lasting <4 months to >10 years. Foxes have been confirmed, using radiotelemetry, as the primary cause of failure of reintroductions of several further species of medium-sized mammals and birds, including common ringtail possums *Pseudocheirus peregrinus*, common brushtail possums *Trichosurus vulpecula* and malleefowl *Leipoa ocellata* (Priddel & Wheeler 1994, Serena 1995). There is some evidence that rate of predation by foxes is slowed if reintroductions take place into structurally complex habitats such as rock outcrops (Short et al. 1992), and increased in open or fragmented habitats where shelter is depleted (Priddel & Wheeler 1994).

The strongest evidence for fox impact on native fauna comes from controlled and replicated fox removal or reduction experiments. The first, and most extensive of these (Kinnear et al. 1988), showed that black-footed rock-wallabies *Petrogale lateralis* increased in abundance at fox removal sites and also occupied a broader range of habitats. Population increase was 4-5 fold over eight years (Fig. 2). Similar increases in numbers and range of habitats used have been documented recently for red-necked wallabies *Macropus rufogriseus* and eastern grey kangaroos *M. giganteus* (P. Banks, pers. comm.). In further, unreplicated experiments, Rothschild's rock-wallaby *Petrogale rothschildi* increased nearly 30 fold following fox control on an island in the Dampier Archipelago (J.E. Kinnear, in Saunders et al. 1995), while brushtail possums, brush-tailed bettongs, tammar wallabies *Macropus eugenii* and chuditch *Dasyurus geoffroii* increased following fox control in southwest Western Australia (Saunders et al. 1995). At one of these latter sites, Dryandra State Forest, numbats increased some 50 fold in relative abundance following partial and then complete removal of foxes from the forest area (Friend & Thomas 1995). Interestingly, no experimental study has reported any changes in numbers of small mammals (<200 g), birds or other fauna following fox removal; in one study no change in small mammal abundance was found (P. Banks, pers. comm.).

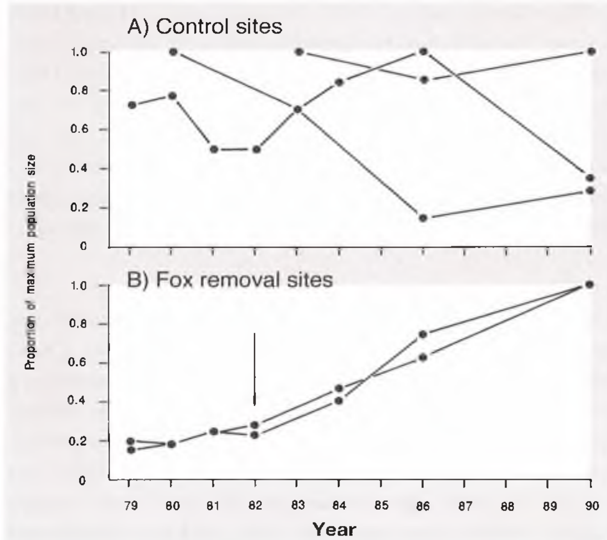

Figure 2. Effects of fox removal on populations of rock-wallabies *Petrogale lateralis* in Western Australia from 1979-1990. (A) gives the proportional population size at control sites (N = 3), and (B) at fox removal sites (N = 2); the arrow indicates when removals began. Numbers of wallabies at each site are shown as a proportion of the maximum obtained in yearly census estimates, to adjust for between-site differences in abundance. Redrawn from Kinnear et al. (1988) and Saunders et al. (1995).

Dingo *Canis lupus dingo*

Introduction and establishment

The dingo was introduced to Australia 3,500 - 4,000 years ago by Asian seafarers. It spread rapidly and completely across the mainland, probably assisted by Aborigines (Corbett 1995). At least 14 offshore islands are occupied by dingoes (Dickman 1992a), but some of the largest islands, including Tasmania, remain dingo-free (see Fig. 1C). Densities do not usually exceed 1/km² even in favoured forest regions of eastern Australia, and are close to zero in sheep farming areas of the southeast and southwest due to exclusion by a dingo fence and intensive human persecution (Newsome & Coman 1989).

