FINAL REPORT FOR THE AUSTRALIAN GOVERNMENT DEPARTMENT OF THE ENVIRONMENT AND HERITAGE

Interactions between feral cats, foxes, native carnivores, and rabbits in Australia.

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Natural Heritage Trust
Helping Communities Helping Australia
An Australian Government Initiative

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Table of contents

Figures and Tables

Executive summary and recommendations

Through the Natural Heritage Trust, the Department of the Environment and Heritage (DEH) is working to develop and implement coordinated actions to reduce damage to the natural environment and primary production caused by feral animals.

Predation by foxes (*Vulpes vulpes*) and feral cats (*Felis catus)* have been identified as known or perceived threats to 34 and 38 native species, respectively, in threat abatement plans provided for under the *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act). Land degradation and competition with native species by European rabbits (*Oryctolagus cuniculus*) is also listed as a key threatening process under the EPBC Act.

The aim of this report is to review the evidence of the interactions between these three pest species, their control and the impact they have on Australian native species. The objectives of this report are:

1. To determine the nature of interactions between feral cats and foxes (competition and/or predation), especially in relation to control of either or both species, and the associated impacts on native species and ecological communities (especially those listed as threatened under the EPBC Act), and feral rabbit populations within Australian habitats/regions.

2. To determine the implications of feral rabbit control to feral cat, fox and native prey populations, and the importance of rabbits for maintaining high feral cat and fox numbers within Australian habitats/regions.

3. To determine the interactions between feral cats, foxes and native carnivores and relative significance of competition and predation by feral cats and foxes to these native species.

Based on the degree of overlap in distribution and diet of feral cats and foxes, there is a potential for competitive interactions. There is circumstantial evidence of foxes excluding feral cats from food resources, and of foxes killing feral cats. No studies have experimentally demonstrated an increase in the rate of predation by feral cats on native species following a reduction in fox abundance in Australia. Several studies have described increases in cat abundance following reductions in fox numbers resulting from control operations. However, the evidence for an increase in abundance in cat abundance following fox control is inconsistent between studies and may be confounded by inadequate monitoring techniques and behavioural changes.

A potential cost of predator control is an increase in rabbit abundance, which may cause increased competition for food and other resources with native herbivores. Several studies suggest that predators can exert prolonged regulating pressure on rabbits at low densities and can impede recovery of rabbit populations. Particularly when populations have already been significantly reduced through external factors such as disease, drought, high or low rainfall, floods or warren ripping. However, predator manipulation studies over a wide range of habitats have provided inconsistent evidence of predator regulation of rabbits. Predation appears to play an important role in regulating rabbit populations in arid and semi-arid systems under certain conditions (e.g. after drought has reduced rabbit populations), but has weaker effects in more temperate environments or when environmental conditions improve and rabbits escape regulation. It is important to note that many of the studies that have shaped our understanding of population regulation of rabbits in Australia were undertaken prior to the escape of Rabbit Haemorrhagic disease (RHD) in Australia. The potential regulatory effect of RHD on rabbit populations and the effect this could have on rabbit–predator interactions is largely unknown. The impact of rabbits on flora and soils is well documented, but the impact on native mammal species is poorly understood.

The impact of changes in predators and their primary prey on native mammal species has been the focus of few experimental studies. Studies that have discussed the role of foxes and feral cats in regulating rabbit populations have largely not investigated the benefits or costs of predator control to native species. Other studies that have investigated the impact of fox and cat control on native mammal species have reported benefits from pest control; however, there are many acknowledged limitations of these studies. While several studies have reported that fox removal has benefited a range of native species, many have not assessed pre-control population parameters, do not have control sites, are not replicated, and have not attempted to test alternative hypotheses to predation, such as competition by herbivores. Also there are several notable exceptions to a general response to fox control (e.g. mixed responses of small mammal

abundance from Operation FoxGlove WA, Project Eden, WA and Project Deliverance, Vic). While the limitations cited above might have resulted from limited budgets and logistical constraints associated with large-scale operations, the inferences that can be drawn are limited nevertheless.

From the studies reviewed it is unclear what the impact of a decline in rabbits is on native species. In the studies reviewed in this report, both feral cats and foxes shift consumption to the next most abundant prey item (e.g. invertebrates, reptiles, or birds) in the absence or decline of rabbits. There is no evidence that as a result of a decrease in rabbits there is an increase in predation rates on populations of rare or endangered species.

The interactions between rabbits and predators in arid and semi-arid environments have been relatively well studied in comparison to more temperate parts of Australia. Our level of understanding of these interactions and the impact on native species in arid and semi-arid and temperate environments is less well understood. In temperate environments the relationship between changes in rabbit abundance and declines in either feral cats or foxes has not been clearly demonstrated. Also, no studies showed that a decline in rabbit abundance leads to an increased rate of predation on native species. It appears that in systems where rabbits are not the staple prey item, changes in rabbit abundance have little impact on populations of feral cats or foxes.

Little quantitative information is available on the interactions between introduced predators and native carnivores. Available data suggests that dingoes (*Canis lupus dingo*), may be capable of suppressing fox populations, but that this is likely to be mediated by specific environmental conditions such as drought. There is some evidence to suggest that foxes spatially and temporally avoid wild dogs and that only during times of limited resources do the two come into direct conflict. Similarly, there is a lack of knowledge on the impacts of feral cats and foxes on native predators.

We used simulation models to explore the potential interactions between rabbits, foxes and feral cats. The sensitivity of the model to small changes in rainfall suggests a more detailed understanding of the relationships is required. More specifically, there is a need to quantify the relationship between rabbits and foxes and feral cats. Numerical responses for the two predators should be determined in relation to both the abundance of rabbits (or juvenile rabbits) and simultaneously the abundance of alternative food sources. To properly quantify and model the

impact of foxes and feral cats on both rabbits and native prey requires kill rates of these prey to be assessed in relation to the availability of all prey types. This is particularly important for native prey. It is also important to understand the population dynamics of native Australian prey and the population dynamics of rabbits following the arrival of RHD, in the absence of predation from introduced predators.

The limited data available for temperate systems suggest fox population dynamics may not be linked as strongly to rabbit dynamics as they appear to be in semi-arid systems. Alternative models are thus required for temperate systems. These models will almost certainly require data on the interactions of predators and a wide variety of foods. Feral cats are rarely seen in spotlight counts in temperate systems and no quantitative numerical relationships can be established from the available data.

Several studies have reported that integrated control (ripping, RHD or both poison baiting and RHD) has enhanced the decline of predator species, but to our knowledge no studies have investigated the costs and benefits of integrated feral animal control. A risk-averse approach would be to undertake integrated control wherever feral cats, foxes and rabbits co-occur. However, this may not be practical or possible due to limitations on resources. At present we have no clear understanding of the costs and benefits associated with integrated control programs.

Despite a number of studies that have provided valuable insights into the impacts that changes in prey abundance can have on populations of introduced predators, and how predators can influence the abundance of prey species, there are many gaps in our understanding of predator-prey interactions.

The four main areas where further information would improve our understanding of the interactions between feral cats, foxes, rabbits, their control and the impacts on native species are:

1. How to effectively monitor changes in abundance of introduced predators, particularly feral cats. At this point in time we are limited in our ability to control feral cats over large areas, although this is an area of current research.

2. The impact of predator control operations on the population dynamics and social organisation of sympatric predators and the impacts on native species and communities.

3. The role of rabbits in temperate systems in supporting elevated numbers of foxes and feral cats.

4. The effects of disease (RHD and myxomatosis), particularly in temperate environments, on the interactions between predators and their prey

A combination of focused research programs on the more tractable parameters of the above identified gaps, and larger scale experiments conducted over appropriate temporal and spatial scales is likely to produce important advances in our understanding of the interactions between feral cats, foxes, rabbits, their control and native species. It is recommended that at the completion of such studies the information gained is used to update the models of the systems as presented in this review, that the results be peer reviewed and made widely available, and the outcomes from the models should be used to direct management strategies for these pest species.

1 Background

The Department of the Environment and Heritage (DEH) is the Australian Government's major environmental agency and is responsible for achieving the Government's environmental objectives. Through the Natural Heritage Trust, DEH is working to develop and implement coordinated actions to reduce damage to the natural environment caused by pest animals.

Since their arrival in Australia over a century ago, introduced herbivores such as the European rabbit (*Oryctolagus cuniculus*) and introduced predators like the feral cat (*Felis cattus*) and red fox (*Vulpes vulpes*) are thought to be responsible for the extinction or decline of a wide range of native species. Foxes and feral cats have been identified as known or perceived threats to 34 and 38 native species, respectively, in threat abatement plans provided for under the *Environmental Protection and Biodiversity Conservation Act 1999* (EPBC Act). Competition and land degradation by rabbits is also listed as a key threatening process under the EPBC Act. Both State and Federal governments annually commit significant funds to manage the impact that these pest animals have on our environment. Between 1992 and 1999 the Federal government committed $4.7, $1.2 and $2.1 million to fox, feral cat and rabbit research and control programs, respectively.

Understanding the mechanisms that influence the abundance of these pest species, and the nature of the interactions between pest species and native species is critical to increasing our capacity to manage the threats they pose, and to optimise expenditure on pest animals management.

Feral Cat (Felis catus) Photo: Department of Natural Resources, Mines and Energy, Queensland.

Red Fox (*Vulpes vulpes*) Photo: P.Menkhorst.

Dingo (*Canis lupus lupus*) Photo: DSE

European Rabbits *(Oryctolagus cuniculus*) in plague numbers, South Australia. Photo: P. Bird.

Spotted-tailed Quoll (*Dasyurus maculatus) Photo: DSE*

2 Objectives

Predation by the feral cat and the red fox, and competition and habitat modification by the European rabbit have been listed as threatening processes by the Commonwealth under the *EPBC Act 1999.* State legislation also recognises these species as threats to biodiversity while control to mitigate their impacts is conducted throughout Australia. The role the rabbit plays in supporting populations of feral cats and foxes, and the effect of control of one or more of these species has in altering their impact on native species, is poorly understood. The aim of this report is to review the evidence of interactions between these pest species, their control and the impact on Australian native species. The objectives of this report are:

- To determine the nature of interactions between feral cats and foxes (competition and/or predation), especially in relation to control of either or both species, and the associated impacts on native species and ecological communities (especially those listed as threatened under the EPBC Act), and feral rabbit populations within Australian habitats and regions.

- To determine the implications of feral rabbit control on feral cat, fox and native prey populations, and the importance of rabbits for maintaining high feral cat and fox numbers within Australian habitats and regions.

- To determine the interactions between feral cats, foxes and native carnivores and relative significance of competition and predation by feral cats and foxes to these native species.

3 Introduction

Since the European settlement of Australia in 1788, 59 species (24%) of the mammalian fauna have become rare, vulnerable or extinct (Short and Smith 1994). These extinctions and declines have not been spread evenly across the continent, with a greater number of extinctions being recorded in the semi-arid and arid parts of Australia than in the more temperate areas (Woinarski and Braithwaite 1990).

There has been considerable debate as to the cause of these extinctions. As early as 1856–57, observations were made of the decline in a range of native species. Finlayson (1961) writes on observations he made in Central Australia between 1931–35 and 1950–56. He notes the role of the "three major scourges, the rabbit, the fox and the feral house cat", and he describes their impact as catastrophic, the rabbit by "competition for food plants and the latter two by direct predation". Evidence that predation by introduced predators is the primary cause of extinction and decline in populations of native species has gathered momentum in the past decade (Dickman et al. 1993; Short and Smith 1994; Smith and Quinn 1996; Short 1998). This is mainly the result of the experimental demonstration of the impacts of predators on remnant populations of mammals (Kinnear et al. 1988, 2002; Friend 1990) and their impact on reintroduced mammals (Friend 1990; Short et al. 1992).

Rabbits: European rabbits first established in Australia near Geelong in Victoria, in 1859. The rapid spread of rabbits across mainland Australia was probably aided by the presence of burrows of native species, the lack of predators, changes made by the development of land for agriculture, and in some cases by their deliberate transportation. Rabbits have caused significant damage to the environment directly, preventing the regeneration of some plant species, and indirectly by impacting on bird and mammal populations through altering vegetation community structure, damage to soils (erosion, loss of fertility, and increased run-off). The impacts of rabbits have been most significant in the rangelands of central Australia, where numerous plant species and the animals that are dependent on them are threatened with extinction or are suffering range reductions (Williams et al. 1995). Rabbits can compete with sheep for pasture, particularly when biomass falls below a threshold (estimated at below 259 kg ha^{-1}, Short 1985). The estimated impact of rabbits in lost production for the wool industry in 1989 was $115 million per annum (Williams et al. 1995).

Foxes: The first reliable record of a successful fox release was near Geelong, in 1871, where rabbits had been released a few years earlier. The subsequent spread of foxes across Australia is closely linked to the spread of rabbits. Australian studies on the food habits of foxes (Coman and Brunner 1972; Myers and Parker 1975a,b, Brooker 1977; Jones and Coman 1981; Catling 1988; Paltridge et al. 1997; Risbey et al. 1999) highlighted the importance of rabbit in their diet, and data on the early spread of foxes suggested the spread was more rapid where rabbits were present (Saunders et al. 1995).

Feral cats: The timing of the arrival of domestic cats in Australia is less clear. Baldwin (1980) suggested that cats could have been introduced to north-western Australia by Indonesian trading vessels as early as the sixteenth century. However, Abbott (2002) reviewed historical sources and found no evidence that the cat was present on mainland Australia prior to settlement by Europeans. He reported that cats spread from multiple coastal introductions in the period 1824–86 and by 1890 nearly the entire continent had been colonised. Abbott (2002) concluded that the evidence for early impacts of feral cats causing major and widespread declines in native fauna is considered tenuous and unconvincing.

Populations of feral cats were increased in the nineteenth century by the planned release of thousands of feral cats (Rolls 1969) in an attempt to control mice (Dickman 1996), rabbits (Rolls 1969; Fuller 1970) and native rats (Bennett 1879 in Dickman 1996). The impact of feral cats on native fauna has not been critically investigated, but numerous historical and circumstantial accounts suggested that feral cats may have deleterious effects on native fauna (e.g. Dickman et al.1993; Dickman 1996).

Interactions: Understanding the dynamics of predator–prey systems is fundamental to effectively managing the threats and benefits that introduced predators pose to Australia's conservation and agricultural values. The interactions between feral cats and the red fox, and their reliance on introduced mammals, especially European rabbits as their primary prey are of key importance. Abundance of primary prey can influence the extent to which these predators impact on secondary prey, many of which are indigenous species.

Predator–prey interactions also have significant implications for Australia's agricultural industries. For example, foxes can kill lambs (Lugton 1991; Saunders et al. 1995: Greentree et al. 2000) but predation by foxes and feral cats can also regulate rabbit numbers and help reduce their impact on farm production by reducing

competition with livestock and reducing the costs of rabbit control (Williams *et al.* 1995).

3.1 Information Used

This review draws on many studies from a wide range of environments across Australia. We have included research programs or control operations that were useful in addressing the objectives of the study. Although we were not given approval to include several unpublished studies by some government organisations, a number of these are reputedly close to publication and should provide additional information soon.

The majority of information we review is from experiments or control operations that have either reduced or removed predators or their primary prey. We do not review studies of the diet of feral cats or foxes *per se* as this does not provide direct evidence of the nature of the interactions between these species and prey species. However, we include studies that describe the diets of multiple predator species, or those that include shifts in diet in response to changes in the abundance of primary prey and predators, either via deliberate experimental manipulation or as a result of management actions. These studies are included as they may provide information on the potential for competition between predator species.

