Influence of Fragmentation and Disturbance on the Potential Impact of Feral Predators on Native Fauna in Australian Forest Ecosystems

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Abstract

We review current knowledge of the diet and predator-prey relationships of the feral cat (Felis catus), fox (Vulpes vulpes) and dingo (Canis familiaris dingo) (including wild dogs), and consider how forest fragmentation by roads may influence the use of native forest ecosystems by these species and the significance of this for native fauna. The cat, fox and dingo are significant predators in Australia that interact with native fauna in various ways, including predation, competition for resources, and transmission of disease. On the basis of current knowledge, it is clear that the nature and impact of predation by the cat, fox and dingo on native fauna are primarily determined by prey availability, although there are exceptions to this rule. Generally, dingoes prey upon large to medium-sized prey species (e.g. wallabies, common wombats and possums), foxes prey upon medium-sized to small prey (e.g. possums and rats) and consume a significant component of scavenged material and vegetation, while cats also prey upon medium-sized to small prey, but may have a greater proportion of reptiles and birds in their diet. The cat is generally considered to be an opportunistic predator and to have contributed to the demise of a number of mammals. The fox is considered more of a threat to small native mammals than is the cat and it has been asserted that all species of mammals that fall within the critical weight range (CWR) of 120-5000 g are at risk of local extinction when the fox is present. The severity of the impact of the dingo upon the native fauna is considered to be minimal, at least in comparison with the impact that the cat and fox can have on populations. The dingo is not considered a threat to CWR mammals in undisturbed environments. The fox, feral cat and dingo are all considered to have the ability to selectively prey upon species and, to some extent, individual sexes and age-classes of a number of larger prey species.

Although many of Australia's forested areas are relatively heavily fragmented by roads, there are no published studies specifically investigating the use of roads by feral predators. Information on the distribution and abundance of foxes, cats and dingoes in these ecosystems, their ecology and their impact on native fauna is particularly limited. Further, the extent to which roads influence the distribution and abundance of these species and the consequences of these for native fauna are poorly known. Given this, we suggest that one of the most important research needs is to establish the relative impact that exotic predators may have on native fauna under varying degrees of road construction within native forests. For example, are areas with and without roads in forests used differently by exotic predators and what is the significance of this in terms of the potential impact on fauna? The extent to which feral predators forage away from roads needs further investigation, as does the rates of predation within edges, because this may have several consequences for the design, location and size of retained strips and wildlife corridors as well as restoration programmes. Further observations on regional differences influencing predator–prey interactions are required, as is research on the potential impacts on native fauna resulting from prey selection in forests subjected to various degrees of fragmentation and modification.

Introduction

The cat (*Felis catus*), fox (*Vulpes vulpes*) and dog (*Canis familiaris*) are important feral predators in Australia that interact with native fauna in various ways, including predation, competition for resources, and transmission of disease. Knowledge of the impact that these interactions have on native wildlife is limited and is obscured by factors such as habitat destruction, fragmentation and altered fire regimes (all of which can adversely affect native species), and the lack of documentation of the status of many native species when Europeans

first arrived. There is a growing body of anecdotal and empirical evidence, however, to indicate that feral predators can have a significant impact upon native fauna at the local, regional and national scale. Terrestrial mammals with an adult body weight between 35 and 5500 g appear to be particularly threatened by feral cats and foxes. Small and medium-sized mammals (termed critical weight range species, or CWR species) constitute the majority of the mammalian fauna that has become extinct or is considered to be rare and endangered with extinction (Burbidge and McKenzie 1989). Although feral predators cannot be identified as solely responsible for the demise of many of these species, there is evidence implicating these feral species, particularly the fox and the feral cat, as significant threats to the survival of remaining populations of rare and endangered native fauna.

Feral predators rely primarily on native fauna for food in forests. Unfortunately, information on the distribution and abundance of foxes, cats and dingoes (*Canis familiaris dingo*) in these ecosystems, their ecology and their impact on native fauna is particularly limited. (The dingo was introduced into Australia some 4000 years ago and has interbred with feral dogs to the extent that it is not practical to distinguish between the two, which are referred to collectively here as dingoes). Further, the extent to which management activities such as road construction influence the distribution and abundance of these species and their potential impact on native fauna is poorly known. In this paper we (i) review current knowledge of the diet and predator–prey relationships of the feral cat, fox and dingo, and (ii) consider how disturbance in the form of road construction may influence the use of native forest ecosystems by these species and the significance of this for native fauna. Our intent is not to present an exhaustive review but rather to indicate what is, and what is not, known and to emphasise some of the major gaps in knowledge that need to be addressed if the management of feral predators in native forests is to have a firmer scientific base.