Diet

Prey range from invertebrates and vegetation to wild horses and buffalo. However, mammals comprise the major part of the diet in all regions where dingoes have been studied, and some 70% of these represent species weighing 500 g or more (Corbett 1995). Dietary variation between regions reflects prey availability: native rats and geese are taken in tropical northern Australia, wallabies are taken predominantly in forested regions, while rabbits, large kangaroos and cattle are taken in arid and semiarid areas. Dingoes hunt solitarily for small prey but form packs to bring down larger species such as kangaroos (Thomson 1992).

Impact

Dingoes probably had major impacts on native animals soon after their introduction to Australia, and exert continuing effects. Like cats and foxes, impact is mediated primarily via direct predation. However, unlike the smaller carnivores, dingoes may impact positively as well as negatively on native animals by keeping fox and cat populations in check.

Predation

Evidence for predatory impact by dingoes is historical and circumstantial rather than experimental, but nonetheless plausible. Thus, Corbett (1995) incriminated dingoes in the demise of up to 10 medium-sized species of mammals in central Australia after 1930, arguing that predation increased following expansion of the pastoral industry and the establishment of rabbits. The resulting depletion of pastures would have exposed shelter-dependent native mammals, increasing their risk of predation. According to Corbett (1995) these species would have been most at risk from dingoes, especially during drought, when populations of other carnivores crash.

Most other studies suggest that dingoes have major impacts on native species >15,000 g. For example, Caughley et al. (1980) showed that red kangaroos *Macropus rufus* and emus *Dromaius novaehollandiae* increased dramatically in abundance in northwestern New South Wales following exclusion of dingoes by a boundary fence. Densities of both species in the dingo-free region remain higher (emus by 5-26 fold, kangaroos by 16-166 fold) than in areas north and west of the fence where dingoes still occur. In northeastern New South Wales increased abundance of dingoes is associated with reduced survival of young eastern grey kangaroos and swamp wallabies *Wallabia bicolor* (Robertshaw & Harden 1986, Jarman et al. 1987). Following drought or disturbance such as fire, when populations of native prey species are depleted, dingoes can suppress prey recovery or even eliminate local populations of large macropods provided that alternative prey are available (Newsome et al. 1983).

Dingoes usually exhibit an inverse numerical relationship with foxes and perhaps with feral cats (Newsome & Coman 1989, Catling & Burt 1994), fostering belief that dingoes directly suppress populations of the smaller carnivores. Foxes are most abundant in dingo-free regions in southeastern and southwestern Australia, and increase sharply in density inside the dingo-exclusion fence in New South Wales (Wilson et al. 1992). Local declines in dingo numbers may also allow dramatic increases in cat populations (Pettigrew 1993). Suppression of foxes and cats by dingoes could occur by competition for food but more likely by direct predation; dingoes include both species of smaller predators in their diet in all regions where they co-occur (Corbett 1995). Whatever the process, if suppression of foxes and feral cats by dingoes is effective and sustained in any area, the net impact of dingoes on small and perhaps medium-sized animals could be positive. This intriguing possibility requires testing.

Competition

There is no clear evidence that dingoes compete with native animals for any resources. However, there is speculation that dingoes outcompeted Tasmanian devils *Sarcophilus harrisii* and thylacines *Thylacinus cynocephalus* on the mainland of Australia soon after their introduction. Both marsupials disappeared some 500 - 3,000 years ago from the mainland, surviving only in Tasmania which is dingo-free (Corbett 1995).

Disease

Dingoes carry the hydatid tapeworm *Echinococcus granulosus*, which may kill wallabies in its encysted intermediate form. They also carry *Spirometra erinacei* and mange (Newsome & Coman 1989). As with the red fox, however, there is no evidence that these parasites cause population-level effects on native animals.

Impacts of predators in human-modified environments

Foxes and cats have been shown to impact negatively on native animals in Australia, whereas dingoes may have positive as well as negative effects. Some evidence suggests that these impacts are exacerbated by human activity, especially by removal or fragmentation of native vegetation and by introduction of alternative prey such as the rabbit.