We use models of trophic interactions to: a) formally identify the various interactions and their inter-relationships, b) identify where there are gaps in our current understanding, and c) investigate the outcome of various management scenarios of integrated control and the potential benefits to native species.

Finally, we outline areas for future investigations including experimental designs to address the identified critical gaps in knowledge for various geographical locations around Australia.

3.2 Background to Predator and Predator–Prey Interactions

This section provides a brief overview of predator–prey interactions, as these concepts provide the background upon which the rest of the report is based.

Untangling the complex nature of the population dynamics of predators and their prey is difficult (Figure 1).
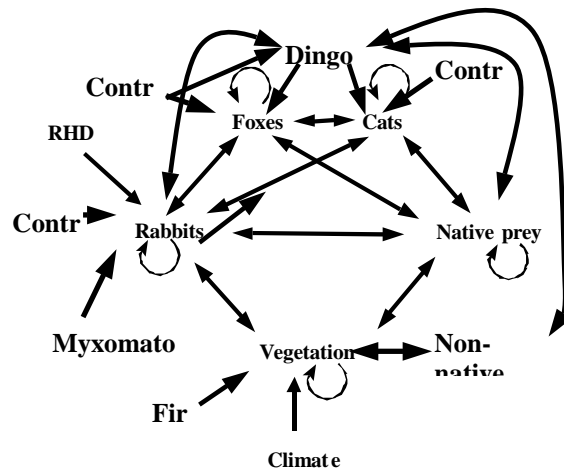
Figure 1. Some key processes that may affect interactions between predators and their prey.

The arrows represent the direction, but not the strength of the interaction. Circular arrows indicate density-dependant regulation. Factors that disrupt any one of these interactions can result in flow on effects to other parts of the system. For example, reducing the abundance of foxes may influence the interactions between: feral cats, rabbits and native prey; native prey and rabbits; rabbits, native prey and vegetation; vegetation and native prey; and so on.

The interactions between predators and their prey, and the implications for conserving species that are threatened by predation have been extensively written about (Holt 1977; Sinclair *et al.* 1990; Pech *et al.* 1992, 1995; Sinclair and Pech 1996; Pech and Hood 1998).

Predation can either limit a prey population's growth, or it can act to regulate a population's abundance. This review is not concerned with the mechanisms that might limit a population, as all forms of mortality and reproductive loss set a limit about which populations fluctuate (Sinclair and Pech 1996). Understanding if predation regulates prey does provide insights into the risks faced by populations of native species (i.e. small populations are potentially at greater risk of extinction), and it also provides information on how a population might respond to the removal of predation pressure. The role that primary prey (i.e. rabbits) plays in population increase of predators and the flow on effect to alternative prey is also important.

Understanding the interaction between feral cats, foxes and their prey relies on knowing how changes in predator abundance (numerical response) and the rate at which they depredate prey (functional response) relate to changes in prey density (Solomon 1949; Sinclair *et al.* 1990; Pech *et al.* 1992). It also requires an understanding of the role that primary prey (especially rabbits) has in maintaining the

abundance of both foxes and feral cats, and whether this alters predation rates on alternative (native) prey species.

Two different types of functional response are commonly used to describe the way in which the number of prey consumed per predator changes as prey density changes (Holling 1959; 1965). A Type II functional response predicts that predators will have a progressively decreasing effect on prey as prey abundance increases (i.e. inversely density-dependent, Sinclair *et al.* 1990; Pech *et al.* 1992). A Type III response can be represented by a threshold S-shaped curve. At low-prey densities the proportion of prey consumed increases as prey density increases (i.e. density-dependent response). This arises through prey-switching behaviour or decreased social and territorial constraints of predators when prey becomes more abundant (Pech *et al.* 1992). At high-prey density the proportion of prey consumed slows, with a similar response to a Type II curve (Pech *et al.* 1992; Sinclair and Krebs 2003).

The numerical response follows the basic shape of functional responses, whereby the number of predators increases in response to increases in prey density through mechanisms such as reproduction and immigration. Predator numbers can also reach an asymptote due to reproductive and social constraints such as territoriality and emigration (Sinclair *et al.* 1990; Thompson 1994).

In practice, it is difficult with empirical data to distinguish between Type II and Type III responses. The total response of predators is the product of the functional and numerical response and is shaped by the types of functional and numerical response experienced by the predator. If there is no density dependence in either functional or numerical response, then the proportional effect of the total response is uniformly inversely density-dependent and is of Type II form (Figure 2). If there is density dependence then the shape of the total response is of Type III form and shows density dependence at low-prey densities while remaining depensatory at high-prey densities (Sinclair 1989; Sinclair *et al.* 1998).

A prey species' instantaneous rate of increase (i.e. the difference between net recruitment and predation) can be used to assess the impacts of a Type II and Type III predator total response. Figure 2a shows prey rates of increase relative to population size (number of prey) for a range of Type II total predator responses (level 1–3). Figure 2b shows the equivalent curves (level 1–4) for Type III total response (Sinclair and Krebs 2003). In Figure 2a, at high-prey density, low levels of predation (level 1) do not regulate the prey species, and there is one stable point (C) at

which prey is regulated by food. At higher levels of predation, prey rate of increase is positive between points B and C, if prey numbers fall below point B prey species can be driven to extinction. At very high levels of predation, prey will go extinct. These curves represent the situation where prey species are secondary prey items and predators are reliant on some other staple prey(e.g. rabbits).

For the Type III total response (Figure 2b), there are a number of outcomes from different predation rates. At low levels of predation the outcome is the same as in a Type II response and prey are not regulated by predation (point C). As predation levels increase there can be two possible stable points: firstly (points A, C), where predation is regulating prey at point A and food or some other factor at point C; and secondly a single stable point (A) where predation alone is regulating prey, or prey are not able to persist due to predation rates being too high (level 4). Point B is an unstable threshold (level 2) where populations move either towards point A or C.

a)

b)
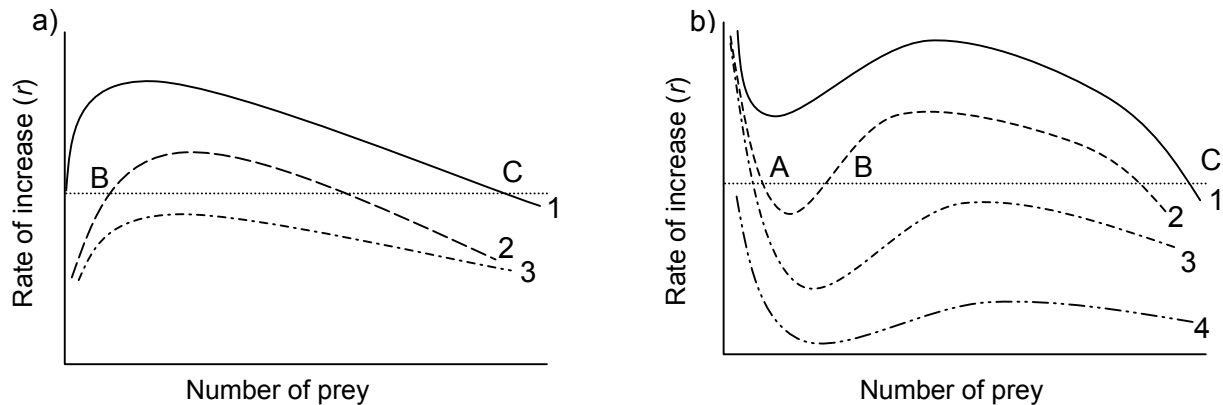
Figure 2. Total response curves for (a) type II and (b) type III responses (from Sinclair and Krebs 2003). The instantaneous rates of change of the prey population experiencing different levels of (a) Type II and (b) Type III predation. Point A represents a stable point from regulation by predators, point C a stable point due to regulation from food with predation not regulating, and point B is an unstable threshold. Curves 1-4 represent different intensities of predation: 1, lowest predation level; 4, highest predation level.

Recent theoretical developments have highlighted some of the limitations of functional and numerical responses in understanding predator–prey dynamics (Alonzo 2002). These developments suggest that prey vulnerability can play an important role in how predators maximise their foraging efficiency by selecting prey based on poor anti-predator behaviour (Quinn and Cresswell 2004).

Prey species weigh up the cost of an activity against the risks of predation. The impacts of these decisions manifest in a reduced amount of time spent foraging, reducing the food intake of a prey species, which in turn can act to reduce health and fecundity. For example, rodents and gerbils reduced foraging and shift foraging activity when the risk of predation was high (Brown 1988; Kolter *et al.* 1991; Hughes *et al.* 1994) and *Antechinus* species in Australia displayed different foraging effort under risk of predation (Stokes *et al.* 2004; Arthur 2001; Arthur and Pech 2003). Arthur *et al.* (2003) showed that populations of house mice reproduced earlier and reached higher densities in locations where the risk of predation was low compared to areas where it was high.

We need to understand the types of interactions that currently exist. This includes the types of response predators' experience from changes in prey abundance that might change the abundance of predators or alter the rates of predation on native species. Several authors have suggested that the best approach to determine which response describes the interaction between predators and their prey is through perturbation experiments (Sinclair 1989; Pech *et al.* 1995; Cappuccino and Harrison 1996; Korpimaki and Krebs 1996; Sinclair 1996; Krebs *et al.* 2001).

Non-manipulative studies have demonstrated that predation plays a role in limiting primary prey populations, but they cannot be used to unequivocally assess whether predation is a regulating factor because of the potential confounding effect of other factors. Sinclair (1989) suggested that predator regulation of prey can be tested by removing predators, and then, after the prey has increased permitting predators to reinvade. If predators are regulating prey numbers, the return of predators should result in prey populations returning to pre-predator removal densities (assuming that all other factors are equal). Pech *et al.* (1995) and Krebs *et al.* (2001) described the possible manipulations of prey, which include changes in prey density through reintroduction's, altering food supply or the abundance of alternative prey species and predators.

In addition to interactions between predators and prey, predators that share food resources can compete, either via intraspecific competition or intraguild predation. Changes to the composition of the predator assemblage can result in altered rates of predation on prey species (see section 4 for further details).

In complex systems with multiple predators and a range of prey species, community food web models may prove to be more insightful (Chase 2003; Navarrete and Castilla 2003). These are areas of active research and development that may provide increased understanding of the interaction between predators, prey and their management in the future; however, they are not discussed further in this report.

4 Literature Review

4.1 Change in Abundance of Predators

The control of introduced predator species, particularly foxes, is widespread throughout Australia for both agricultural and conservation reasons. Preliminary results of a review of feral vertebrate pest control operations throughout Australia, commissioned by the DEH, indicate the magnitude of this control. For example, fox control was undertaken on at least 9 million ha of predominantly public land during 2002 (Reddiex *et al.* 2004).

If predation is regulating rabbit abundance, a reduction in the abundance of foxes (and feral cats) could result in an increase in the abundance of rabbits. Rabbits are well suited to respond quickly to the removal of predation, as they have a high rate of increase and respond rapidly to improvements in environmental conditions. This has potential ecological consequences that may indirectly lead to impacts on native fauna through loss of vegetation, soil structure, and changes in nutrient levels (Banks *et al.* 1998) or competition for food (Williams *et al.* 1995). Dawson and Ellis (1979) found considerable overlap in the diet of the rare yellow-footed rock wallaby (*Petrogale xanthopus*) and rabbits in western New South Wales, and Dawson and Ellis (1994) found evidence of competition for food between rabbits and red kangaroos.

Fox control operations aimed at restoring native species or communities have been undertaken across Australia over recent decades. These operations rarely control all pests (i.e. feral cats, foxes and rabbits) or report on the presence of non-target pest species. This hinders the interpretation on the impact that changes in rabbits abundance arising from predator control might have on native species.

4.1.1 Control of both feral cats and foxes (implications for primary and alternative prey)

This section focuses on the effects of changes in the abundance of feral cats and foxes on rabbit populations and on native species or communities. Studies that have experimentally manipulated predator populations receive most attention (Table 1). Interactions between introduced predator species following control of only one of a suite of predator species are also reviewed.

Although predators have been regarded as contributing to population control of low-density rabbit populations worldwide (Newsome *et al.* 1989; Trout and Tittensor 1989; Gibb and Williams 1990; Rogers *et al.* 1994), there have been few experimental tests in Australia to assess whether predation is indeed a regulating factor (Table 1). Trout and Tittensor's (1989) review of the worldwide rabbit–predator literature suggested that predators do not have a regulatory effect on high-density rabbit populations but may regulate low-density populations, in particular those populations that have been reduced by extrinsic factors.

Study 1: Yathong Nature Reserve

Newsome *et al.* (1989) and Pech *et al.* (1992) reported a predator-removal experiment conducted at Yathong Nature Reserve, New South Wales between June 1981 and January 1984. Newsome *et al.* (1989) reported that low-density populations of rabbits increased rapidly where foxes and feral cats were continually shot. After only 14 months, densities of rabbits at the predator-removal sites were 3.5–4 times greater than those sites where predators were not controlled, whereas untreated populations had remained low. Pech *et al.* (1992) subsequently showed that when predators were allowed back into the predator-removal areas, rabbit populations continued to increase and did not decline to the density in the untreated area. These studies demonstrated that predators could regulate rabbit populations at low densities in semi-arid and arid habitats (less than 9–15 per spotlight km), but that populations could escape predator regulation and result in a higher stable state. The mechanism whereby rabbit populations are reduced to enable regulation at low density may vary across: the range of rabbits (eg. drought reducing food resources) in the above studies; or disease such as RHD (Mutze *et al.* 1998; Saunders *et al.* 1998); or conventional rabbit control operations. The importance of environmental stochasticity in enabling regulation of rabbit populations resulted in Newsome *et al.*'s (1989) concept of 'environmentally modulated predation'. Newsome and Sinclair (1995) suggested that predator–prey dynamics in Australia are influenced by El Nino Southern Oscillations (ENSO) causing wide environmental fluctuations (e.g. prolonged periods of drought).

Study 2: Peron Peninsula

Project Eden is an 'operational experiment' with a primary goal of reconstructing the pre-European fauna on Peron Peninsula (100 000 ha), Shark Bay, Western Australia (Thompson and Shepherd

1995). This area can be classified as semi-arid, with a mean annual rainfall of 220 mm. In addition to predator-removal operations over a 1050 km^2 area, herbivores (goats, sheep and rabbits) have also been controlled. The relative abundance of predators and larger native fauna such as euros, echidnas, emus and goannas have been monitored using track transects, where animal tracks are monitored over a 80 km transect, and small mammals have been monitored on six grids using pitfall and Elliott traps.

Aerial baiting to control foxes commenced in 1995, resulting in an approximately 95% reduction in fox abundance, and subsequently an electrified barrier fence was constructed to prevent/reduce reinvasion by foxes. Feral cat control commenced in 1996 and has involved a number of trapping and baiting regimes. Feral cats have been maintained at approximately 30–50% of pre-control levels, a level that is believed to be too high to permit the establishment of many species of small mammal (K. Morris, pers. comm.). Rabbit population did not increase significantly following fox-control. It is possible that rabbits had escaped predator regulation prior to the commencement of fox control operations, and thus a reduction in predators would not have affected the rabbit population. Presence/absence monitoring over eight years following the initial fox control operation indicated a seasonal fluctuation in rabbits, supporting the idea that rabbits were being regulated by food resources and not predation. The release of myxomatosis and more recently RHD on Peron Peninsula in 1996 may confound the effects of fox control on rabbit populations.