Diet and Impacts of Feral Predators

Reliable assessment of the impact of feral predators on species and populations of native fauna is not a trivial task. It is necessary to determine whether feral predators suppress populations of native fauna, with the result that the affected species, or populations, are threatened with extinction or are no longer able to perform their biological functions. Dietary information can indicate taxa that are potentially susceptible to predation but may not reflect the true impact that predation has on a species (Newsome 1991; Paton 1993). Establishing the impact of feral predators on species and populations typically requires detailed long-term investigation as there are many (natural and unnatural) factors that can influence population dynamics. Specific studies investigating predator–prey relationships between feral predators and native wildlife in Australia are limited and have been undertaken only recently. The initial impact that exotic predators may have had on the fauna can be considered more generally, however, by assessing the relationship between the arrival of feral predators and the decline and extinction of species locally, regionally and nationally (e.g. Morton 1990; Recher and Lim 1990).

Felis catus

The cat is generally considered to be an opportunistic predator, with the level of predation being partly dependent on the availability and abundance of prey (Coman and Brunner 1972; Jones 1992). Normally, cats appear to prey upon species that are equal in size or smaller than themselves (Kleinman and Eisenberg 1973; Landré 1977; Paton 1993). Thus, any animal less than 3–4 kg in body weight is potential prey. Most prey species, however, usually weigh less than 100 g (Paton 1996).

Cats differ from canids in several ways: (i) they have a partially arboreal habit; (ii) they have excellent night vision, unlike the canids, which rely heavily on their highly developed olfactory senses; (iii) when live prey are available, they do not require water (Jones 1988; Newsome 1991); (iv) they prey more heavily upon birds and reptiles than do the canids (Bayly 1978; Triggs *et al.* 1984; Catling 1988; Lumsden *et al.* 1991), although the avian component of the

diet is still considered to be minimal (Coman 1973, 1991; Jones 1992); and (v) they appear to be more selective in their choice of prey than are canids (Bayly 1978). Unlike canids, cats are generally not scavengers (Bayly 1978; Jones and Coman 1981).

The potential impact that cats can have on wildlife populations can be estimated crudely by calculating the energy requirements of the average adult cat. Adult cats need to consume 5-8% of their body weight per day, which is equivalent to 300 g of flesh (Jones 1977; Paton 1993). The requirements for a female with litter can be 20% of her body weight per day (Jones 1977). Given this, the average 4-kg cat feeding on animals weighing 50 g would need six animals per day to meet its energetic requirements, which is equivalent to 2188 animals per year. However, the reliability of such estimates is uncertain since the entire prey is not always eaten, especially where they are abundant, and the energy requirements of feral cats can be expected to vary considerably depending on the environment. For example, Muir (1982) reported that 500 g of food were commonly found in the stomachs of cats that he examined. The stomach of one cat contained 24 reptiles, two mice, one bird and two grasshoppers. He concluded that 'The effects on the native fauna of even a low cat density with a diet such as this must be formidable' (Muir 1982, p. 8).

Cats are known to prey upon 186 native bird species, 64 species of native mammal, 87 species of reptiles, 10 species of amphibians, and numerous invertebrates (Paton 1993). Although rabbits appear to be a preferred prey item (Bayly 1978; Jones and Coman 1981; Catling 1988), cats are known to consume individuals of 2–3 native animal species per day even where rabbits are abundant (Paton 1993). Where rabbits are often scarce, such as in forest environments, native species such as the ringtail possum (*Pseudocheirus peregrinus*) and the bush rat (*Rattus fuscipes*) can become important prey (Jones and Coman 1981; Triggs *et al.* 1984).