Interactions with habitat fragmentation

In eastern and western Australia forested environments have been extensively cleared for agriculture and suburban growth, dissected by transport links and modified for production forestry (Lunney 1991). These practices result in fragmentation of natural vegetation across the regional landscape, and declines in abundance and distribution of species unable to exploit cleared land. In habitats subjected to intensive logging or control burning, simplification of vegetation structure may lead to further reductions in species occurrence or to restriction of individuals to remnants with dense cover. Such fragmentation effects have been well documented for terrestrial vertebrates in agricultural areas of eastern and western Australia (Goldney & Bowie 1990, Smith et al. in press), and in production forests (Recher et al. 1987). Recent evidence suggests that fox abundance increases in forests close to disturbed land (Catling & Burt 1995). Where introduced predators persist in both remnant vegetation and modified surrounding land, predator-prey linkages are decoupled and impacts of predators are likely to be severe. The effects of enhanced predation have been documented for fragmented populations of rock-wallabies (Kinnear et al. 1988), brush-tailed bettongs (Christensen 1980) and malleefowl (Priddel & Wheeler 1994) among others.

In arid environments in central Australia where the original vegetation is often open, predator impacts are likely to be enhanced more by temporal than spatial habitat fragmentation. During droughts many native species appear confined to oases or other rich, dependable patches in the landscape (Morton 1990). If introduced predators are better able than native species to move into such patches during drought, *per capita* predation at oases is likely to be temporarily increased. Drought-induced dispersal movements of >100 km have been recorded for both feral cats and dingoes (Pettigrew 1993, Corbett 1995), greatly exceeding those recorded for small and medium-sized native mammals (Dickman et al. 1995). Temporal fragmentation has been exacerbated also by a recent shift in the fire regime in much of central Australia. This shift, from small-scale mosaic burning carried out by Aboriginal people to less frequent but intense broadscale burning following European settlement, has probably resulted in reduced availability of dependable resource patches across the landscape (Morton 1990). Predation at remaining patches could be expected to be intense.

Interactions with alternative prey

Rabbits constitute an important part of the diet of all three species of predators in most areas where they occur (Corbett 1995, Saunders et al. 1995, Dickman 1996). Their importance lies principally in the fact that they support large populations of predators. In temperate Australia rabbits often occur within and outside fragments of remnant vegetation, thus supporting large predator populations on a regional scale and perhaps contributing to suppression of patchily distributed populations of native species (Saunders et al. 1995). In arid Australia intense predation on native species can follow drought-induced collapse of rabbit populations (Newsome et al. 1989), with all three predator species switching their diets from rabbits to native prey. Such predation is likely to have greatest impact at oases if rabbits have depleted vegetation cover (Morton 1990). Cattle carcasses can also support dingoes and sometimes cats through droughts, perhaps providing a similar subsidy effect to that of rabbits in temperate regions.

Conclusions

Much historical and circumstantial evidence suggests that feral cats, foxes and dingoes have had negative, population-level impacts on native vertebrates in Australia. Observational studies infer continuing impacts on native species, and suggest further that impacts may be most intense in modified environments and in the presence of abundant, alternative prey. Research is needed urgently to confirm these inferences, and to quantify levels of impact in different environments and on different components of the native fauna. The most appropriate research entails experimental manipulation of predator abundance, together with monitoring of responses of prey species, and is recommended here as a priority.

Acknowledgements - this paper benefited from discussions with participants at the workshop on exotic wildlife in Ammarnäs. I thank M. Dunier, H. Hokkanen and the OECD Directorate for Food, Agriculture and Fisheries for making possible my attendance at the workshop, and K. Danell, G. Sjöberg and K. Sjöberg for their hospitality. I also thank P. Banks, P. Mahon, C. McKechnie and K. Sjöberg for their comments on earlier versions of the manuscript, and P. Nummi for editorial assistance.

References

Amarasekare, P. 1994: Ecology of introduced small mammals on western Mauna Kea, Hawaii. - Journal of Mammalogy 75: 24-38.

Atkinson, I.A.E. 1985: The spread of commensal species of Rattus to oceanic islands and their effects on island avifaunas. - In: Moors, P.J. (Ed.); Conservation of island birds. International Council for Bird Preservation, Cambridge, pp. 35-81.

Atkinson, I. 1989: Introduced animals and extinctions. - In: Western, D. & Pearl, M.C. (Eds.); Conservation for the twenty-first century. Oxford University Press, Oxford, pp. 54-75.