Trap-catch indices of small native mammals did not appear to have increased significantly after intensive predator-control. In 1995, trap success for all small mammals ranged from 8 to18%, and increased to 40% in 1996 (seasonal rainfall events may have influenced this measurement), but has averaged 10–25% since 1996, except for 2001 when trap success fell to 8% (K. Morris, pers. comm.). Trapping along road transects has also showed variable results, with some species apparently increasing (e.g. hopping mouse [*Notomys spp.*], goanna, bobtail skink and blue tongue skink), and others declining (e.g. bilbies [*Macrotis lagotis*] and woylies [*Bettongia pencillata*]). The relative abundance of reptiles and small mammals on trapping grids might be influenced more by rainfall than predator-control (K. Morris, pers. comm.).

Study 3: Heirisson Prong

Risbey (2000) described a predator-removal experiment undertaken to protect reintroduced native animals at Heirisson Prong, Shark Bay, Western Australia, from 1990 to1994. This area can be classified as semi-arid and coastal, with a mean annual rainfall of 280 mm. The experiment comprised three different 'predator zones': zone 1) an area with low cat and low fox abundance following eradication of foxes and intensive cat control on the northern tip of Heirisson Prong that was isolated by an electrified barrier fence (*c.* 12 km^2); zone 2) an area with low fox abundance, comprising 120–200 km^2 immediately adjacent to the barrier fence; and zone 3) an area with no fox or cat control over an unspecified area adjacent to the previous zone. Spotlight surveys targeting foxes and feral cats were undertaken at three-monthly intervals to assess changes in relative abundance over the three zones. Rabbits were also counted during these surveys. Pitfall traps were monitored one year before and three years after predator control began and were used to determine the relative capture success of small mammals and reptiles between the three zones.

Control of foxes and feral cats in zone 1 resulted in low densities of foxes throughout the study period (<0.05 km^{-1}), whereas feral cat numbers initially increased following the initial drop in spotlight counts of foxes, but then declined when intensive cat control began. In zone 2, fox control resulted in fox abundance remaining low, but spotlight counts of feral cats showed a three-fold increase from 0.06 km^{-1} to 0.18 km^{-1} over three years. Both foxes and feral cats showed no trend in abundance in zone 3.

Indices of rabbit abundance were low (<1 rabbit km^{-1}) in all zones prior to predator control, but increased in both of the predator control zones once control commenced (to a maximum of 7 km^{-1}). There was an apparent difference in the average annual rate of increase between zone 1 and zone 2 ($r = 0.27$, and $r = 0.53$, respectively; calculated from Risbey 2000), with rabbits increasing more rapidly in zone 2. Rabbits were periodically poisoned in zone 1 from 1993 onwards, with the objective of killing feral cats and foxes by secondary poisoning. Risbey (2000) suggested that this may have accounted for low rabbit counts in autumn 1992 and winter 1993. Rabbit abundance remained low in the zone where no predators were controlled.

Risbey (2000) suggested that rabbit populations at Heirisson Prong were regulated by the onset of seasonal rainfall and predation from foxes and feral cats; and that the removal of foxes in particular may have allowed rabbits to escape predator-regulation. However, the observed increase of rabbits following removal of predators was extremely low compared with other studies where regulation has been inferred (Pech *et al.* 1992; Banks 2000).

Risbey *et al.* (1999) stated that their study presents the first experimental evidence that feral cats have a negative impact on populations of small mammals on the mainland of Australia. In zone 1, where foxes and feral cats were maintained at low abundance, captures of small mammals increased over the duration of the study (42 captures in June 1990 to 93 captures in July 1994). However, in zone 2, where only foxes were controlled, small mammals (Ash-grey mouse [*Pseudomys albocinereus*]; Sandy inland mouse [*Pseudomys hermannsburgensis*]; Little long-tailed dunnart [*Sminthopsis dolichura*]; and house mouse [*Mus musculus*]) declined by 80% (55 captures in March 1990 to 7 in March 1994). Small mammals were variable over the study period in the experimental control zone, where foxes and feral cats were not controlled. Changes in indices of predator abundance did not appear to influence capture success of reptiles.

The acknowledged limitations of Risbey *et al.'s* (1999) study included no replication of both experimental and control study sites; incomplete sampling before the manipulation at all sites (experimental control was not monitored pre-manipulation); and the manipulation of rabbit numbers was not replicated across all study zones. These limitations prevent extrapolation of the results outside Heirisson Prong, but provide valuable insights into predator–prey interactions in this system; however, the influence of increasing rabbit abundances after the removal of foxes (and feral cats) remains a confounding factor. CSIRO has continued to control foxes and feral cats in zones 1 and 2, and monitor the changes in abundance of prey species, but at the time of writing, the data were not available for inclusion.

Robley (1999) undertook a study in Risbey's zone 1 between 1995 and 1998 that investigated the interactions between rabbits and burrowing bettongs (*Bettongia lesueur*); the later being reintroduced in 1992. Periodic rabbit control using 1080 poisoned with one-shot oats was discontinued in 1996 with the reintroduction of western barred bandicoots (*Perameles bougainville*). Fox and feral cat control continued through poisoned meat baiting and shooting (Richards and Short 2003). Rabbit populations increased 1 per spotlight km in 1995 to a peak of 13 rabbits per spotlight km in the summer of 1997–1998. The rabbit population collapsed in the months following to approximately 3 per spotlight km in July 1998. This decline was aided by the introduction of RHD and the rabbit population continued to decline and remained at less than 1 per spotlight km to October 1998 (Robley *et al.* 2002).

Robley *et al.* (2001) investigated dietary overlap between bettongs and rabbits between 1996 and 1999 at two levels of rabbit density (medium 13.7 ha^{-1} and high 38 ha^{-1}) in Risbey's zone 1. They found no significant overlap in diet and that bettongs were capable of shifting their diet in response to changes in resource availability while rabbits were far less flexible, resulting in a dramatic population decline. Robley *et al.* (2002) found no difference in burrowing bettong body condition, reproductive output or resource use during the same period.

Between 1992 and 1997, foxes gained entry to the reintroduction site (zone 1) at Heirisson Prong on three separate occasions lasting between several days and several weeks. On each occasion foxes killed between 36 and 77% of the re-established population of burrowing bettongs (Short *et al.* 2002). Foxes engaged in surplus killing of bettongs, rarely consuming any of the carcasses. Foxes killed bettongs despite an abundant rabbit population that, at the time of incursions in 1996 and 997, outnumbered bettongs by 350 and 700 to one, respectively (Short *et al.* 2002). This provides some evidence that predator-naive prey are highly vulnerable to predation regardless of the form of the response predators might have to changes in prey abundance, and that even well-established reintroduction populations are still vulnerable to predation.

Study 4: Arid Recovery Program

The Arid Recovery Program is a joint conservation initiative involving Western Mining Company Resources, Department of Environment and Heritage (South Australia) and the University of Adelaide, and was established in June 1997 (Moseby 2002). An area of 60 km^2 was progressively fenced to exclude rabbits, feral cats and foxes, with all these species removed from inside the reserve between 1997 and 2000.

Small mammal and reptile pitfall trapping from sites inside (n=12) and outside (n=11) the reserve has been undertaken annually since 1998. In the first three years there was no reported difference between the average number of small mammals captured inside and outside the reserve. In 2001 and 2002 a significant difference in the average number of small mammal captures was reported, with a four-fold increase inside the reserve between 2001 and 2002, and in 2002 a similar difference between captures inside and outside the reserve (Moseby 2002). The author also noted an increase in the number of observations of Barn Owls (*Tayo alba*), Frogmouths (*Podargus strigoides*) and Boobook Owls (*Ninox novaeseelandiae*) inside the reserve, and while acknowledging the limitations. Moseby (2002) suggested this might be expected given the increased number of small mammals. The results

for reptiles are more complex and little can be drawn from it at this stage. Moseby (2002) noted a general decline in captures in 2001–2002 and suggested that this may be linked to changes in vegetation structure resulting from the removal of rabbits.

4.1.2 Control of foxes only (implications for primary and alternative prey)

Study 5: Namadgi National Park

Banks *et al.* (1998) described a predator-removal experiment that examined the role of fox predation in suppressing rabbit population growth in Namadgi National Park, Australian Capital Territory, between 1993 and 1995. This area can be classified as sub-alpine forest with reclaimed pasture. The experiment involved suppressing fox abundance on two sites, using 1080 poisoned FoxOff™ over an 18 month period and comparing rabbit responses on these and two other non-treated sites. All sites were approximately 10 km^2 in area. In the two removal sites, foxes declined in abundance, and rabbit populations grew to 6.5 and 12.0 times their initial population size within 18 months. In the untreated sites, rabbit populations showed a very small population increases over the same period (10%). An interesting observation made by these authors was that other non-target predators of rabbits (e.g. feral cats, dingos], wedge-tailed eagles [*Aquila audax*]) appeared unaffected by the fox baiting. The authors noted that feral cats were seen infrequently throughout the study (<1 animal every 2 months).

Banks (2000) reported on a follow up experiment at this site where foxes were permitted to re-invade the two sites where they had previously been removed (at the time of reinvasion rabbit population densities were estimated at 44.2 and 21.6 per spotlight km). On one predator-removal site rabbit populations declined immediately after foxes reinvaded and remained low for 16 months, suggesting that fox predation was effective at regulating numbers. Banks (2000) suggested that part of the observed decline in rabbit numbers might have been attributable to changes in habitat use following the reinvasion of foxes. However, on the other predator-removal site rabbit densities dropped slightly following the reinvasion of foxes, but then continued to increase (23%) over the following 16 months, suggesting that rabbits were not regulated by fox predation.

Spotlight counts, including indices of several native species, have been continued to the current day at Banks' study sites by Environment ACT. These unpublished data are not available for discussion in this report, but one is incorporated into the trophic interaction model (see section 5).

Several other studies have focused on the benefits to native species of controlling foxes. Saunders *et al.* (1995) and Kinnear *et al.* (2002) reviewed predator-removal studies that have attempted to quantify the removal of fox predation on native species. Some of these studies, which have primarily been undertaken in Western Australia, are summarised below.

Study 6: Mt Carolyn

Kinnear *et al.* (1988, 1998) reported on a fox-removal study at Mt. Carolyn commencing in 1979 where foxes were controlled using 1080 baits at two colonies of rock-wallabies (*Petrogale lateralis*), and not controlled at three other colonies. Populations receiving fox control increased four- to five-fold over 8 years, while those not receiving fox control remained at similar levels to pre-control levels in 1990, having remained low or increased and then declined over the duration of the experiment. No information is provided on the presence or abundance of rabbits. Hone (1994) statistically analysed the data from Kinnear *et al.* (1988) using three different approaches (ANOVA, changes in abundance, and changes in rate of increase), only one of which demonstrated a statistically significant effect of fox control on rock-wallaby populations. Kinnear *et al.* (1998) rebutted Hones' analysis by highlighting differences in each of their underlying assumptions for each of the tests that are described by Hone, and suggested an alternative modelling approach to analysing the data. Hone (1999) pointed out that despite the various approaches to analysing the data there are still potential alternative hypothesis that could explain the observed patters, and that it is the acquisition of reliable knowledge that will improve our capacity to understand and manager threatening processes. Sinclair and Krebs (2003) reviewed the results of Kinnear's studies and showed that the rate of increase for these rock-wallabies was higher when predators were absent than when they were present. They suggest that fox predation was inversely density dependant and that foxes were treating rock-wallabies as secondary prey to some more abundant and persistent primary prey.

Study 7: Dolphin Island

Kinnear *et al.* (2002) reported a nearly thirty-fold (1 in 1979 to 27 in 1990) increase in Rothschild's rock-wallabies (*Petrogale rothschildi*) following fox control on Dolphin Island, Western Australia. Over the same time period, rock-wallaby numbers remained constant on fox-free Enderby Island. Counts were undertaken over a single period of several days, and no data on trends in fox abundance, changes in causes of mortality, alternative predators or underlying environmental

conditions are presented. Hence it cannot be concluded that fox predation regulates the abundance of these rock-wallabies.

Study 8: Tutanning Nature Reserve

At Tutanning Nature Reserve (2200 ha), brush-tailed bettongs (*Bettongia penicillata*) increased from 7 captures in 1984, prior to fox baiting, to 64 in 1989 following 5 years of intensive fox control. Numbers of common brushtail possum (*Trichosurus vulpecula*) and tammar wallaby (*Macropus eugenii*) also increased over this period, and it was suggested that fox control enabled the burrowing bettong to inhabit and reproduce successfully in a larger part of the reserve (Kinnear *et al.* 2002).

Study 9: Dryandra State Forest

An intensive fox removal program in Dryandra State Forest, Western Australia, where control was undertaken monthly over 5 years, resulted in a significant increase in numbat (*Mymecobius fasiatus*) in the baited area, but not in the unbaited area, and burrowing bettongs also appeared to increase in the baited area (Friend 1990).

Study 10: Jarrah Forest

Morris *et al.* (1995) reported on an experiment that investigated the impact of foxes on western quoll (or chuditch; *Dasyurus geoffroii*) in a jarrah forest of Western Australia. Fox baiting using 1080 baits was undertaken from 1991-1994 over an initial area of 4 000 ha, which was later increased to 17 000 ha. Ten chuditch were monitored using radio-collars for the first 12 months and then by trapping only. In the first 12 months following fox baiting, trap success rates were stated as increasing significantly. Trap success in the unbaited area was low (0–1.2%) compared to the baited area (1.2–8.6%), however, trap success was not assessed prior to control commencing in the baited area and trap success on the unbaited area was an order of magnitude less than on the treated site. It is therefore possible that chuditch abundance may have naturally varied between baited and unbaited areas and the observed differences may not necessarily be a result of fox predation. Morris *et al.* (1995) also reported an increase in trap success rates of brush-tailed bettongs (or woylie, *Bettongia pencillata*), common brushtail possum and southern brown bandicoots (or quenda, *Isoodon obesulus*) in the baited areas, and in addition to changes in numbers these species broadened their distribution following fox control.

Study 11: Operation FoxGlove

During the 1990's the impact of fox control on native fauna in Western Australia has also been investigated in two large control operations.

Operation Foxglove involved aerial baiting of foxes over 400 000 ha of northern jarrah forest from 1993 to 1999 (de Torres 1999). The control was largely designed to determine the optimal frequency of poison baiting (unbaited versus 2, 4 and 6 baitings per year), with fauna responses to baiting monitored at each site. Monitoring included sand plot indices for fox abundance, radio-telemetry of translocated populations of woylies, radio telemetry of common brushtail possums, and trapping and spotlight counting of a suite of native fauna. Preliminary results in regards to native fauna response to fox baiting are inconsistent, as radio-telemetry monitoring has shown significant differences in survivorship of translocated woylies between treatments, while trapping data showed no significant difference in abundance between treatments for the three most frequently trapped native mammals.

High-intensity (6 baitings per year at 5 baits per km^2) fox control in northern jarrah forest in Western Australia over 6 years has not resulted in a population increase of quokkas (*Setonix brachyurus*). Low recruitment has been suggested as the cause for the lack of response in this species (Hayward *et al.* 2003). However, habitat preferences are suggested as a potential limiting factor with no evidence presented to show that foxes have been killing quokka.

Study 12: Red-tailed Phascogale

Friend and Scanlon (1996) reported on the effect of fox control on populations of red-tailed phascogale (*Phascogale calura*) in the Western Australian wheatbelt. Trapping grids were established to monitor numbers of red-tailed phascogale on nine reserves in 1993, two of which received no fox control, three received fox control since 1985, and four received fox control since 1994. Trap success data from 1994 to1996 suggested that fox control benefited populations of red-tailed phascogale; however, it was also noted that rainfall and population abundance from the previous year are strongly related, which obscures the effect of other factors.