Cats can prey upon mammals that fall within the CWR, and may have contributed, *inter alia*, to the demise of some of these species, such as the broad-faced potoroo (*Potorous platyops*), the desert rat-kangaroo (*Caloprymnus campestris*) and the central hare-wallaby (*Lagorchestes asomatus*), as well as the decline of several bandicoot species and the western quoll (*Dasyurus geoffroii*) (Johnson *et al.* 1989). Cats appear to have been responsible for the extinction of the burrowing bettong (*Bettongia lesueur*) and the banded hare-wallaby (*Lagostrophus fasciatus*) from Dirk Hartog Island, the spectacled hare-wallaby (*Lagorchestes conspicillatus*) from Hermite Island, and the brush-tailed bettong (*Bettongia penicillata*) from St Francis Island (Burbidge 1971; Burbidge and George 1978; Johnson *et al.* 1989; Leader-Williams and Walton 1989; Deeker 1993; Kinnear 1993). All of these species fall within the CWR. However, the cat exists in Tasmania, which is the last stronghold for many CWR species, such as the long-nosed potoroo (*Potorous tridactylus*), the Tasmanian bettong (*Bettongia gaimardi*) and the Tasmanian pademelon (*Thylogale billardierii*) (Johnson *et al.* 1989).

Despite the generalisation that cats tend to prey on the small animals, they are also known to prey on larger species, such as the yellow-footed rock wallaby (*Petrogale xanthopus*) and the unadorned rock-wallaby (*Petrogale inornata*) (Spencer 1990; Sheppard 1990 in Pearson 1992), which have a mean adult body weight of 7 and 4.3 kg, respectively. Cats have been identified as a significant predator of the black-footed rock wallaby (*Petrogale lateralis*) in isolated colonies in Queensland, where smaller prey species are less abundant (Spencer 1990); predation by cats on this population is resulting in depressed recruitment rates of adults into the population, causing the population to decline. The decrease in black-footed rock wallabies coincided with prolonged drought conditions, which may have exacerbated the effects of predation (Spencer 1990).

Further evidence of the impact that cats can have on populations at a local level is also apparent as predation by the feral cat has undermined attempts to reintroduce native animals into parts of their former range. For example, reintroduction programmes for the burrowing bettong (*Bettongia lesueur*) on continental Australia have been unsuccessful because of predation by feral predators (cats and foxes) (Deeker 1993); the reintroduction of the greater stick-nest rat (*Leporillus conditor*) into parts of its former range is constantly under threat from predation by the fox and cat (Copley 1989); and predation by the cat has undermined attempts to reintroduce the rufous hare-wallaby (*Lagorchestes hirsutus*) into parts of its former range (Kinnear 1993). The rate at which populations of native fauna can increase after cats have been removed from an area may be used to assess the impact that the cat can have on populations.

There is no conclusive evidence to support the notion that cats have resulted in large-scale changes to the abundance of native mammals.

Vulpes vulpes

Foxes prey on a wide range of mammals, birds and insects, and consume a range of fruits; as with the cat, where rabbits are abundant they are typically the preferred prey species of foxes (Seebeck 1978; Wallis and Brunner 1986). Where rabbits are less abundant, foxes tend to prey upon possums, the smaller dasyurids, and native rats. Predation on smaller native species is more common in undisturbed habitat, especially in forest environments, because the abundance of small mammals is proportionally higher than elsewhere and rabbit numbers are usually comparatively low (Coman 1973).

Foxes are unlikely to consume more than 10% of their body mass per day (Macdonald 1987). On this basis, Saunders *et al.* (in press) suggested that the average adult fox would consume 380-450 g of food per day. A study by Phillips and Catling (1991) in Nadgee Nature Reserve, south-eastern Australia, found that three foxes preyed upon 20 species. The most common species were the small and medium-sized mammals (52%), particularly *Rattus* species, which were also the most abundant mammals recorded in the area.

The impact of the fox on native fauna is considered to have been profound, although the evidence for this is largely circumstantial. For example, in Western Australia, following colonisation by the fox, the status of the mammal fauna changed profoundly, with many CWR mammals becoming extinct (Kinnear *et al.* 1988). Johnson *et al.* (1989) reported that almost all species of extinct macropods fall within the CWR, and although there is no clear primary cause explaining these extinctions, there is reason to believe that the introduction of the fox was a significant factor. In south-eastern Australia, the decline of many kangaroos, wallabies and rat-kangaroos has been attributed to, *inter alia*, the increase in the abundance of fox populations at the turn of this century (Lunney 1989). Lunney and Leary (1988) commented that extinctions of the small mammals in the Bega area of south-eastern New South Wales coincided with a peak in fox abundance in 1912.