Baerl, C.D.N., Dorit, R., Greenwood, P.H., Freyer, G., Hughes, N., Jackson, P.B.N., Kawanabe, H., Lowe-McConnell, R.H., Nagoshi, M., Ribbink, A.J., Trewavas, E., Witte, F. & Yamaoka, K. 1985: Destruction of fisheries in Africa's lakes. - Nature 315: 19-20.

Baldwin, J.A. 1980: The domestic cat, Felis catus L., in the Pacific islands. - Carnivore Genetics Newsletter 4: 57-66.
Baynes, A. 1987: The original mammal fauna of the Nullarbor and southern peripheral regions: evidence from skeletal remains in superficial cave deposits. - In: McKenzie, N.L. & Robinson, A.C. (Eds.); A biological survey of the Nullarbor region South and Western Australia in 1984. South Australian Department of Environment and Planning, Adelaide, Western Australian Department of Conservation and Land Management, Perth, and Australian National Parks and Wildlife Service, Canberra, pp. 139-152.
Brockie, R.E., Loope, L.L., Usher, M.B. & Hamann, O. 1988: Biological invasions of island nature reserves. - Biological Conservation 44: 9-36.
Burbidge, A.A. 1971: The fauna and flora of the Monte Bello Islands. - Department of Fisheries and Fauna Western Australia, Report No. 9: 1-19.
Burbidge, A.A. & George, A.S. 1978: The flora and fauna of Dirk Hartog Island, Western Australia. - Journal of the Royal Society of Western Australia 60: 71-90.
Burbidge, A.A., Johnson, K.A., Fuller, P.J. & Southgate, R.I. 1988: Aboriginal knowledge of the mammals of the central deserts of Australia. - Australian Wildlife Research 15: 9-39.
Burbidge, A.A. & McKenzie, N.L. 1989: Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. - Biological Conservation 50: 143-198.
Catling, P.C. 1988: Similarities and contrasts in the diets of foxes, Vulpes vulpes, and cats, Felis catus, relative to fluctuating prey populations and drought. - Australian Wildlife Research 15: 307-317.
Catling, P.C. & Burt, R.J. 1994: Studies of the ground-dwelling mammals of eucalypt forests in south-eastern New South Wales: the species, their abundance and distribution. - Wildlife Research 21: 219-239.
Catling, P.C. & Burt, R.J. 1995: Why are red foxes absent from some eucalypt forests in eastern New South Wales? - Wildlife Research 22: 535-546.
Caughley, G., Grigg, G.C., Caughley, J. & Hill, G.J.E. 1980: Does dingo predation control the densities of kangaroos and emus? - Australian Wildlife Research 7: 1-12.
Caughley, J. 1980: Native quolls and tiger quolls. - In: Haigh, C. (Ed.); Endangered animals of New South Wales. NSW National Parks and Wildlife Service, Sydney, pp. 45-48.
Christensen, P.E.S. 1980: A sad day for native fauna. - Forest Focus 23: 3-12.
Corbett, L.K. 1995: The dingo in Australia and Asia. - University of New South Wales Press, Sydney, 200 pp.
Covacevich, J. & Archer, M. 1975: The distribution of the cane toad Bufo marinus in Australia and its effects on indigenous vertebrates. - Memoirs of the Queensland Museum 17: 305-310.
Croft, J.D. & Hone, L.J. 1978: The stomach contents of foxes, Vulpes vulpes, collected in New South Wales. - Australian Wildlife Research 5: 85-92.
Cross, J. 1990: The feral cat - justification for its control. - Thesis, Charles Sturt University, Riverina, 83 pp.
Darwin, C.R. 1859: The origin of species by means of natural selection or the preservation of favoured races in the struggle for life. - J. Murray, London, 692 pp.
Diamond, A.W. 1987: Studies of Mascarene Island birds. - Cambridge University Press, Cambridge, 458 pp.