Study 13: Western Shield

Project Western Shield, is a fox management program that involves the application of poison baits (4 baitings per year at 5 baits km^2) on 3.6 million ha of Western Australia. This project was formally launched in 1996 and is currently in operation. Native species (particularly small mammal) abundance is monitored at 40 sites, using a range of techniques including trapping and spotlighting, and nest boxes to monitor fauna not readily trapped. Mammal reintroductions have also occurred at sites where foxes are being controlled, and these reintroductions are also monitored. At the time of writing the results of this

project were being prepared for publication by the Department of Conservation and Land Management, Western Australia (CALM) and were not available for inclusion in this review.

Study 14: Project Deliverance

In 1995, Project Deliverance was established in Eastern Victoria. This project aimed to measure the response of medium-sized native mammals to broad-scale fox control. Three locations, the West Coast, East Coast and Stony Peak sites were established (A. Murray, pers. comm.). Each location comprised a poisoned 'treatment site' and a paired unpoisoned 'non-treatment' site. 1080 FoxOff bait was buried in bait stations spaced at 1 km intervals, with baits being replaced every 3-4 weeks. Non-poisoned baits were laid at the same rate and intensity on the non-treatment sites (A. Murray, pers. comm.). The sites were between 7000 and 14000 ha and were paired to match dominant vegetation community and structure, topography and geographic location.

Medium-sized mammals were cage-trapped on both treated and non-treated sites by placing 60 cage traps at 300 m intervals along a single transect in each treatment and non-treatment site. Traps were operated for several days four times per year from 1998 to 2003.

Preliminary results from this project indicate that long-nosed potoroos (*Potorous tridactylus*) and southern brown bandicoots (*Isoodon obesulus*) may have responded positively to the fox control treatment.

Summary

The assumption underlying these fox control operations is that species thought to be at risk will respond to a reduction in fox abundance. While there have been increases in population estimates for some species at some locations, the response has been variable. Many of the studies reviewed have not assessed pre-control population parameters, lack control sites, have no replication, do not attempt to assess changes in fox and/or cat abundance, and plausible alternative hypothesis remain untested. Little is known on the impact of changes in rabbit abundance following predator control on native species, and the importance of differences in underling prey vulnerability to predation.

The rock-wallaby studies in Western Australia serves to highlight the difficulty in interpreting the results from studies into predator–prey interactions, and the need for well designed and implemented programs that will enable robust analysis resulting in reliable information.

There still remains uncertainty of the effect of fox control on 'at-risk' species and uncertainty about the consequences for rabbit, and cat populations, and their impacts on 'at-risk' species despite decades of publicly funded research. Some of this uncertainty may be addressed if funding providers insisted on peer-reviewed publication of results.

4.1.3 Control of feral cats only (implications for primary and alternative prey)

Feral cats are thought to have had a destructive impact on a wide array of native vertebrate fauna (Atkinson 1985, Dickman 1996). The impact of feral cats have been most obvious on islands (Nogales *et al.* 2004), in part, as native species have evolved in the absence of such a predator, and due to a general lack of appropriate anti-predator behaviour.

Feral cats either acting alone or in association with factors such as rabbits or rats and mice, has been considered responsible for the local extinction of a number of species on islands. For example, predation by feral cats, that were supported by high numbers of introduced rabbits, was the mechanism that caused the extinction of the Macquarie parakeet, (*Cyanoramphs novaezelandiae erythrotis*) on Macquarie Island (Taylor 1979). This pattern is considered to be widespread across Australian islands (Burbidge 2002).

The eradication of feral cats from islands has been achieved a number of times on islands around Australia and the world (Algar *et al.* 2002Harper and Dobbins 2002; Wood *et al.* 2002; Rauzon *et al.* 2002). The impact of feral cats on mainland Australia is poorly understood. They are cited as the primary cause for the failure of a reintroduction program of Rufous hare-wallabies (*Lagorchestes hirsutus*) in the Tanami Desert in Western Australia (Gibson *et al.* 1994; Christensen and Burrows 1995).

Despite several years of research (Algar and Sinagra 1996; Algar *et al.* 1999), control programs aimed at reducing feral cat abundance are hindered by a number of factors, including the limited reliability of the available indices to accurately assess changes in abundance, and by the lack of efficient control techniques.

We know of no control operations or research that has specifically investigated the relationship between feral cats and rabbits in isolation from foxes and/or dingoes. It is unclear whether or not feral cats are capable of regulating rabbits, or that feral cat populations show a numerical response to a reduction in rabbit numbers. It is also unclear what effect feral cat control alone has on populations of native species.

Table 1. Examples of studies in Australia that have experimentally assessed the impact of predation on rabbit population densities through manipulations of predator densities. T = Treatment, NT = Non-treatment sites.

Study	Location	Study area	Habitat	Duration of study (years)	Experimental treatment	Techniques used	T & NT sites	eplication	Key rabbit population density changes	Factors other than predation considered
Newsome *et al.* (1989)	New South Wales	3 sites, 50–180 km^2 per site	Semi-arid	2	Fox and cat removal	Rabbit and predator abundance	Yes	n=1–2^b	Increased 11.7 times on T sites compared with 2.8 times on NT sites	Drought Food supply
Pech *et al.* (1992)	New South Wales	3 sites, 50–180 km^2 per site	Semi-arid	5	Fox and cat removal^a, followed by no predator removal	Rabbit and predator abundance, Predator diet	Yes	n=1–2^b	T site populations remained higher than the NT sites, despite reintroduction of predators	Drought Myxomatosis
Banks *et al.* (1998)	Canberra	4 sites, 10 km^2 per site	Sub-alpine Forest	2	Fox removal	Rabbit and predator abundance	Yes	n=2	T sites increased 6.5 and 12 times compared to 2 times and a decline on NT sites	None
Banks (2000)	Canberra	4 sites, 10 km^2 per site	Sub-alpine Forest	1 ½	Allowed foxes to re-invade sites	Rabbit and predator abundance	Yes	n=2	One T site declined and remained low following predator reinvasion. Other T site declined, then increased by 23%	None
Risbey (2000)	Heirisson Prong	3 sites, 120 - >200 km^2	Semi-arid	5	Fox and cat removal	Predator abundance	Yes	No	Two T sites increased while no change on NT site.	Rainfall

^{a} Predator removal was carried out by Newsome *et al.* (1989) ^{b} Level of replication changed during the study.

Summary

Improving the level of reliable knowledge on the interactions between feral cats, foxes and rabbits will increase our capacity to manage the impact of predation on populations of native species and when to undertake integrated control.

A potential cost of predator control is the release of rabbits from regulation resulting in a numerical increase in rabbit abundance, which may cause increased competition for food with native herbivores (Dawson and Ellis 1979; Dawson and Ellis 1994). The damage by rabbits is well documented (Williams *et al.* 1995), but the impact of rabbits on native species is poorly understood (Robley *et al.* 2001, 2002).

Several studies suggest that predators can exert prolonged regulating pressure on rabbits at low densities and can impede recovery of rabbit populations. This is particularly so when those populations have already been significantly reduced through external perturbations of density-independent extrinsic factors such as disease, drought, high or low rainfall, floods, and warren ripping (Newsome *et al.* 1989). However, predator manipulation studies over a wide range of habitats have provided inconsistent evidence of predator regulation of rabbits. Predation appears to play an important role in regulating prey populations in some arid systems under certain conditions (e.g. after drought has reduced rabbit populations), but has weaker effects in more temperate environments or when environmental conditions improve and prey escape regulation. In contrast, in New Zealand, Reddiex (2004) found that predation, at least when combined with RHD, is a significantly stronger process in temperate than semi-arid regions. It is important to note that many of these studies were undertaken prior to the escape of RHD in Australia. The potential regulatory effect of RHD on rabbit populations and the effect this could have on rabbit–predator interactions are largely unknown.

The impact of changes in predator and primary prey abundance on native mammal species has been the focus of few experimental studies. Several studies that have discussed the role of predation (feral cats and foxes) in regulating rabbit populations have not investigated the benefits or costs of predator control to native species. Other studies that have investigated the impact of fox and cat control on native small mammal species reported benefits from pest control; however, there are many acknowledged limitations of these studies. Many of the studies did not assess pre-control population parameters, did not have control sites, were not replicated, and did not attempt to test alternative hypotheses, such as competition by herbivores.

Several studies have reported that fox removal has benefited a range of native species. However, there are several notable exceptions (e.g. mixed responses of small mammal abundance from Operation FoxGlove, Project Eden, and Project Deliverance).

The only site we reviewed where foxes, feral cats and rabbits were controlled was the Arid Recovery Program in South Australia (Moseby 2002). A positive response in small mammal species was reported at this site; however, we have not seen detailed results from the study. An interesting observation of the study was the reported increase in avian predators and the shift in the reptile community structure, possibly in response to changes in vegetation brought on by the removal of rabbits (Moseby 2002). This highlights the complex and interactive nature of ecosystem management.

One of the major limitations in the manipulative experiments described above is the short time frame of the studies. For example, Banks (2000) monitored rabbit and predator populations for 16 months following re-colonisation of study sites by foxes; however, this period only covered one breeding season for foxes. Ideally, manipulation studies should cover a time period sufficient to allow variation in temporal trends to be accounted for in the analysis. Also, many studies lack either a treatment and non-treatment comparison or at least before and after measures of abundance. The latter is not ideal, as direct comparisons are confounded by temporal changes (e.g. rainfall from the previous year, Friend and Scanlon 1996). Another difficulty is that most studies reviewed did not quantify the abundance of alternative predators (e.g. feral cats or native predators) or whether they were even present in the study areas. The potential influence of these species may confound the interpretation of the reported results.

There is a need for more manipulative experiments to examine the role of predation in regulating rabbits, particularly in temperate environments, and the impacts a range of rabbit abundances have on native prey species. These studies need to control for the effects of other regulating factors if they are to test unequivocally the role of predation in altering rabbit abundance and the impacts on native species and/or communities. These studies need to operate at a spatial and temporal scale that encompasses the full range of environmental factors that are likely to influence the dynamics of rabbit populations in a given area, and those of their predators. However, it may be difficult to temporally or spatially manipulate some

potential regulating factors (e.g. diseases) on an appropriate scale.

Alternatives to large-scale experimental manipulations include engaging management agencies to use control operations as large-scale experiments (Walters 1986, NSW NPWS 2001, Robley and Wright. 2003). Another approach is the development of predictive population models. These models can be used to explore the sensitivity of the various parameters that are critical to predator–prey dynamics, and identify areas on which management and experiments should focus.

4.2 Interactions Between Feral Cats and Foxes

In Australia, little is known of the relationships between feral cats and foxes. Mesopredator release (*sensu* Soulé *et al.*1988) occurs when a dominant predator is reduced in abundance, thus allowing a population increase in lower-order predators that results in an increase in predation on shared prey species. Mesopredator release has been documented in a range of studies. For example (in the following format: dominant predator, lower order predators, prey): Coyotes (*Canis latrans*), foxes (*Vulpes* spp.), skunks (*Mephitis* spp.), domestic cats and small birds (Soulé *et al.* 1988; Estes 1996); Iberian lynx (*Felis pardina*), mongoose (*Herpestes ichneumon*), and rabbits (Palomares *et al.* 1995); coyote, red fox, and duck (Sovada *et al.* 1995); coyote, badger, gray fox, bobcats, jack-rabbits and rodents (Henke and Bryant 1999); coyote, gray fox, cat, opossum, and scrub-feeding birds (Crooks and Soulé 1999). Several other studies have inferred potential mesopredator release from changes in abundance of sympatric predator species (e.g. Dekker 1986; Litvaitis and Harrison 1989; Sargeant *et al.* 1993; Lindstrom *et al.* 1995). The key mechanism that may enable a dominant predator to have an effect on mesopredator populations is interspecific competition (e.g. exploitation or interference competition) and/or intraguild predation (e.g. direct predation).

The potential for mesopredator release of feral cats as a result of changes in fox abundance is of most concern, but poorly understood. These species overlap in their distribution (Figure 3), there are many areas where fox control is undertaken throughout Australia and where these species co-occur (Figure 4) and very few control operations directly target feral cats. The potential for interspecific competition between foxes and feral cats is supported by the numerous studies that have described a strong dietary overlap between the two species from the same sites (Table 2).

The majority of studies reviewed reported that the diets of both feral cat and foxes included rabbits, birds, reptiles, rodents, invertebrates, and plant material. Most of these studies have been undertaken in systems where rabbits were the dominant dietary species (i.e. primary prey; but see Sandell 1999).

Several studies observed that the relative importance of secondary prey species varied between predators (Bayly 1978; Catling 1988; Risbey *et al.* 1999). For example, Risbey *et al.* (1999) found that sheep carrion and invertebrates were more prevalent in the diet of foxes, and native rodents, birds and reptiles were more prevalent in the diet of feral cats. Molsher (1999) reported an overall dietary overlap between foxes and feral cats of 75%, but also reported that foxes and feral cats used many of the same prey types in different proportions. The removal of foxes from one of Molsher's (1999) sites resulted in a significant increase in the frequency of carrion consumption by feral cats compared with the sites where foxes were not controlled, but there were no other significant differences for any of the other prey types. It is believed that foxes and feral cats co-exist in many areas due to specialisation of different age classes of rabbits, with feral cats focusing on juvenile rabbits and foxes on adult rabbits (Catling 1988). Jones (1977) and Liberg (1984) have also reported a preference of feral cats for juvenile rabbits.

The potential for dietary competition between foxes and feral cats may be exacerbated in periods such as droughts or following disease outbreaks (e.g. myxomatosis or RHD) where food resources, particularly young rabbits, become limited. Few of the studies listed in Table 2 attempted to compare diet with prey availability, and those that have focused on rabbit abundance (e.g. Molsher 1999; Read and Bowen 2001; Holden and Mutze 2002). Molsher (1999) reported a positive correlation between the occurrence of rabbit in the diet of both feral cats and foxes and rabbit abundance. Read and Bowen (2001) reported that diet between foxes and feral cats were similar when rabbit numbers were high, but varied substantially when rabbit numbers were low. Holden and Mutze (2002) investigated the impact of RHD on feral cat and fox diet in South Australia. Fox diet changed to include substantially less rabbit, and more invertebrates and carrion, while there was little change in cat diet.

In general, diet studies showing a high degree of overlap support the concept of interspecific competition between feral cats and foxes, but they do not demonstrate such a relationship.

Dietary studies aside, little is known about the interaction between feral cats and canids (Dickman

1996). Dingoes have been reported to directly predate feral cats (Corbett 1995) and foxes (Coman 1973; Molsher 1999; Risbey *et al.* 1999), however, the incidence was extremely low. From a sample of 15 dietary studies covering Victoria, New South Wales, Northern Territory and Western Australia, and comprising 2133 fox stomachs and 7718 fox scats, the remains of feral cats occurred only four times. There is no evidence to determine whether these were a result of direct predation or scavenging dead individuals, though Risbey *et al.* (1999) suggested that direct predation was likely in their study.

Several studies have described increases in cat abundance following reductions in fox numbers resulting from control operations (Algar and Smith 1998; Catling and Reid 2003), and following local declines in dingo abundance in Queensland (Pettigrew 1993). Christensen and Burrows (1995) observed a three-fold increase in the abundance of feral cats in the Gibson Desert, and suggested this increase was likely a result of exceptional rainfall resulting in a large numerical response of rabbits. Catling and Burt (1995) have also reported that the abundance of feral cats is negatively correlated with both foxes and dingoes at a site in New South Wales. Read and Bowen (2001) did not manipulate predators, but reported that cat abundance peaked when fox numbers were low and when rabbit numbers were relatively high.