Dietary studies support the notion that foxes can have a profound impact upon prey species, particularly those within the CWR. These studies have shown that foxes prey upon macropods, and that foxes can be considered locally significant predators, threatening many of the smaller macropod species. This threat is exacerbated when ground cover is removed (Robertshaw and Harden 1989). The most dramatic reductions of medium-sized mammals in south-western Western Australia has occurred where there is a fairly open understorey. These mammals include the brush-tailed bettong or woylie (*Bettongia penicillata*), the quokka (*Setonix brachyurus*) and the western quoll (*Dasyurus geoffroii*) (Christensen 1980). Other indirect evidence that the fox has facilitated the decline and extinction of some species, particularly some species of macropods, is the absence of extinctions of macropod species in areas where there are few or no foxes (e.g. the wet-dry tropics of northern Australia and Tasmania) (Johnson *et al.* 1989).

Kinnear *et al.* (1988) presented experimental evidence demonstrating that foxes can severely depress rock wallaby populations. Initial research suggested that remnant populations of rock wallabies in the wheatbelt of Western Australia were declining and that the fox was involved in this. Following fox control in some of these areas, populations of rock wallabies increased by up to 223%. Kinnear *et al.* (1988) also demonstrated the importance of identifying the source areas of feral predator species; foxes were migrating into an area of 2 km² as quickly as those within were being eliminated.

Fox control in other areas has also aided the recovery of populations of some native species. For example, in Dryandra State Forest in Western Australia, populations of ringtail possums, brushtail possums and other native mammals have increased markedly following fox baiting (Christensen 1980). Fox control is also deemed necessary in areas where the re-establishment of the numbat (*Myrmecobius fasciatus*) is being conducted (Burbidge and Friend 1989). Research such as this implies that the fox has been a major factor in the decline of many native species and that their incursion into many areas puts extant populations of many native species at risk (Kinnear *et al.* 1988). Foxes may pose a greater threat to these species during severe drought. Newsome *et al.* (1983), for example, observed greater predation pressure on macropods during drought.

In forest environments, many species are considered to be threatened by predation by the fox. In the forests of south-eastern New South Wales, for example, threatened species include the southern brown bandicoot (Isoodon obesulus) and the rare long-footed potoroo (Potorous longipes). Vulnerable species such as the white-footed dunnart (Sminthopsis leucopus), the brush-tailed phascogale (Phascogale tapoatafa), the long-nosed potoroo (Potorous tridactylus) and the brush-tailed rock wallaby (*Petrogale penicillata*) are also likely to be affected by predation by feral predators (Forestry Commission of New South Wales 1992). In the forests of north-eastern New South Wales, species listed as rare and endangered, such as the long-nosed potoroo, the parma wallaby (Macropus parma), the rufous bettong (Aepyprymnus rufescens) and the red-legged pademelon (Thylogale stigmatica), are sensitive to predation by foxes (Smith et al. 1992). Smith et al. (1992) believed that predation by foxes on Potorous tridactylus in northern New South Wales is threatening the survival of the species regionally. Many groundnesting birds are also considered vulnerable to predation (Kinnear 1993). Ground-dwelling birds such as the lyrebird (Menura novaehollandiae) are also susceptible to predation by foxes. Lill (1980) found that the fox was a major predator of young lyrebirds. As a result of the high mortality of young lyrebirds, the population examined suffered from depressed recruitment rates. This finding is particularly significant for species, such as the lyrebird, that naturally have low reproductive rates.

Limited published evidence suggests that foxes may selectively prey upon individuals within a mammal population. In Western Australia, for example, Dickman (1988) found that a population of the southern brown bandicoot (*Isoodon obesulus*) experienced high predation from foxes. On the basis of the fox scats collected and analysed, female bandicoots were being preyed upon more frequently than were males despite being outnumbered by about two to one by males. The preliminary investigation of Claridge *et al.* (1991) on *I. obesulus* in south-eastern New South Wales was consistent with Dickman's finding.

Although the fox is linked to the decline of many native animals, some species nevertheless persist in the presence of this predator. For example, in Western Australia, the brush-tailed bettong (*Bettongia penicillata*) can survive in areas where foxes are common, but has vanished from other areas where the fox is apparently less abundant (Johnson *et al.* 1989). The reasons for these observations remain to be determined precisely.

Canis familiaris dingo

The impact of the dingo on native fauna is poorly known. While the native fauna have co-existed with the dingo to some extent for several thousands of years, the present pattern of distribution and abundance of the dingo relative to the native fauna is unlikely to be similar to that experienced in the past. Similarly, the environment within which these species interact has changed markedly. It has been suggested that the dingo competed with the thylacine (*Thylacinus cynocephalus*) and indirectly with the Tasmanian devil (*Sarcophilus harrisii*) to the extent that these species became extinct on the mainland but survived in Tasmania, where the dingo is absent (Davies 1979; Thompson *et al.* 1987; Robertshaw and Harden 1989).