Dickman, C.R. 1988a: Detection of physical contact interactions among free-living mammals. - Journal of Mammalogy 69: 865-868.
Dickman, C.R. 1988b: The quokka Setonyx brachyurus. - Rottnest Island Authority, Perth, 8 pp.
Dickman, C.R. 1992a: Conservation of mammals in the Australasian region: the importance of islands. - In: Coles, J.N. & Drew, J.M. (Eds.); Australia and the global environmental crisis. Academy Press, Canberra, pp. 175-214.
Dickman, C.R. 1992b: Commensal and mutualistic interactions among terrestrial vertebrates. - Trends in Ecology and Evolution 7: 194-197.
Dickman, C.R. 1993a: Raiders of the last ark: cats in island Australia. - Australian Natural History 24: 44-52.
Dickman, C.R. 1993b: The biology and management of native rodents of the arid zone in New South Wales. - NSW National Parks and Wildlife Service, Sydney, 149 pp.
Dickman, C.R. 1996: Overview of the impact of feral cats on Australian native fauna. - Australian Nature Conservation Agency, Canberra, 92 pp.
Dickman, C.R., Predavec, M. & Downey, F.J. 1995: Long-range movements of small mammals in arid Australia: implications for land management. - Journal of Arid Environments 31: 441-452.
Dickman, C.R., Pressey, R.L., Lim, L. & Parnaby, H.E. 1993: Mammals of particular conservation concern in the Western Division of New South Wales. - Biological Conservation 65: 219-248.
Dickman, C.R. & Read, D.G. 1992: The biology and management of dasyurids of the arid zone in New South Wales. - NSW National Parks and Wildlife Service, Sydney, 112 pp.
Disney, H.J. de S. & Smithers, C.N. 1972: The distribution of terrestrial and freshwater birds on Lord Howe Island, in comparison with Norfolk Island. - Australian Zoologist 17: 1-11.
Ebenhard, T. 1988: Introduced birds and mammals and their ecological effects. - Viltrevy 13: 1-107.
Faragher, R.A. & Harris, J.H. 1994: The historical and current status of freshwater fish in New South Wales. - Australian Zoologist 29: 166-176.
Finlayson, H.H. 1943: The red centre. - Angus & Robertson, Sydney, 153 pp.
Finlayson, H.H. 1961: On central Australian mammals, Part IV. The distribution and status of central Australian species. - Records of the South Australian Museum 41: 141-191.
Fitzgerald, B.M., Karl, B.J. & Veitch, C.R. 1991: The diet of feral cats (Felis catus) on Raoul Island, Kermadec group. - New Zealand Journal of Ecology 15: 123-129.
Friend, J.A. & Thomas, N.D. 1995: Reintroduction and the numbat recovery programme. - In: Serena, M. (Ed.); Reintroduction biology of Australian and New Zealand fauna. Surrey Beatty & Sons, Sydney, pp. 189-198.
Gibson, D.F., Lundie-Jenkins, G., Langford, D.G., Cole, J.R., Clarke, D.E. & Johnson, K.A. 1994: Predation by feral cats, Felis catus, on the rufous hare-wallaby, Lagorchestes hirsutus, in the Tanami Desert. - Australian Mammalogy 17: 103-107.
Goldney, D.C. & Bowie, I.J.S. 1990: Some management implications for the conservation of vegetation remnants and associated fauna in the central western region of New South Wales. - Proceedings of the Ecological Society of Australia 16: 427-440.
Green, K. & Osborne, W.S. 1981: The diet of foxes, Vulpes vulpes (L.), in relation to abundance of prey above the winter snowline in New South Wales. - Australian Wildlife Research 8: 349-360.
Grey, G. 1841: Journals of two expeditions of discovery in northwest and western Australia, during the years 1837, 38 and 39, under the authority of Her Majesty's government. - T. & W. Boone, London. Vol. I, 412 pp. Vol. II, 482 pp.