Risbey *et al.* (1999) suggested that fox control at Heirisson Prong could lead to a mesopredator-like response resulting in an increase in cat abundance. This prediction was based on the observation of cat remains in fox diet studies, and hence it was inferred that intraguild predation occurred. This prediction was tested in a subsequent study, (Risbey *et al.* 1999) where fox and cat numbers were counted on spotlight transects and small mammals were surveyed by live capture methods in areas where fox and cat populations were controlled (see section 4 study 3 for further detail on the experimental design of this study). At the site where only foxes were controlled, spotlight counts of feral cats increased three-fold over three years, but small mammals declined in numbers (indexed by captures/100 trap nights).

Despite the limitations in the experimental design of this project (Risbey *et al.* 1999), they believed that the above results were sufficient to infer that fox control may lead to increased abundance of feral cats. Molsher *et al.* (1999) investigated the potential for competition between feral cats and foxes by concurrently comparing diet, home range and habitat use, and using video observation and simultaneous radio-tracking to study avoidance and aggression between both feral cats and foxes at Lake Burrendong, New South Wales, between 1994 and 1997. The extent of the perceived interspecific competition was investigated using a fox-removal experiment. The study area comprised two treated areas, foxes were removed on one and reduced by 50-75% on the second, and two untreated areas, where foxes were not controlled.
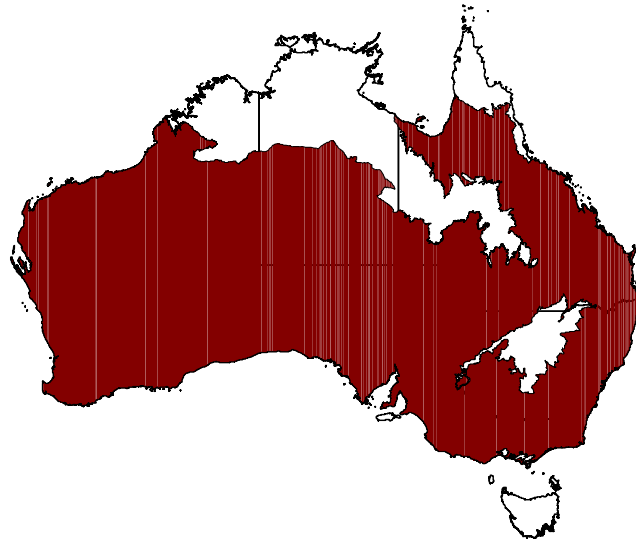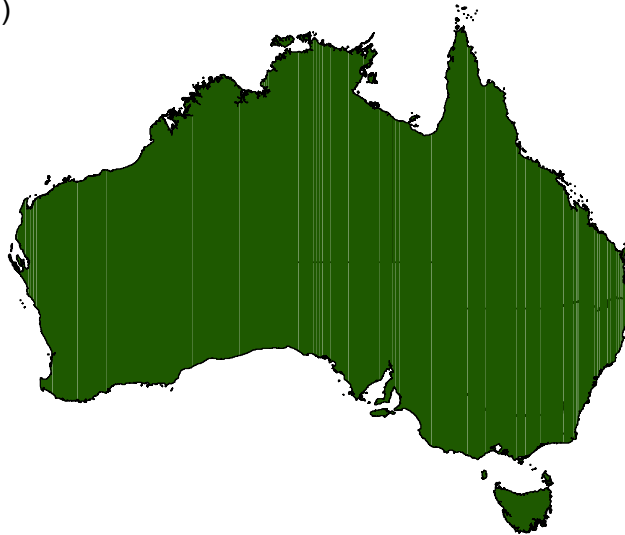
Figure 3. Distribution of a) fox, b) feral cat and c) European rabbits in Australia.
(Source: Environmental Resource Information Network, Department of the Environment and Heritage).

Figure 4. Location and extent of a) feral cat (n =96) and b) fox control (n = 777) operations in Australia.
(Reddiex *et al.* 2004). Area of control operations (ha) not shown to scale.

Table 2. Examples of comparative feral cat and fox diet studies in areas where rabbits are present.

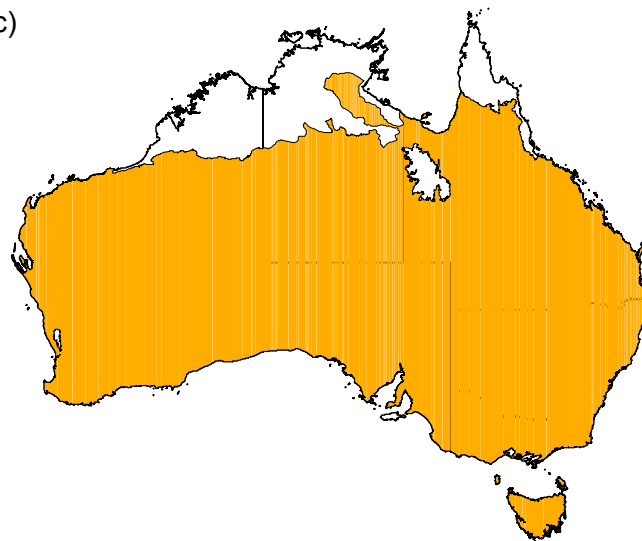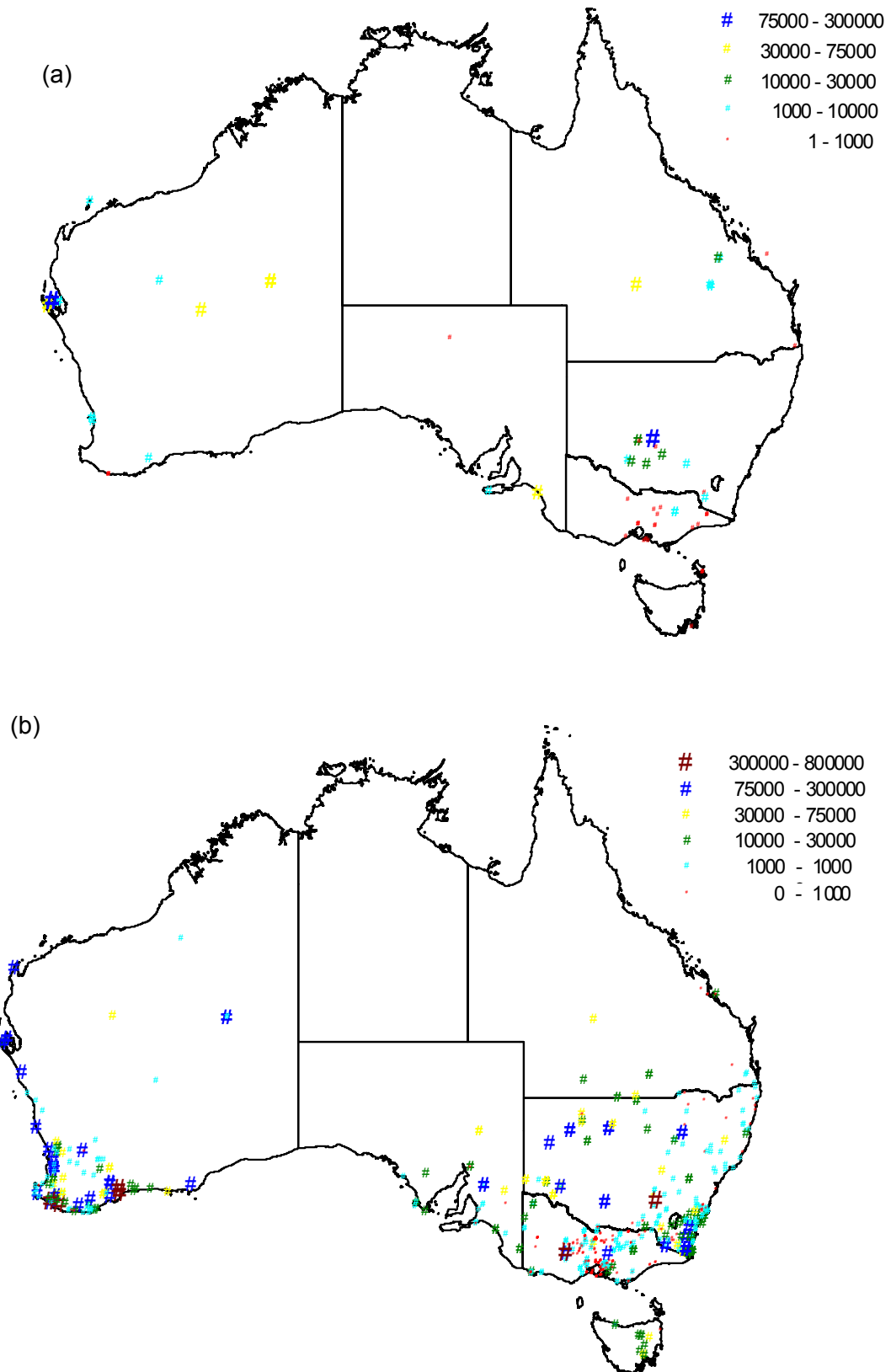| Study	Location	Stomach or scat	Technique used to assess diet	Number of fox samples	Rabbit in fox diet (% occurrence)	Number of cat samples	Rabbit in cat diet (% occurrence)
Bayly (1978)	Mt Lyndhurst, SA	Stomach	Percent occurrence	29	44.5	21	68.2
Catling (1988)	Yathong Nature Reserve, NSW	Stomach	Percent occurrence	288	45.1	112	54.0
Molsher (1999)	Lake Burrendong, NSW	Scats	Percent occurrence & Volume	343	52.2	499	81.6
Risbey *et al.* (1999)	Heirisson Prong, WA	Stomach	Percent occurrence	47	76.6	171[A]	49.1
Read and Bowen (2001)	Roxby Downs, SA	Stomach	Percent occurrence	105	~0-100	516	~22-70
Holden & Mutze (2002)	Flinders Ranges, SA	Stomach	Percent occurrence	Pre-RHD 105 Post-RHD 774	Pre-RHD 63.1 Post-RHD 6.9-15.7	Pre-RHD 73 Post-RHD 294	Pre-RHD 37.3-46.2 Post-RHD 9.8-35.6

[A] Feral cats (n=109) and Semi-feral cats (n=62) combine

A large overlap in resource use, home range and diet between feral cats and foxes suggested a high potential for competition. In both areas where foxes were controlled there were significant behavioural changes, including increased use of carrion and increased use of grassland habitat. Molsher *et al.* (1999) suggested that these behavioural changes indicated interspecific competition; however, as acknowledged by the author, there was no increase in cat abundance over the 2.5 years following the control of foxes, therefore mesopredator release cannot be demonstrated statistically. Interference competition was also recorded, with three radio-collared feral cats believed to be killed by foxes, and foxes were observed acting aggressively towards feral cats. However, no cat remains were found in any of 255 fox stomachs or 343 fox scats, suggesting that if intraguild predation did occur it was relatively rare.

A major limitation of many of the above mentioned studies is that reported increases in cat abundance following fox control may in fact be an artefact of the census methods rather than an actual increase in cat abundance. Indices of cat abundance using track counts may increase following a reduction in foxes; however, this may be related to changes in cat activity patterns not changes in abundance (Molsher 1999). While spotlighting is often undertaken over an inappropriate transect length for predators and/or is assessed at an appropriate scale for rabbits, but not predators.

Monitoring changes in abundance of introduced predators can be expensive and problematic as these species are often cryptic, elusive and occur in low densities. It is often not necessary to measure the actual number of individuals in a population or the number within a given area, as these measurements can be labour intensive and expensive, and in the majority of ecological investigations unnecessary (Krebs 1999). Instead, indices of density that are correlated with absolute density are useful (Caughley 1977). Unfortunately, the current techniques available (bait take, spotlight counts, sand plot activity and scat counts) are generally imprecise, and/or have restrictions on their application. The relationship between changes in the index and actual abundance remains untested. There is a need for further development of more reliable techniques to accurately assess changes in the abundance of predator species in Australia.

Summary

Feral cats and foxes overlap in distribution and diet, and there is circumstantial evidence of interspecific competition, where foxes may competitively exclude feral cats from food resources, and of intraguild predation where foxes may prey upon feral cats.

Foxes, but not feral cats have been controlled over large areas, and there is a possibility that impacts on shared prey can increase following fox control if feral cat numbers increase after fox control.

Several studies have described increases in cat abundance following reductions in fox numbers resulting from control operations. However, the evidence for a numerical response in cat abundance following fox control is inconsistent between studies and may be confounded by inadequate survey techniques and behavioural changes that may influence cat activity.

There remains a great deal of uncertainty on mesopredator release of feral cats following fox control, but it would not be surprising if adequately tested, given the above circumstantial evidence.

4.3 Change in Abundance of Primary Prey (Rabbits)

The European rabbit, which occupies 90% of Australia (Figure 3), forms the major component of the diet of feral cats and foxes in many areas, particularly the pastoral zones of southern Australia (Coman and Brunner 1972; Myers and Parker 1975a,b; Brooker 1977; Jones and Coman 1981; Jarman 1986; Catling 1988; Dickman 1996; Paltridge *et al.* 1997; Molsher *et al.* 1999; Risbey *et al.* 1999).

Rabbits may influence the persistence of native species by increasing the population size of a shared predator. In their review of patterns of decline and extinction of Australian rodents, Smith and Quin (1996) concluded that high levels of rabbits and house mice may have supported foxes and feral cats leading to declines and extinctions of native prey species; they term this process, 'hyperpredation'. Jarman (1986) noted that where rabbits supported numerous foxes, more vulnerable species such as rat-kangaroos or bandicoots may be subjected to unsupportable levels of predation. In north-eastern New South Wales, Rufous rat-kangaroos (*Aepyprymnus rufescens*) persist only where foxes and rabbits were scarce (Schlager 1981), and Christensen (1980) argued that densities of brushtailed bettongs (or woylies *Bettongia penicillata*), foxes and rabbits are similarly related in south-western Western Australia. It was thought that predation by feral cats (supported by high numbers of introduced rabbits) was the mechanism that caused the extinction of the Macquarie parakeet) on Macquarie Island (Taylor 1979). Parakeets and feral cats coexisted for 60 years before rabbits were introduced onto the island, with feral cats being presumably controlled by density-dependant mechanisms. Within 20 years of the introduction of rabbits, parakeets and banded rails had become extinct. It was suggested that rabbits provided a year round food supply, supporting feral cats at high densities, thus increasing predation on alternative prey.

Smith and Quin (1996) suggested that declines and extinctions in native species are more likely: to occur in areas where rabbits, rats and mice are abundant and the alternative prey species are terrestrial; fall within the prey-size class of dingoes (which can predate almost any prey-size), foxes and feral cats (that are restricted to small and medium-sized prey); and have low reproductive

rates with poorly developed anti-predator behaviour.

In many parts of Australia, particularly semi-arid and arid areas where drought is common, rabbit populations fluctuate markedly (Williams *et al.* 1995), and a lagged increase in predator numbers can result (Saunders *et al.* 1995; Read and Bowen 2001). However, when rabbits decline, either as a result of drought or disease, or through rabbit control operations, it is possible that predators may switch their consumption to the next most abundant alternative prey (Pech and Hood 1998; Table 3).

Prey switching occurs when the proportional contribution of a species to a predators diet does not match its relative abundance (Murdoch 1969; Murdoch and Oaten 1975). While prey switching has not been demonstrated for feral cats or foxes in Australia, some work has been undertaken on their numerical and dietary response to changes in rabbit abundance and in some instances the changes in abundance of alternative prey (see section 4.3).