Dingoes require some 1.4 kg of food per day, or about 7% of their own body weight per day, to meet their energetic requirements (Green and Catling 1977), although they have been observed consuming much more than this (Newsome *et al.* 1983). To meet these needs they

may hunt alone or in packs (Newsome *et al.* 1983; Triggs *et al.* 1984). They are solitary hunters, particularly when smaller prey is abundant, but tend to hunt co-operatively when larger prey is available, or when the abundance of smaller prey is low (Newsome 1988). Robertshaw and Harden (1986) reported that dingoes switched to hunting in packs when their numbers were high, which resulted in dingoes concentrating their efforts on hunting large macropods. Hunting in packs may increase foraging efficiency and so is likely to be a useful behaviour during drought and other stressful environmental conditions that may influence the availability of prey. As a result, the dingo is able to exploit macropods occurring at low and high population densities (Newsome *et al.* 1983).

Generally, dingoes prey upon larger mammals such as the swamp wallaby (Wallabia bicolor), the red-necked wallaby (Macropus rufogriseus) and the common wombat (Vombatus ursinus) (Triggs et al. 1984; Robertshaw and Harden 1986). Studies of the feeding ecology of dingoes in south-eastern New South Wales by Newsome et al. (1983) found that they preyed on 23 mammal species, nine bird species and a variety of fish and insects, and consumed some plant material. The mammals fell into three broad weight categories: 0.1 kg (rat size); 1.25 kg (possum size); and 16 kg (wallaby size). The larger mammals were the most common prey item found in the scats of the dingo (48%). It was also apparent that the abundances of prey species were not always reflected in their frequency of occurrence in the dingo scats, suggesting a level of selectivity in foraging by the dingo. It was also found that the range of species preyed upon did not increase during periods of low prey abundance. Rather, the animals appeared to concentrate their efforts on the larger species. Newsome et al. (1983) considered medium-sized mammals to be the staple prey because of their dependability, despite the larger swamp wallaby being the most abundant prey species. The rest of the native species in the diet were considered 'supplementary' (larger prey), 'opportune' (small prey) and scavenged. Other studies have indicated that large animals, such as macropods, are the staple prey of the dingo (Robertshaw and Harden 1985, 1986, 1989). The diet of dingoes in north-eastern New South Wales, for example, was shown to consist of a wide array of species, but 76% of the diet consisted of five prey items: the swamp wallaby, the red-necked wallaby, the parma wallaby, the bush rat and species of Antechinus (Robertshaw and Harden 1986). Both Lunney (1989) and Triggs et al. (1984) reported that the swamp wallaby (Wallabia bicolor) was the most common prey species in canid scats in south-eastern Australia.

Newsome *et al.* (1983) documented the ability of the dingo to switch prey species. Following severe wildfire, dingoes switched from a diet consisting mainly of medium-sized prey species to a diet of larger mammals. This may have suppressed populations of wallabies and kangaroos for 2-3 years following the fire, until other sources of prey became abundant. Jarman *et al.* (1987) also regarded dingoes as having an important role in regulating the number of wallabies. Despite the low abundance of all prey species following fire and drought during their study, the presence of swamp wallabies in scats remained high.

Dingoes do prey upon rare species (Davies 1979) and Robertshaw and Harden (1986) found that dingoes preyed upon macropodids in greater proportion than their availability, with the swamp wallaby apparently preferentially selected amongst the macropods (Robertshaw and Harden 1986, 1989). The brushtail possum (*Trichosurus vulpecula*) and the ringtail possum (*Pseudocheirus peregrinus*) were found to be the most common possum species in the scats of dingoes in forests of south-eastern New South Wales (Lunney 1987). Other possum prey species present in scats included the greater glider (*Petauroides volans*), the yellow-bellied glider (*Petaurus australis*), the sugar glider (*Petaurus breviceps*), the feathertail glider (*Acrobates pygmaeus*) and the eastern pygmy-possum (*Cercartetus nanus*). There is also evidence that dingoes selectively prey upon young animals and subadult females of native mammals (Robertshaw and Harden 1989).