Hayde, K.A. 1992: Ecology of the feral cat Felis catus on Great Dog Island. - Thesis, University of Tasmania, Hobart, 120 pp.

Jarman, P. 1986: The red fox - an exotic large predator. - In: Kitching, R.L. (Ed.); The ecology of exotic animals and plants. John Wiley & Sons, Brisbane, pp. 43-61.

Jarman, P.J., Johnson, C.N., Southwell, C.J. & Stuart-Dick, R. 1987: Macropod studies at Wallaby Creek 1. The area and animals. - Australian Wildlife Research 14: 1-14.

Jones, F.W. 1924: The mammals of South Australia. Part II. The bandicoots and the herbivorous marsupials. - Government Printer, Adelaide, 458 pp.

King, D.R., Oliver, A.J. & Mead, R.J. 1981: Bettongia and fluoroacetate: a role for 1080 in fauna management. - Australian Wildlife Research 8: 529-536.

King, D.R. & Smith, L.A. 1985: The distribution of the European red fox (Vulpes vulpes) in Western Australia. - Records of the Western Australian Museum 12: 197-205.

Kinnear, J.E., Onus, M.L. & Bromilow, R.N. 1988: Fox control and rock-wallaby population dynamics. - Australian Wildlife Research 15: 435-450.

Lenghaus, C., Obendorf, D.L. & Wright, F.H. 1990: Veterinary aspects of Perameles gunnii biology with special reference to species conservation.- In: Clark, T.W. & Seebeck, J.H. (Eds.); Management and conservation of small populations. Chicago Zoological Society, Brookfield, pp. 89-108.

Long, J.L. 1988: Introduced birds and mammals in Western Australia. - Agriculture Protection Board of Western Australia, Perth, 56 pp.

Lunney, D. (Ed.) 1991: Conservation of Australia's forest fauna. Royal Zoological Society of New South Wales, Sydney, 418 pp.

Moodie, E. 1995: The potential for biological control of feral cats in Australia. - Australian Nature Conservation Agency, Canberra, 159 pp.

Morris, K. 1992: Return of the chuditch. - Landscope 8: 11-15.

Morton, S.R. 1990: The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. - Proceedings of the Ecological Society of Australia 16: 201-213.

Newsome, A.E., Catling, P.C. & Corbett, L.K. 1983: The feeding ecology of the dingo II. Dietary and numerical relationship with fluctuating prey populations in south-eastern Australia. - Australian Journal of Ecology 8: 345-366.

Newsome, A.E. & Coman, B.J. 1989: Canidae. - In: Walton, D.W. & Richardson, B.J. (Eds.); Fauna of Australia, volume 1B, Mammalia. Australian Government Publishing Service, Canberra, pp. 993-1005.

Newsome, A.E., Parer, I. & Catling, P.C. 1989: Prolonged prey suppression by carnivores-predator-removal experiments. - Oecologia 78: 458-467.

Pavlov, P.M. 1995: Pig Sus scrofa. - In: Strahan, R. (Ed.); The mammals of Australia. Reed Books, Sydney, pp. 715-717.

Pettigrew, J.D. 1993: A burst of feral cats in the Diamantina - a lesson for the management of pest species? - In: Siepen, G. & Owens, C. (Eds.); Cat management workshop proceedings - 1993. Queensland Department of Environment and Heritage, Brisbane, pp. 25-32.

Pollard, D.A. (Ed.) 1989: Introduced and translocated fishes and their ecological effects. - Bureau of Rural Resources, Canberra, 181 pp.

Priddel, D. & Wheeler, R. 1994: Mortality of captive-raised malleefowl, Leipoa ocellata, released into a mallee remnant within the wheat-belt of New South Wales. - Wildlife Research 21: 543-552.

Ramsay, B.J. 1994: Commercial use of wild animals in Australia. - Australian Government Publishing Service, Canberra, 185 pp.

Recher, H.F., Shields, J., Kavanagh, R. & Webb, G. 1987: Retaining remnant mature forest for nature conservation at Eden, New South Wales: a review of theory and practice. - In: Saunders, D.A., Arnold, G.W., Burbidge, A.A. & Hopkins, A.J.M. (Eds.); Nature conservation: The role of remnants of native vegetation. Surrey Beatty & Sons, Sydney, pp. 177-194.

Ride, W.D.L., Mees, G.F., Douglas, A.M., Royce, R.D. & Tyndale-Biscoe, C.H. 1962: The results of an expedition to Bernier and Dorre Islands Shark Bay, Western Australia, in July, 1959. - Government Printer, Perth, 131 pp.

Robertshaw, J.D. & Harden, R.H. 1986: The ecology of the dingo in north-eastern New South Wales IV. Prey selection by dingoes, and its effect on the major prey species, the swamp wallaby, Wallabia bicolor (Desmarest). - Australian Wildlife Research 13: 141-163.