In a review of the potential impacts on Australian native fauna of RHD, Newsome *et al.* (1997) noted that there was little rigorous evidence of impacts of predation on wildlife populations as primary prey (rabbits) collapse. This was regardless of the mechanism that caused the crash (i.e. drought, myxomatosis or conventional control). Their report was commissioned as RHD escaped Wardang Island of the South Australian coast in 1995 and was spreading across the Flinders Ranges in South Australia. Since then, there have been a number of studies on the impacts of reduced rabbit numbers (mainly) resulting from RHD on the abundance of feral cats and foxes. Far fewer studies have simultaneously investigated changes in predator diet and the flow-on effects to alternative prey species, and many of these have been conducted over short (<2 years) timeframes.

This section reviews the interactions between a reduction in primary prey (rabbit) on feral cats, foxes and native carnivores and the effects of these predators on alternative prey. We review the impact on each predator individually and the potential impact on alternative prey.

4.3.1 Effects of changes in abundance of primary prey on feral cat abundance and impacts on native prey

There are a limited number of examples in the published literature that illustrates the relationship between a change in rabbit abundance and a change in the abundance of feral cats. By far the majority of evidence comes from studies in semi-arid and arid Australia.

Study 1: Yathong Nature Reserve

Newsome *et al.* (1989) and later Pech *et al.* (1992) reported on a predator-removal experiment at Yathong Nature Reserve, New South Wales, conducted between June 1981 and January 1984. This area can be classified as semi-arid, with a mean annual rainfall of 200–350 mm. The experimental design for the Newsome *et al.* (1989) study was, 1) removal of predators over one area of 70 km^2 (Block A), 2) no predator control was undertaken on two areas of 180 and 50 km^2 (Blocks B & C, respectively). After one year of the study Block B was sub-divided and predator control commenced over a 90-km^2 area (Block B1) of the Block to examine repeatability and site specificity of the results. No predator control was undertaken on the remaining area (Block B2). Pech *et al.* (1992) advanced the above study by analysing an additional experiment beginning in mid-1983. Predator-removal continued in Block A, but only limited predator-removal occurred in Block B1. Control of predators ceased in all sites in August 1983 and they were allowed to reinvade the experimental blocks. In both studies densities of rabbit and predator populations were assessed on all sites by spotlight counts. The effects of predator-removal on native prey were not assessed in either of these experiments. On sites where no predator control was undertaken spotlight counts of feral cats were highest (1.5 km^{-1}) in 1979, corresponding with the period of highest rabbit numbers (310 km^{-1}). Pech *et al.* (1992) report that feral cat abundance was linked to the maximum density of rabbits in the previous three months.

Study 15: Flinders Rangers National Park

In the Flinders Ranges National Park, South Australia, Holden and Mutze (2002) reported on a study investigating the impact of RHD on introduced predators from 1994 to 2000. The study involved a combination of fox baiting across the entire park and rabbit control operations (warren ripping) covering 10% of the park. An experimental site was established in 1992, containing eight treatment blocks (each 3–4 km^2). Rabbits were controlled on half the plots. RHD reached the area in 1995. Spotlight transects, each running 2 km long, were established in each treatment block, concentrating on strips 30–60m wide. In addition to this study they conducted a broad-scale study of introduced predators. This covered three areas, a fox baited area, an unbaited area adjacent to the park, and a remote unbaited area. No details of the size of these areas were provided.

On the experimental plots, feral cat numbers declined from ~15 feral cats sighted per 100 km to an average of 3.2, six to ten months after rabbit

populations had declined by 85% due to RHD (Holden and Mutze 2002). No information was provided on changes in cat numbers on the broad-scale sites. In the year following the arrival of RHD, the previously distinctive seasonal dispersal peaks in cat abundance were absent. The lack of rabbits to support recruitment into the population was cited as a major reason for the decline in feral cat numbers across all areas of this study. However, the authors noted that cat numbers increased through 1996-97 in the National Park concurrent with an increase in house mice in the diet. No measure of changes in abundance were made for house mice, thus this result needs to be interpreted with caution.

Study 16 Roxby Downs

Read and Bowen (2001) reported on the population dynamics of feral cats and foxes in relation to changes in rabbit abundance over a ten-year period between 1989 and 1999. Outbreaks of myxomatosis and RHD occurred in 1993 and 1996, respectively. Changes in feral cat, fox and rabbit abundance were monitored using spotlight counts along two 20 km transects.

Feral cats reached a peak density of 3 km^{-2} prior to the release of RHD. Rabbit populations declined following the release of RHD (Read and Bowen 2001), and cat populations were reported to have subsequently declined. However, no figures were provided on the relative abundance of feral cats post-RHD.

Study 17: Lake Burrendong

At Lake Burrendong, in central New South Wales, Molsher *et al.* (1999) reported no clear change in the abundance of feral cats to changes in rabbit abundance. Rabbits at Lake Burrendong declined following the arrival of RHD from ~18 km^{-1} to <5 km^{-1} six months later. Cat numbers were low six months after high rabbit numbers. However, changes in feral cat numbers were also weakly correlated with the abundance of carrion, small mammals (4-month lag), reptiles (1-month and 2-month lag), and grasshoppers (3-month lag). These authors suggest that behavioural responses altering the sightability of feral cats may account for recorded changes in population size rather than actual numerical responses associated with changes in prey abundance.

Study 18: Northern Territory

Edwards *et al.* (2002a) report on population trends in rabbits and other wildlife following the arrival of RHD in the Northern Territory. They used spotlight counts conducted at 3-monthly intervals along 10 km transects over two successive nights. They recorded an 85% reduction in rabbit numbers across six locations in the Northern Territory, but no detectable decline in feral cat numbers. The

authors noted that a weakness in their study was the lack of a control site where RHD was not present, and that they could not separate out environmental effects.

In a related study that covered 2.5 years, Edwards *et al.* (2002b) established paired ripped and unripped warren plots on four of the above sites. Rabbits were monitored via spotlight counts along a fixed transect of 10 km, and populations of feral cats, foxes, and dingoes were monitored using track counts along the same transect. Both before and after the arrival of RHD, there was significantly less sign of feral cats on sites where rabbit warrens were ripped compared to unripped sites.

Study 19: RHD Monitoring Program

The RHD Monitoring and Surveillance Program was established to monitor the impacts of the spread of RHD on biodiversity (Neave 1999). This program covered 10 intensive (Table 3) and 54 broad-scale monitoring sites, collectively covering all the principal biomes occupied by rabbits in Australia. At each of the intensive monitoring sites, attempts were made to assess changes in the abundance of rabbits, small to medium-sized mammal fauna, other fauna (birds, macropods and wombats), predators and vegetation (pasture and perennials). The RHD science sub-committee set standard methods for the collection of data at each of the ten sites (Neave 1999). However, on many of the sites native species response monitoring was stopped after a year or two due to a lack of response or a shortfall in funding.

Sandell and Start (1999) summarised the results from the Australia-wide RHD monitoring program and the implications for biodiversity. They reported that a decline in feral cat numbers following the arrival of RHD was recorded on 6 of 10 intensive monitoring sites. These were the Nullarbor Plain (anecdotal only), the Northern Territory (one of which was included in Edwards *et al.* 2002b above), the Flinders Ranges (one being reported by Holden and Mutze 2002 above), on the central tablelands of New South Wales, and at Hattah-Kulkyne National Park. At this latter site, sightings of feral cats during the course of rabbit spotlight transects were the only measure available. An average of 0.025 feral cats per km was recorded from ten spotlight counts prior to the arrival of RHD (137 km of transect). An average of 0.01 feral cats per km was recorded from six spotlight counts post-RHD (Sandell and Start 1999).

At two of the RHD monitoring sites there was no pre-RHD data available and reports of decline were only anecdotal. It was not possible to establish control sites (i.e. RHD absent) at any of the monitoring locations.

However, several sites had pre-RHD data on rabbit numbers, in some cases predator numbers, and only at Lake Burrendong, in parts of Hattah-Kulkyne, Flinders Ranges and Nullarbor was there any information on native fauna pre-RHD in relation to feral cat and rabbit abundance.

4.3.2 Effects of changes in abundance of primary prey on feral cat diet and impacts on native prey

Feral cats have a catholic diet, but prefer live prey. Younger rabbits appear to be a staple of their diet when abundant, but a number of diet studies indicate that they are capable of eating a variety of items including small mammals, birds, reptiles, invertebrates and carrion (Dickman 1996).

Study 1: Yathong Nature Reserve

Catling (1988) found that feral cats displayed a Type III functional response (see section 4) to rabbits at Yathong Nature Reserve, New South Wales but only during the rabbit-breeding season. Cats ate fewer rabbits when the rabbit population was low and when fewer young rabbits were in the population, but more when the rabbit population was increasing. When rabbits were scarce (or declined after the breeding season), feral cats changed their diet to include (in order of importance) invertebrates, birds, reptiles and small mammals. This resulted in an annual prey cycle. Catling (1988) made no assessment of alternate prey species abundance so it is not possible to infer what the impact of this change in diet would have on populations of native species.

Study 15: Flinders Rangers National Park

In the Flinders Ranges, (South Australia), Holden and Mutze (2002) reported that despite a significant decline in rabbit abundance following RHD, the remaining cat population continued to prefer rabbits in their diet (pre-RHD rabbits occurred in 42% of cat stomachs n=73, versus 24%, n=293 post-RHD). Reptiles and birds were consumed at a similar rate pre- and post-RHD, but invertebrates became a more frequent item in feral cat diet post-RHD. No assessment was made of changes in the abundance of alternative prey, so the potential impact cannot be discussed.

Study 20: Roxby Downs

At Roxby Downs, South Australia, rabbits were the most important component of feral cat diet when rabbit counts exceeded 10 km^{-2}; below this figure other vertebrates increased in importance (Read and Bowen 2001). The authors suggested that the decline in cat abundance, following the decline in rabbits, was buffered by the ability of feral cats to shift their hunting to include a wide range of native vertebrates. Generally, feral cats were reported to

consume prey in proportion to its availability, thus when rabbit populations crashed feral cats consumed small sand-dwelling lizards, with house mice and small passerines also contributing to their diet (Read and Bowen 2001). The impact on alternative prey cannot be discussed, as changes in abundance of alternative prey were not assessed during this study.

Study 17: Lake Burrendong

At Lake Burrendong, New South Wales, rabbits remained the dominant prey type of feral cats despite a 90% reduction in rabbit numbers (Molsher *et al.* 1999). There was no evidence of feral cat numbers proportionally increasing consumption of reptiles, invertebrates or small native mammals after rabbit abundance had declined. However, house mice were found to form a significant component (100% occurrence in scats in autumn and 43% in winter) of the cat diet 10 months post-RHD. Previously, house mice had not occurred in more than 19% of cat diet.

Study 21: Hattah-Kulkyne National Park

Cavanagh (1998) and Sandell (1999) assessed changes in feral cat diet pre- and post-RHD at Hattah-Kulkyne National Park. Four cat stomachs were collected pre-RHD and eleven were collected post-RHD. Feral cats consumed mammals, invertebrates, reptiles, and birds, with rabbits being the staple prey item. The authors acknowledged that sample sizes were small but suggested that post-RHD feral cats shifted their diet from rabbits to birds (50% by occurrence and 16% by volume pre-RHD to 67% and 88% post-RHD).

Study 22: Tanami Desert

Paltridge (2002) investigated the diet of feral cats, foxes and dingoes in relation to prey availability at two separate sites in the Tanami Desert, Northern Territory, between 1995 and 1997. Rabbits were absent from this study area. Monitoring focused on changes in abundance of invertebrates, reptiles, and small mammals via pitfall and Elliott trapping 3 times per year. Bird species were monitored along 1 km walked transects using distance sampling methods. Macropods, goannas and bilbies were monitored by track counts along 10 km track transects. The diet of predators was assessed (frequency of occurrence) through analysis of scats collected along the track transects and from active searches.

In the absence of rabbits, feral cats relied on reptiles as a summer staple with an increased reliance on birds during winter when reptiles where less active. In most cases the relative abundance of prey items in the diet of feral cats followed that of their relative availability. The consumption of small mammals (both sites) and skinks (one site) was strongly correlated with their field abundance.

Feral cats showed a marked increase in the consumption of birds, prior to an increase being detected in the field. However, the author suggested that bird abundance had actually increased but the survey technique failed to record the increase.

4.3.3 Effects of changes in abundance of primary prey on fox abundance and impacts on native species

The fate of foxes and rabbits has been linked since their introduction to Australia some 130 years ago. It has been suggested that the spread of the fox across Australia was in part facilitated by the presence of rabbits, which had been introduced earlier (Saunders *et al.* 1995). However, the interactions between rabbit abundance and foxes and the impacts on native fauna have only been investigated more recently.

Study 19: RHD Monitoring Program

Declines in spotlight counts of foxes were reported following the arrival of RHD at four (Nullarbor Plains, Muncoonie, Hattah-Kulkyne and Tablelands) of the nine national RHD monitoring sites (Sandell and Start 1999; an additional site was located in Tasmania where foxes were absent)(Table 3). At two sites (Nullarbor and Flinders Ranges subsite) the reports of decline were only anecdotal. Two sites reported no long-term change in fox abundance (Lake Burrendong and Northern Territory aggregated sites) and one site was not assessed due to low fox densities (Coorong). As mentioned earlier, these findings need to be interpreted with caution.

Study 16: Roxby Downs

At Roxby Downs, high fox numbers coincided with peaks in rabbit abundance. Fox densities peaked at >3 km^{-2} one year after rabbit densities peaked at ~375 km^{-2}, but declined to <0.5 km^{-1} several months after rabbit populations crashed following the arrival of RHD. Foxes were rarely seen for the two years of this study (Read and Bowen 2001).

Study 15: Flinders Rangers National Park

In the Flinders Ranges National Park, Holden and Mutze (2002) reported that fox numbers were reduced by 96% (54 per 100 spotlight km to 7.8 spotlight km) following a fox-baiting program. After the arrival of RHD fox abundance declined to 1.6 per 100 spotlight km with a lag of about 6 months. The authors suggested that the reduction in rabbit numbers was partially responsible for the additional decline. The authors noted that a critical impact on fox numbers was the lack of rabbits during the rabbit-breeding season; this resulted in no peak in rabbit numbers, which normally

supports recruitment of juvenile foxes (Holden and Mutze 2002).

Study 18: Northern Territory:

In contrast to the above studies, Edwards *et al.* (2002a) reported that following an 85% reduction in rabbit numbers across six locations in the Northern Territory there was no detectable decline in fox numbers (see section 4.3.1 for comments on the limitations of this study).

Sandell (1999) reports on the changes in rabbit, fox and native species following the arrival of RHD at Hattah-Kulkyne, Victoria. This site comprised six sub-sites, at which rabbits were monitored via spotlight counts and active warren entrance counts. Warren entrance counts did not commence until after the arrival of RHD, as did spotlight counts at one of the six sites. Spotlight counts were conducted over a total of 108 km per annum from 1991 to 1999, with sampling repeated at least once.

Sandell (1999) reports that at two of the sites in the Hattah-Kulkyne National Park, pre-RHD spotlight counts for rabbits ranged between 2 and 8 km^{-1}, but have remained below 0.5 km^{-1} since the arrival of RHD. At the site in the Murray Sunset National Park, pre-RHD counts ranged from 0.2 to 6 km^{-1}, while post-RHD counts did not exceed 0.3 km^{-1}. On the dryland agricultural site rabbit counts declined from an average of 4 per km pre-RHD to 1.2 per km over a two year period following the arrival of RHD.