Forest Fragmentation, Roads and Feral Predators

Fragmentation, defined as 'the loss of continuity', occurs when habitat is cleared to the extent that remaining habitat exists in patches isolated from each other by a matrix unlike the

original. Fragmentation also results in an increase of the perimeter-to-interior ratio, or edge, of the habitat. In forest ecosystems managed for timber production, original forest habitat can become fragmented as a result of many factors, including the construction of roads, timber extraction, and prescribed burning (fuel-reduction burning). Roads and the secondary regrowth of vegetation that follows timber extraction and fuel-reduction burns may effectively isolate forest habitat. In many regions of eastern Australia, native forests managed for timber production can be viewed as patches of old-growth habitat within a matrix of successional forest of various ages and floristic composition. Given this, it would appear important to understand the extent to which road construction and the 'edges' created by this form of disturbance influence the potential impact of feral predators on native forest fauna.

Roads

Roads have several potential consequences for wildlife inhabiting any given area, including habitat loss, intrusion of edge effects (see below), barrier effects and increased mortality due to collisions with vehicles (Simberloff and Cox 1987; Bennett 1991). Roads may also facilitate access to food, or indirectly increase food supply, for various taxa (Oxley *et al.* 1973). It has been widely accepted that the construction of roads has the potential to facilitate the ingress of predators (including carnivorous mammals, birds and reptiles) into forest environments previously inaccessible to them (Andrews 1990; Fanning and Mills 1990; Gilmore 1990; Copson 1991) or, at least, that the use of roads by feral predators for hunting and movement is commonplace since roads provide easy travelling conditions (Bennett 1990; Cunningham 1990; Lumsden *et al.* 1991). Andrews (1990) proposed that feral animals are easily introduced into areas where there are roads, as the accompanying edge effect favours species with generalised ecological requirements. Arnold *et al.* (1987) reported that the narrow roadside verges in Western Australia are characterised by weeds and feral animals.

Evidence exists to support the observation that feral predators utilise roads for foraging and movement, particularly in areas where the vegetation is dense, which may hinder the movement of large animals. Taylor et al. (1985), during a mammal survey within dense vegetation in the Upper Henty River region in western Tasmania, found that large carnivores were trapped only along roads or beside creeks. They concluded that roads may facilitate the ease with which large carnivorous mammals can move into areas with possible consequences for predation levels, particularly on the fauna living close to the road or track. Newsome et al. (1983) reported that highly mobile species appeared to use roads and beaches as 'rights of way', '... the dingo certainly did so' (p. 349). Feral cats and foxes have been observed hunting along river edges in Victoria (Lumsden et al. 1991). Harden (1985) found that dingoes in the forests of north-eastern New South Wales frequently travelled along ridgetops, creeks and firetrails. Claridge et al. (1991) reported that fox and dingo activity was consistently observed along the roads adjacent to their study area, as well as along a nearby river. Bennett (1990) noted that cats were often sighted hunting and moving along forest roadsides. The scats and tracks of feral predators are frequently found on roads (May, unpublished observations), providing evidence that roads are used by these species; however, the extent to which roads are used by feral predators compared with habitat lacking roads is not known.

Evidence from research in England indicates that foxes, especially males, will use railway lines for dispersal and movement (Trewhella and Harris 1990). Kolb (1984) found that, where railway lines are present, male foxes may use these as convenient pathways for movement within their home range. The use of linear features for dispersal is not apparent in open environments, such as in urban settings. In closed environments, however, it is possible that roads are a convenient means of movement.

Roads, and the associated roadside verge, can influence the structure of small-mammal communities. For example, a study in the USA found that there were more species of small mammals along roadside verges than in the adjacent habitat, and that most of the species that preferred the roadside verges and accompanying edge habitat were grassland and generalist species (Adams and Geis 1983; Adams 1984). There were also greater population densities of animals in the roadside habitat than in the adjacent habitat.

Grass along roadside verges provides attractive grazing conditions for mammalian herbivores such as the eastern grey kangaroo (*Macropus giganteus*) and the common wombat (*Vombatus ursinus*) (Bennett 1991). This makes these species vulnerable to vehicular collision and roadside predation (Bellis and Graves 1971; McIlroy 1978; Bennett 1991). Roadkills are more commonplace on heavily used roads and the resulting carcasses are a potential food source for feral predators such as cats, dingoes and foxes (Vestjens 1973). An increase in the abundance of grazing species at road edges, as well as the potential preponderance of carcasses, may support higher populations of predators locally. These predators can kill animals attracted to food available along the roadside verges. The extent to which these predators forage away from roads, however, is not known.