Robinson, A.C. & Smyth, M.E.B. 1976: The vertebrate fauna of Nuyts Archipelago, South Australia. - Transactions of the Royal Society of South Australia 100: 171-176.

Rolls, E.C. 1969: They all ran wild. - Angus & Robertson, Sydney, 546 pp.

Ryan, G.E. 1976: Helminth parasites of the fox (Vulpes vulpes) in New South Wales. - Australian Veterinary Journal 52: 126-131.

Saunders, G., Coman, B., Kinnear, J. & Braysher, M. 1995: Managing vertebrate pests: foxes. - Australian Government Publishing Service, Canberra, 141 pp.

Savidge, J.A. 1987: Extinction of an island forest avifauna by an introduced snake. - Ecology 68: 660-668.

Serena, M. (Ed.) 1995: Reintroduction biology of Australian and New Zealand fauna.- Surrey Beatty & Sons, Sydney, 264 pp.

Serena, M., Soderquist, T.R. & Morris, K. 1991: The chuditch (Dasyurus geoffroii). - Department of Conservation and Land Management, Perth, 32 pp.

Short, J., Bradshaw, S.D., Giles, J., Prince, R.I.T. & Wilson, G.R. 1992: Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia - a review. - Biological Conservation 62: 189-204.

Smith, A.P. & Quin, D.G. 1996: Patterns and causes of extinction and decline in Australian conilurine rodents. - Biological Conservation 77: 243-267.

Smith, G.T., Leone, J. & Dickman, C.R. in press: Small terrestrial vertebrate communities in remnant vegetation in the central wheatbelt of Western Australia. - Western Australian Naturalist.

Smith, P.J., Pressey, R.L. & Smith, J.E. 1994: Birds of particular conservation concern in the Western Division of New South Wales. - Biological Conservation 69: 315-338.

Smithers, C.N. & Disney, H.J. de S. 1969: The distribution of terrestrial and freshwater birds on Norfolk Island. - Australian Zoologist 15: 127-140.

Spiller, D.A. & Schoener, T.W. 1994: Effects of top and intermediate predators in a terrestrial food web. - Ecology 75: 182-196.

Stodart, E. & Parer, I. 1988: Colonisation of Australia by the rabbit Oryctolagus cuniculus (L.). - Commonwealth Scientific and Industrial Research Organisation, Canberra, 21 pp.

Stone, P.A., Snell, H.L. & Snell, H.M. 1994: Behavioral diversity as biological diversity: introduced cats and lava lizard wariness. - Conservation Biology 8: 569-573.

Sturt, C. 1833: Two expeditions into the interior of southern Australia, during the years 1828, 1829, 1830, and 1831: with observations on the soil, climate, and general resources of the colony of New South Wales. - Smith, Elder and Co., London, Vol. I, 219 pp. Vol. II, 271 pp.

Thompson, M.B. 1983: Populations of the Murray River tortoise, Emydura (Chelodina): the effect of egg predation by the red fox, Vulpes vulpes. - Australian Wildlife Research 10: 363-371.

Thomson, P.C. 1992: The behavioural ecology of dingoes in north-western Australia. III. Hunting and feeding behaviour, and diet. - Wildlife Research 19: 531-541.

Tidemann, C.R., Yorkston, H.D. & Russock, A.J. 1994: The diet of cats, Felis catus, on Christmas Island, Indian Ocean. - Wildlife Research 21: 279-286.

Watts, C.H.S. & Aslin, H.J. 1981: The rodents of Australia. - Angus & Robertson, Sydney, 321 pp.

White, S.R. 1952: The occurrence of the quokka in the south-west. - Western Australian Naturalist 3: 101-103.

Wiley, J.W. 1985: The Puerto Rican parrot and competition for its nest sites. - In: Moors, P.J. (Ed.); Conservation of island birds. - International Council for Bird Preservation, Cambridge, pp. 213-223.

Wilson, G., Dexter, N., O'Brien, P. & Bomford, M. 1992: Pest animals in Australia. A survey of introduced wild mammals. - Bureau of Rural Resources and Kangaroo Press, Kenthurst, 64 pp.