Fox abundance was assessed during quarterly spotlight counts for rabbits between 1990 and 1999. Sandell (1999) reports that there was no decline in fox abundance coincident with the decline in rabbits following the arrival of RHD. The data are aggregated from a series of transects in the Murray Sunset National Park totalling 137 km. Cavanagh (1998) reports that rabbits did not appear to be the staple prey item of foxes pre-RHD, rather foxes relied on carrion and reptiles, which buffered the impact of rabbit population decline on the fox population.

Scats collected on an annual basis between 1995 and 1999 from Mallee Fowl (*Leipoa ocellata*) nests were also used to assess a change in relative abundance of foxes (n=568). Sandell (1999) concluded that there was a significant decline in the proportion of nests at which fox scats were collected and attributed this to a decline in fox abundance. Sandell (1999) also assessed active fox dens quarterly on five Mallee Fowl monitoring grids between 1996 and 1999 by repeat visits. The average proportion of dens occupied decreased through time. The author suggested that the combined information from scat counts and active dens indicate a steady decline in fox abundance

following the arrival of RHD. However, for both of these observations no statistical tests or details of variance in the data were presented. Several alternative hypotheses for changes in scat accumulation and den activity are possible. It is possible that repeat visits to the same dens may have resulted in the decline in occupancy by foxes through time, and that changes in food resources, environmental conditions or fox population structure may have influenced defecation rates.

4.3.4 Effects of changes in abundance of primary prey on fox diet and impacts on native prey

At Yathong Nature Reserve, New South Wales, foxes appeared to display a Type III functional response (Pech *et al.* 1992) to increasing rabbit numbers during winter and spring, eating more rabbits during the rabbit breeding season than during the non-breeding season. Once the rabbit breeding season had finished, foxes relied more on supplementary prey items (in decreasing order of importance): invertebrates, reptiles, carrion and birds (Catling 1988). However, no assessment of abundance was provided and it is therefore not possible to properly quantify the functional response of foxes to alternative prey.

When rabbits were abundant (>10 km^{-2}) at Roxby Downs, South Australia, they formed the major dietary component for foxes, occurring in more than 70% of fox stomachs. Post-RHD, when rabbit abundance declined, foxes shifted from their pre-RHD reliance on rabbits to mainly invertebrates and slow moving fossorial reptiles (Read and Bowen 2001). Despite the presence of a range of small native mammals (three native mice, two hopping-mice and two dunnart species) house mice was the only small mammal species consumed by foxes (Read and Bowen 2001).

In the Flinders Ranges National Park, South Australia, rabbit was the most common prey item taken by foxes pre-RHD, occurring in 65% of stomachs (n = 105). Post-RHD, where rabbit populations were reduced by 85%, the occurrence of rabbit in fox stomachs was only 16% (n = 774; Holden and Mutze 2002). The authors reported an apparent shift in diet towards more invertebrates, reptiles and kangaroo (carrion from harvesting operations). The authors acknowledged that the limited availability of pre-RHD dietary data made it difficult to determine clearly the change in fox diet (Holden and Mutze 2002).

Sandell (1999) assessed changes in fox diet at the Hattah-Kulkyne RHD monitoring sites in Victoria, by analysing stomach and scat contents. Eleven stomachs were collected pre-RHD and 57 post-RHD. Foxes consumed mammals, reptiles, birds,

fish/crustaceans, invertebrates and vegetation. Sandell (1999) found that carrion was the most important component of fox diet pre-RHD (55% by occurrence and 36% by volume) and that this did not change post-RHD (52% and 41% respectively). Cavanagh (1997) further analysed these data and concluded that the risk of foxes shifting from rabbits to other prey post-RHD was minimal.

Saunders *et al.* (2004) looked at changes in fox diet pre and post RHD. They collected fox stomachs from undulating to hilly lowland country, around Orange, NSW. The area has an annual rainfall of between 500 and 800 mm. RHD arrived at the site in 1996 and was widely established by the end of that year. The authors state that RHD had an effect in the rabbit population but do not provide data on the size of the effect. Foxes were shot at night throughout the year between 1995 and 1998. Foxes were divided into pre (n=240) and post (n=269) RHD samples.

Dietary data was analysed as both percentage occurrence (%O) and percentage by volume (%BV). These authors found no dramatic RHD-induced differences in fox diet. Rabbit comprised 20.8 %O and 16.2 %BV pre-RHD and 19.3 %O and 16.1 %BV post-RHD. There was an increase in the %BV consumption of rodent. This was related to an eruption of house mice numbers. There was no detectable shift to increase predation rates on other prey (sheep, macropod, possum, bird, reptile, invertebrate or plant).

Saunders *et al.* (2004) suggested that the combination of drought (which preceded the arrival of RHD) and RHD had acted in concert to suppress rabbit abundance below a critical threshold resulting in a lack of shift in dietary selection.

Paltridge (2002) monitored changes in the diet of foxes in two areas of the Tanami Desert, where rabbits do not occur. The author found that in contrast to dietary studies elsewhere in Australia, reptiles were an important component of the diets of foxes and should be classified as seasonal staples. When reptiles were less active during winter, birds increased in importance in the diet of foxes.

Of the dietary studies reviewed, only Edwards *et al.* (2002a) described changes in the abundance of native carnivores and alternative prey with a decline in primary prey (rabbit abundance). They report that there were more dingoes and varanids post-RHD and less wedge-tailed eagles. The authors noted that the data for wedge-tailed eagles was highly variable and should be interpreted with caution. Similarly, they report no change in the relative abundance of red kangaroos or small mammals, but that these data are also highly variable. This variability combined with a lack of

experimental non-treatment sites, means that these results need to be interpreted cautiously.

In the Northern Territory, Edwards *et al.* (2002b) studied the effect of warren ripping on rabbits and other wildlife. They found that there was less sign of foxes and feral cats on ripped plots than on unripped plots, but could not detect a change in the abundance of red kangaroos, small mammals or raptors following a decline in rabbit numbers.

Summary

Rabbits are common throughout 90% of Australia and have been associated with the spread of the fox since its arrival 130 years ago. The association between the abundance of rabbits and feral cats is less well understood.

Increased predator density may result from a reliance on abundant staple prey (e.g. rabbits). This may result in a numerical increase in predator species, which may have implications for predation rates on some native species if the predator species that increases specialises in certain prey types. Perturbation experiments looking at changes in staple prey abundance and dietary responses of predators, in conjunction with population studies of predators and prey would provide a test for this hypothesis.

The use of predator manipulation studies or the monitoring of RHD outbreaks has provided insights into the interaction between changes in the abundance of rabbits and the flow-on effects to predators and alternative prey. The level of our understanding of the interactions varies between biogeographical regions in Australia.

In semi-arid and arid areas of Australia, where rabbits are the primary prey of feral cats and foxes, the abundance of both predator species appears to be strongly correlated with rabbit abundance. The abundance of both predators is associated with peaks and troughs in rabbit abundance, and both predator species show a lagged decline in abundance of 6 to 12 months after rabbits are substantially reduced. In temperate environments this relationship is less well understood, and in the few studies in these habitats foxes and feral cats have not shown the same marked response to changes in rabbit abundance. In areas where rabbits are not the primary prey, or where environmental conditions and/or disease have suppressed rabbit populations below a critical threshold, the decline in rabbits has had no measurable effect on the abundance of these predators.

In a few examples the use of integrated control (ripping, RHD or poison baiting and RHD) has enhanced the decline in predator species.

A number of studies have assessed changes in the diet of feral cats and foxes with changes in rabbit abundance. In arid and semi-arid systems, where rabbits were abundant, feral cats were able to kill rabbits even at low densities or to shift to alternative prey species, including lizards, house mice and birds when rabbits were less abundant providing some buffering against declining rabbit populations. In temperate habitats, house mice may play an important role in supporting feral cat abundance, acting as staple prey. Foxes in these areas appeared less capable of killing rabbits at low densities and relied more on invertebrates and reptiles.

In areas where rabbit populations had been suppressed, either by environmental conditions, disease, or in areas where rabbit populations are 'naturally' at low densities, it appears that changes in rabbit abundance have little effect on the diet of foxes. Little is known about feral cat diet in this situation.

Feral cats and foxes also occur in areas where rabbits are either absent or uncommon. In arid areas where rabbits are absent, invertebrates and reptiles comprise the bulk of the diet of foxes, with rare or endangered small mammals comprising a relatively small proportion of their diet (Paltridge 2002). Rabbits are uncommon in the higher altitude areas of Australia where prey availability varies seasonally (Osborne *et al.* 1978). In these areas invertebrates are the major dietary item of foxes in snow free months, with native small mammals found in all months but reported as the winter staple (Green and Osborne 1981).

From the studies reviewed it is unclear what the impact of a decline in primary prey is on native species. In the studies reviewed in this report, both feral cats and foxes shift consumption to the next most abundant prey item, (e.g. mice, invertebrates, reptiles, or birds). There is no evidence that as a result of a decrease in primary prey there is an increase in predation rates on populations of rare or endangered species. We are not discounting that this is a real possibility. Rather, we were unable to find or access studies that demonstrate such an effect.

Our level of understanding of the interactions between feral cats, foxes and rabbits in temperate environments is less clear. The relationship between changes in rabbit abundance and declines in either feral cats or foxes has not been clearly demonstrated and no information is available that demonstrates that a change in rabbit abundance leads to increased rates of predation on native species.

Table 3. Examples of studies that have assessed the impact of changes in rabbit population densities on predators and alternative prey.

T = Treatment and NT = Non-Treatment.

Study	Location (# sites)	Study Area (ha)	Habitat	Duration (months)	Treatment	Technique Used	T & NT Sites	Replication Yes / No	Key Changes in population	Changes in alternative prey
Pech et al. 1992	Yathong, NSW		Semi-arid	30	Pre-control	Spotlight counts	Y	Y	Increase in # rabbits	Not monitored
Holden and Mutze 2002	Flinders Ranges NP, SA	400 each	Arid	36	RHD	Spotlight counts	P&P	n = 10	Decline in feral cats	Monitored
Read and Bowen 2001	Roxby Downs, SA	20 km transects	Arid	10 yrs	RHD	Spotlight counts	P&P	N	Decline in feral cats	
Molsher et al. 1999	Lake Burrendong, NSW	90 km^2 30 km transects	Temperate	3 yrs	RHD	Spotlight counts Small Mammal Trapping Active searches	P&P	N	Decline in feral cats	Monitored
Edwards et al. 2002a	Multiple sites, NT	10 km transects	Arid	2.5 yrs	RHD	Spotlight counts	P&P	n = 4	No Decline in feral cats	
Edwards et al. 2002b	Multiple sites, NT	20 – 140 km^2	Arid	2.5 yrs	RHD / Warren ripping	Spotlight counts Track Counts Small Mammal Trapping	Y (Warren ripping only)	n = 4	Decline in feral cats	
Sandell and Start 1999	Nullarbor Plain, WA	25 km transect 21 km transect	Arid	16	RHD	Spotlight counts	N	N	Decline in feral cats and foxes	Monitored
	Central Australia sites	400 each	Arid	36	RHD	Spotlight counts	P&P	n = 4	Decline in foxes but not in cats	Monitored
	Muncoonie Lake, QLD	1050	Arid	24	RHD	Spotlight counts	N	N	Decline in foxes, not in feral cats	Monitored
	Balcanoona / Wertaloon, SA	400 each	Arid	24	RHD	Spotlight counts	N	n = 4	[A]Decline in foxes and feral cats	Monitored
	Hattah, VIC	~700 each	Semi-arid	24 - 84	RHD	Spotlight counts	P&P	n = 6	Decline in foxes, not in feral cats	Monitored

P&P = Pre and Post treatment monitoring, A = Anecdotal, NA = not assessed due to low numbers

Table 3 cont/.

Study	Location (# sites)	Study Area (ha)	Habitat	Duration (months)	Treatment	Technique Used	T & NT Sites	Replication Yes / No	Key Changes in population	Changes in alternative prey
	Coorong, SA	60–120	Temperate	24	RHD	Spotlight counts	Y	N = 2	NA	Monitored
	Lake Burrendong, NSW	800–1200	Temperate	24	RHD	Spotlight counts	N	N	No decline in foxes	Monitored
	Central Tablelands, NSW	250 each	Temperate	48	RHD	Spotlight counts	P&P	n = 3	Decline in foxes and cats	Monitored
	North Tasmania	1500	Temperate	24	RHD	Spotlight counts	P&P	N	No decline in feral cats	Monitored
Catling 1988	Yathong, NSW		Semi-arid	30	Pre-control	Spotlight counts	Y	Y	Cat & Fox show Type III response to rabbits	Not monitored
					Diet study	Freq. Occur				
Cavanagh 1998 & Sandell 1999	Hattah, VIC	~700 each	Semi-arid	24–84	RHD	Spotlight counts	P&P	n = 6	Cat shift in diet from rabbit to birds	Monitored
					Diet Study	Freq. Occur/vol.				

P&P = Pre and Post treatment monitoring, A = Anecdotal, NA = not assessed due to low numbers

4.4 Interactions Between Native and Introduced Predators, and Rabbits

4.4.1 Canids

Dingoes, domestic dogs (*Canis lupus familiaris*) and their hybrids (collectively known as wild dogs) occur throughout most of mainland Australia, and while dingoes can be considered native species, the functional role hybrids play in the ecosystem may be sufficiently similar for them to be considered as acting like native dingoes. The distribution wild dogs overlaps with both feral cats and foxes (Fleming *et al.* 2001) and rabbits (Figure 3).

Over the past 30 years, the diet of wild dogs has been extensively studied. While over 170 species have been identified (Corbett 1995), 80% of the diet of dingoes comprised only 10 species. These were: red kangaroos (*Macropus rufus*), rabbit, swamp wallaby (*Wallabia bicolor*), cattle, dusky rat (*Rattus colletti*), magpie goose (*Anseranas semipalmata*), common brushtail possum long-haired rat (*Rattus villosismus*), agile wallaby (*Macropus agilis*) and common wombat (*Vombatus ursinus*) (Corbett 1995).

Mitchell (2003) studied the dietary and spatial overlap of wild dogs and foxes in the Greater Blue Mountains. He examined scats collected from 10 sites in autumn and winter 2002 (a minimum of 25 scats were collected for each species from each site). Mitchell (2003) also undertook a meta-analysis of 19 previous studies from eucalypt woodland/forest areas that compared fox and wild dog diets. Mitchell concludes that the diets of foxes and wild dogs showed a high degree of overlap, and suggested that this was evidence for potential competition. This author also found that at a fine scale there was some indication of temporal avoidance, but that at a landscape scale foxes and wild dogs co-existed.

Given the potential for dietary overlap and the overlap in distribution of all three predators, there is potential for wild dogs to suppress, either through competition or direct predation, populations of feral cats and/or foxes (Jarman 1986; Robertshaw and Harden 1985; Thompson 1992; Corbett 1995; Fleming *et al.* 2001). However, this has yet to be confirmed experimentally.

On the Nullarbor Plain, Western Australia, foxes and wild dogs were reported to be able to co-exist because foxes were able to hunt rabbits inside wild dog territories and possibly escape conflict by using rabbit warrens (Thomson and Marsack unpubl. data in Fleming *et al.* 2001). In forested areas in south-eastern Australia, there was no evidence of exclusion or avoidance by foxes of wild dogs (Catling and Burt 1995). Thus, it is possible that only when resources are limited that foxes and wild dogs come into conflict. Foxes appear to avoid wild dogs in central Australia at sparsely separated watering points (Fleming *et al.* 2001) and at carcasses of kangaroos and cattle during drought (Corbett 1995).