Rabbits, which have been shown to be preferentially selected as prey by predators such as the fox and cat, are capable of establishing permanent and sizeable populations along roads in forest environments (May, unpublished data). This is a consequence of the improved grazing conditions along the roadside verges. Rabbits may attract feral predators into such areas, thereby increasing the likelihood of impacts on native species. These native animals can include rare species such as potoroos, which may utilise forest edges for foraging, and parma wallabies, which have been sighted at the edges of tracks and at the forest edge (Mount King Ecological Surveys 1992). Mount King Ecological Surveys (1992) reported that the movement of feral animals into previously unlogged forest may affect the conservation status of some potoroo species and it seems highly likely that this is applicable to a number of other native species as well.

Habitat Edges and Predation

The forest edge environment is unique and distinguishable from forest interior conditions and the surrounding environment. Biological and physical variables respond to these boundaries, producing what is commonly referred to as 'edge effects' (i.e. ecological phenomena associated with the edge of a forest) (Chen *et al.* in press). Edges affect ecosystem structure and productivity, understorey species, wildlife habitat, species composition and distribution, and microclimatic conditions (Fritschen *et al.* 1970; Thomas *et al.* 1979; Hansen and Horvah 1990; Chen 1991; Chen *et al.* 1992; Frost 1992). Biological responses to the creation of forest edges depend on the type of forest ecosystem, position in the landscape, orientation, patch size and shape, topographic features, nature of the surrounding matrix, and distance from the edge (Wales 1972; Ranney 1977; Williams-Linera 1990). The response of wildlife to edge conditions is dependent upon a variety of factors including microclimate, predation and food availability (Chen *et al.* 1992).

Changes to the structure and composition of the vegetation affect the resource base, or carrying capacity, of the environment for the fauna of an area. Edges, particularly in temperate regions, usually contain the highest species richness (Thomas *et al.* 1979; Lovejoy *et al.* 1986; Harris 1988), but do not represent the entire suite of species that may inhabit an area, as some fauna are able to take advantage of the changed ecological conditions, whereas others cannot.

Overseas studies have demonstrated that fragmentation of habitat results in large edge-toarea ratios and subsequent high predation rates by predators originating from outside the habitat patches and/or within the edge environment (Gates and Gysel 1978; Andrén *et al.* 1985; Wilcove 1985). For example, Andrén *et al.* (1985) found that predation on nests was positively correlated to the degree of fragmentation of the forest habitat. The incidence of predation within the edge environment can be much higher than that in the interior habitat (Yahner 1988). There have been many studies investigating the rate of predation within the edge environment (e.g. Gates and Gysel 1978; Andrén *et al.* 1985; Wilcove 1985; Andrén and Angelstram 1988; Møller 1988; Gibbs 1991; Andrén 1992). Andrén and Angelstam (1988) found that predation rates increased and levelled off 200–500 m from the edge, while Wilcove (1985) demonstrated that an edge-related increase in predation may extend up to 600 m into the forest. The risk of nest predation is influenced by habitat features at the site, such as vegetation complexity and nest placement (Bowman and Harris 1980; Martin 1988; Møller 1988). A study by Gibbs (1991) in tropical wet forest concluded that the greatest risk of nest predation occurred in forest edges surrounded by secondary succession, and that this was amplified in smaller forest patches. Also, evidence exists suggesting that nests are robbed by different predator species in approximate proportion to the relative abundances of the nest-robbing species (Angelstam 1986). Angelstam (1986) suggested that the productivity of the environment may also allow higher population densities of generalist predators to exist, which affects the amount of nest predation that may occur across an edge.

Areas of unlogged or retained forest in production forests in eastern Australia often have substantial perimeters. These can facilitate degradation of the patch through changed microclimatic conditions and enhanced rates of predation by feral predators (Recher *et al.* 1987; Gilmore 1990). Newsome *et al.* (1983) noted that dingoes occupied a broad range of habitat types within the forests of south-eastern New South Wales, but that they were particularly prevalent in the ecotones between forests and grasslands and heathlands. The ground cover near the edges of these patches may be modified by changed fire regimes and other factors. Ground cover is known to be important for most of the ground-dwelling fauna because it provides shelter and breeding resources and protection from predation. Birds, for example, select habitat sites based partly on the availability of nest sites that minimise the risk of nest predation (Martin 1988).

Conclusions and Research Issues

On the basis of current knowledge, it is clear that the nature and impact of predation by the cat, fox and dingo on native fauna are primarily determined by prey availability, although there are exceptions to this rule. Generally, dingoes prey upon large to medium-sized prey species (e.g. wallabies, common wombats and possums), foxes prey upon medium-sized to small prey (e.g. possums and rats) and consume a significant component of scavenged material and vegetation, while cats also prey upon medium-sized to small prey but may take a greater proportion of reptiles and birds (Triggs *et al.* 1984; Lumsden *et al.* 1991). The severity of the impact of the dingo upon the native fauna is considered to be minimal, at least in comparison with the impact that cats and foxes can have on populations, and the dingo is not considered a threat to CWR mammals in undisturbed environments (Smith *et al.* 1992).

In Australia, the fox-prey relationship is not cyclic but there is a pattern. In open environments, such as semi-arid environments, the presence of the fox has coincided with the loss of significant portions of the native mammal fauna, and, where species do survive, their numbers are invariably low (Kinnear 1993). However, other factors such as habitat destruction obscure the degree to which the fox may be responsible for the demise of native fauna in these areas (Burbidge and McKenzie 1989).

Given that the continent has been devoid of a fox-sized predator for the last 20000–30000 years (Johnson *et al.* 1989), it would seem reasonable to suggest that the impact of the fox on the native fauna could be very significant in terms of the long-term survival of many species. Anecdotal evidence suggests that, in the absence of predators, mammals tend to become less cautious in their habits and therefore may be more susceptible to predation when exotic predators invade an area (Johnson *et al.* 1989). Dickman (1992) found that mice from areas that harboured predators such as foxes, cats and quolls avoided traps with predator odours and generally confined themselves to areas with dense vegetation, in contrast to predator-naive mice. Kinnear *et al.* (1988) established that, in the absence of foxes, rock wallabies increased the distance they ventured from shelter. This suggests that the fox may not only contribute to the decline and extinction of many wildlife populations, but may also significantly affect the dimensions of the realised niche of a species by exaggerating the requirements for shelter and the need for food to be nearby. Kinnear *et al.* (1988) considered that this effect may also restrict the capacity of an individual to outbreed, thereby effectively isolating populations exposed to these conditions. Overall, it is reasonable to assume that road construction in and fragmentation

of undisturbed habitat may expose local populations of native animals to predation by exotic predators, particularly in habitats that may otherwise be inaccessible to exotic predators, such as dense forest environments.

Research Issues

Although many forested areas of Australia are relatively heavily fragmented by roads, no published studies specifically investigate the use of roads by feral predators. Further, many of the published observations of the use of roads by feral predators are biased to some extent, as field studies are often conducted in proximity to roads and true comparisons with areas completely free of roads have not been undertaken. Similarly, studies of the influence of the other aspects of forest fragmentation and disturbance on feral predators, particularly their patterns of foraging and the potential impact on native fauna, are scant. In light of the above, several issues are worthy of research.

One of the most important needs is to establish the relative impact that exotic predators may have on native fauna under varying degrees of road construction and other forms of fragmentation (including prescribed burning or fuel-reduction burning) within native forests. For example, are areas with and without roads in forests used differently by exotic predators and what is the significance of this in terms of the potential impact on fauna? The extent to which feral predators forage away from disturbed sites needs further investigation, as do the rates of predation within edges, as this may have several consequences for the design, location and size of retained strips and wildlife corridors, as well as priorities for future programmes for habitat/ecosystem restoration.

Evidence suggests that prey species can co-exist with the fox as long as fox populations remain low and the prey population is given a chance to recover (Kinnear 1993). For example, at low densities, foxes in areas in northern New South Wales appear to be able to 'co-exist' with several species of CWR mammals (Jarman and Johnson 1977), despite evidence from elsewhere documenting the significant detrimental impact the fox can have on these species. These observations may be attributed to regional differences that affect predator-prey interactions but need investigation.

Much evidence exists to implicate the cat in the decline and extinction of many populations of native fauna, especially island populations. Kinnear (1993, p. 27) stressed 'The absence of a pattern linking feral cats to wholesale faunal declines and extinctions suggests that cat predation is likely to be more species-specific than the fox'. This possibility deserves more attention and we suggest that much more research and monitoring of the feral cat and the response of fauna to the presence of this feral predator be undertaken.

The fox, feral cat and dingo are all considered to have the ability to selectively prey upon species and, to some extent, individual sexes and age-classes of a number of larger prey species. This aspect can be expected to be potentially very important for the population dynamics and persistence of many prey species, especially those occurring at a naturally low population density and as metapopulations. Research on the potential impacts on native fauna resulting from prey selection in forests subjected to various degrees of fragmentation and modification will be important.

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