The interactions between feral cats and wild dogs are poorly understood. The two species co-occur in many areas of Australia (Figure 3) and wild dogs are capable of consuming food items that are also eaten by feral cats, and wild dogs have been recorded occasionally eating feral cats (Fleming *et al.* 2001).

The distribution of wild dogs and the spotted-tailed (*Dasyurus maculatus)*, western (*Dasyurus geoffroii)*, and northern quoll (*Dasyurus hallucatus*) overlap, but the nature of any interactions between wild dog and quoll species is not understood.

4.4.2 Dasyurids

4.4.2.1 Quolls

No studies have investigated the interactions of any of the quoll species with foxes, feral cats or changes in primary prey abundance. This is despite the fact that at least two of the four species of quoll kill rabbits when available (Belcher 1995).

Quolls are smaller than both feral cats and foxes, with the spotted-tailed quoll, the largest quoll species ranging from 1.5 to 4 kg. The eastern quoll (*Dasyurus viverrinus*) ranges from 0.8 to 1.3 kg, the northern quoll ranges from 0.5 to 0.8 kg and the western quoll (or chuditch) ranges form 0.8 to 1.3 kg. In comparison, adult red foxes weigh between 4.5 and 8.3 kg (Coman 1983), and adult feral cats have been reported to weigh as much as 6.2 kg (Jones 1983).

Potential interactions between quoll species and introduced predators could arise through interspecific competition (e.g. exclusion via aggressive competition) and/or intraguild predation (e.g. direct predation). Given the overlap in diet (see below) and size differences: competition or predation remains an untested possibility. It is also possible that with a reduction in feral cats and/or foxes, quoll species may increase in abundance (i.e. mesopredator release; see section 3.2).

Spotted-tailed Quolls

Belcher (1995) studied the diet of the spotted-tailed quoll in East Gippsland, Victoria, and found it to be largely dependent on medium-sized mammals (0.5 to 5 kg). The most important prey

species were the European rabbit, the common brushtail possum and the common ringtail possum (*Pseudocheirus peregrinus*). Other prey included *Antechinus* species, bush rats (*Rattus fuscipes*), echidnas (*Tachyglossus aculeatus*), macropods, wombats (*Vombatus ursinus*), birds, invertebrates, and reptiles. A shift in diet between years was attributed to the variation in rainfall and the effect this had on prey species abundance, suggesting that this predator, like foxes and feral cats (see above) selects prey items in relation to their abundance. Significant differences in diet were found between adult and sub-adult quolls. Sub-adult quolls consumed significantly more small mammals, ringtail possums, invertebrates and reptiles, and significantly fewer rabbits than adult quolls. Belcher (1995) found that medium-sized prey contributed more than 80% of the biomass of prey consumed.

Two unpublished studies provide additional information on dietary overlap and interactions with introduced predators. Alistair Glen at the Institute of Wildlife Research, University of Sydney, New South Wales, is currently investigating comparative diet and habitat use of foxes and spotted-tailed quoll in coastal forest in New South Wales. Unpublished data from this study indicates that quolls are killing rabbits near the margins of the forests (A. Glen pers. comm.). The New South Wales National Parks and Wildlife Service is investigating the impact of bush fires on quolls, in particular diet in the Byadbo region. Preliminary results suggest that the abundance of rabbits and possums decreased immediately post-fire, but the proportions of rabbit in the quoll diet increased (J. Dawson, pers. comm.). Interestingly, the remains of a cat were found in a single quoll scat in this study. Whether this was carrion or not is unknown.

At Lake Burrendong in New South Wales, Molsher *et al.* (1999) compared the diet of feral cats and spotted-tailed quolls and suggested that there was enough overlap for potentially exploitative competition, although the author notes that the sample size of quoll scats was small (n=12). The author found that rabbits were the main prey item of both species with invertebrates second in importance.

Other Quoll Species

Little information is available on the interactions between the remaining quoll species and feral cats and foxes. The three smaller species are active hunters, preying on invertebrates, small mammals, birds, lizards, frogs and plant matter. Invertebrates, particularly arthropods, form an important component of their diet (Blackball 1980; Godsell 1982; Johnson and Roff 1982; Begg 1983; Serena *et al.* 1991; Soderquist and Serena 1994).

Oakwood (2000) studied reproduction and demography in northern quolls and reported that the most common proximate cause of mortality was predation, probably by dingoes Morris *et al.* (2003) suggested that the western quoll (or chuditch) could be detrimentally impacted by foxes through direct predation of young quolls, and/or competition for food as both species overlap in diet (Coman 1973; Lunney *et al.* 1990; Soderquist and Serena 1994).

4.4.3 Raptors

Newsome *et al.* (1997) provides a comprehensive review of the potential impacts of a decline in rabbits on raptors in Australia. They identified that four of the 24 raptor species in Australia relied on rabbits as a major dietary item and another five utilise rabbits as alternative prey when abundant. In order of significance the top four are the wedge-tailed eagle (*Aquila audax*), little eagle (*Hieraaetus morphnoides*), brown falcon (*Falco berigora*) and brown goshawk (*Accipiter fasciatus*).

Newsome *et al.* (1997) reported that, in general, in areas where wedge-tailed eagles rely on rabbits, a decline in rabbits would result in a decline in either the number of adult birds, clutch size or young produced. Evidence presented by Ridpath and Brooker (1986) indicates that wedge-tailed eagles would not breed if rabbit abundance fell below 60 km^{-2}. At the Western Mining Company Olympic Dam site 4–5 wedge-tailed eagle nests were regularly observed to raise 2 chicks each prior to the arrival of RHD. Post-RHD no successful nests were seen for 4 years (John Read pers. comm.).

Little eagles are probably reptile specialists, but take advantage of abundant rabbit populations. They can survive almost exclusively by feeding on young rabbits in spring. It has been reported that peaks in laying season coincide with the peak in rabbit breeding season (Baker-Gabb 1984; Mallinson *et al.* 1990; Olsen and Marples 1992 in Newsome *et al.* 1997). The potential impact of a reduction in rabbit abundance on this species is poorly understood.

Apart from utilising rabbits in both winter and spring little else is known about the interactions between brown falcons and rabbits. Like brown falcons, the brown goshawk consumes a considerable amount of rabbit during winter and spring, and where rabbits are not available birds, reptiles and invertebrates form the major dietary components (Newsome *et al.* 1997).

Raptors were monitored at several of the RHD monitoring sites (see section 4.3), but no clear relationship between short-term changes in abundance and breeding output and declines in rabbits was demonstrated (Sandell and Start

1999). This was partly due to the high degree of variation in density of territories, breeding pairs and the number of young produced per year, the size of monitoring sites, small samples sizes, seasonal variations in climatic conditions, and no measures of alternative prey consumption.

Edwards *et al.* (2002a) reported that in the Northern Territory, although populations of raptors (including wedge-tailed eagles, little eagle, brown falcon and brown goshawk) fluctuated post-RHD, no significant reduction in populations were detected. In a related study, Edwards *et al.* (2002b) investigated the impacts of warren ripping on rabbits and other wildlife. They reported that rabbits were less abundant on ripped plots both before and after the arrival of RHD, but that there was no treatment effect on the abundance of raptors, including brown falcons and brown goshawks. A limitation on this study was that it only ran for 2 to 3 years, and that ripped areas were relatively small compared to the territories of large raptors. This may not have been long enough to detect numerical changes in populations following declines in rabbit abundance.

4.4.4 Varanids

No studies have investigated the interactions of any of the varanids with foxes, feral cats or changes in primary prey abundance. There are 26 described species of goanna (the terms 'monitor' and 'goanna' are interchangeable) in Australia. All are carnivorous, consuming almost anything that can be caught and eaten. Varanids are active diurnal hunters which stalk, run down or dig out their animal prey: smaller species take larger insects, spiders and small frogs, lizards and snakes; larger species hunt lizards, snakes, small birds and mammals but also feed on carrion. Species that are capable of or known to consume rabbits include the perentie (*Varanus giganteus*), sand monitor (*Varanus gouldii*), lace monitor (*Varanus varius*), and yellow-spotted monitor (*Varanus panoptes*) (King and Green 1999).

Most species are active for only six months of the year, but become most active during late spring and summer, which coincide with the emergence of young rabbits and increases in rabbit numbers. Williams *et al.* (1995) made reference to an increase in numbers of goannas with an increase of rabbits. If rabbits comprise a significant component of their diet then these varanids might be affected by a decline in rabbit numbers.

Summary

Little quantitative information is available on the interactions between introduced predators and native carnivores. The information that is available suggests that dingoes and wild dogs may be capable of suppressing fox populations, but that this is likely to be mediated by specific environmental conditions such as drought. There is perhaps stronger evidence to suggest that foxes spatially and temporally avoid wild dogs and that only during times of limited resources do the two come into direct conflict.

Similarly, there is a lack of knowledge on the impacts of feral cats and foxes on quoll species. While there is some information to indicate that there is potential for a negative effect through competition or direct predation, this is also likely to be moderated by specific environmental conditions (e.g. drought or fire altering prey composition or abundance).

A reduction in the abundance of a shared primary prey item (e.g. rabbits) may result in increased competition, direct aggression, increased levels of predation on alternative prey (both from native and introduced carnivores), any of which has the potential to negatively impact on native carnivore populations.

The available evidence suggests that wedge-tailed eagles are likely to experience a reduction in numbers if a reduction in rabbit abundance is significant and sustained. While other raptor species (little eagle, brown falcon and brown goshawk) utilise rabbit when abundant or at particular times of the year, it is less clear what the outcome would be for these species. Further quantitative information is required for these species.

The current detail of information available for varanids is insufficient to be able to draw any conclusions about the impact of changes in these predators or rabbit abundance. Studies on the role varanids play in the predator–prey dynamics of the Australian ecosystem are required.

5   Interactive models of pest population dynamics

A major aim in ecology is to produce dynamic models that allow us to predict the effects of changing parts of the system. To date this has proved largely unattainable, particularly in natural systems (Abrams 2001). Part of the problem lies in the complex nature of these systems, but also in a lack of focus on the components of many of the relationships such as the functional response (Abrams 2001).

Interactive models

Interactive models attempt to model the relationships advocated by Abrams (2001) and have been used in Australian systems because of the strong environmental variability characteristic of these systems. They were pioneered in Australia by Caughley (1987) and colleagues (Bayliss 1987), who used them to model kangaroo population dynamics. At the base of the model is rainfall, (Figure 5) which drives pasture production and pasture senescence. Herbivore offtake from pasture is determined by the functional response of the herbivore to pasture. The numerical response, or instantaneous rate of increase of the herbivore, is expressed in terms of the biomass of grassland vegetation. For a more mechanistic approach rate of increase should be expressed in terms of intake rate, rather than the density of the resource.

Pech and Hood (1998) developed a three trophic level interactive model for a semi-arid system: with grassland vegetation at the bottom level, rabbits and a model native Australian prey in the middle level, and foxes at the top level. Their model was developed to explore whether reduced rabbit abundance due to RHD was likely to benefit or negatively affect native prey subject to fox predation. Their model calculated rabbit population rate of increase as a function of pasture biomass, but adds a term to account for fox predation on rabbits.

They made numerous assumptions because of the lack of detailed information on many of the critical parameters for a model of this type. The first major assumption was that there is a relationship between fox population rate of increase and rabbit density, which we explore below.

Another key parameter was determined in their model by trial and error, to produce population dynamics broadly consistent with those that occur in the field. They set minimum densities on rabbit and fox populations to stop them going extinct in the model. These assumptions make the predictive power of these early models uncertain,

and it is likely the conclusions from them are qualitative rather than quantitative.

Here we set out to refine and extend the Pech and Hood (1998) model. We aim to make the model more predictive, but recognise this will be constrained by whether we can identify critical interactions for these species, and by the data available. The simplest models express rates of increase of consumer species in terms of the abundance (or intake) of resources ('prey'), so our initial intention was to find relationships between rates of increase for foxes and/or feral cats in relation to the abundance of rabbits. Unfortunately, data were not available to do this. We focus initially on semi-arid systems, because the original model was developed for these systems, but we also explore temperate systems.

One of the problems we have with developing models for these systems is that we don't really know what the population dynamics of the different species are. For rabbits we have a reasonable idea, but for predators our understanding of their population dynamics is very uncertain. A ~20 year data set of Brian Cooke's (unpubl. data) indicates that rabbit populations were generally low (<20 per spotlight km), but showed sharp increases, sometimes up to 400 per spotlight km, and sharp declines in density. This suggests rabbits respond rapidly to good conditions and then crash just as rapidly when conditions deteriorate. Whether rabbits are regulated by predators under certain conditions is not really known, but was suggested by some of the results from Yathong (Newsome *et al.* 1989; Pech *et al.* 1992). For predators, we don't really know whether their populations fluctuate markedly or are reasonably stable despite large fluctuations in rabbit density. We may expect with predators to see recruitment peaks in late summer/autumn, because of their seasonal breeding. This was observed in the Flinders Ranges, but spotlight counts there were over extremely long distances (Holden and Mutze 2002). In many other areas these recruitment peaks are not apparent, possibly reflecting the short spotlight distances and the limitations of spotlight counts for tracking changes in the true density of predator populations.

A modelling framework

We begin with the premise that the important interactions that drive the population dynamics of the species in this system are those shown in Figure 5 and we discuss each of these interactions in detail. This diagram is not exhaustive. For

example, we have ignored native predators in the system.
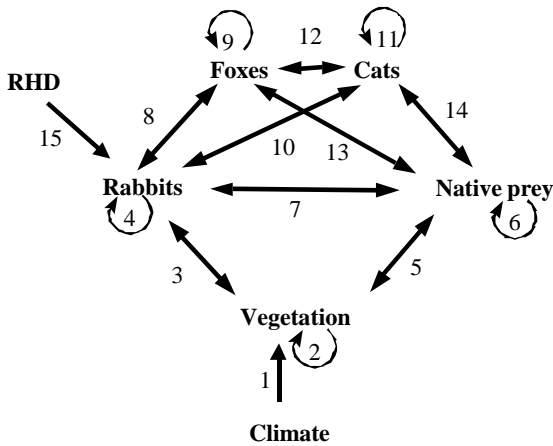
Figure 5. **Interactions in a simplified system.**
Two-way arrows represent interactions that operate in both directions e.g. vegetation affects the growth of rabbit populations and rabbit populations affect the growth of vegetation by consuming it. They do not imply equal strength of the interaction in each direction.

Interactions 1 and 2

The effect of climate on vegetation biomass and growth in Australia in semi-arid systems was quantified by Robertson (1987). Most published interactive models for semi-arid systems in Australia (Caughley 1987; Choquenot 1998; Pech and Hood 1998) have used Caughley's modification of Robertson's (1987) pasture growth model (Caughley 1987; Appendix 1). The model accounts for the fact that pasture growth is determined by both rainfall and standing biomass at the start of the growth period. The latter component represents intra- and inter-specific competition within the plant community (Interaction 2). The model ignores any changes in pasture composition, and assumes an even spatial distribution of pasture biomass.

Interaction 3

Effects of rabbits on vegetation
The effect of rabbits on vegetation was measured by (Short 1987) using an intensive grazing trial in Kinchega National Park. The daily per capita consumption of pasture by rabbits, adjusted for body weight and expressed as kg animal^{-1} day^{-1} is given by equation 2 in Appendix 1. This is an Ivlev form of a type II functional response. No other assessments of the rabbit functional response to vegetation in semi-arid systems were available at the time of writing.

This type of functional response is known as 'prey dependent' because intake for a given body size is

determined by the availability of prey (in this case pasture) only. Other authors have used 'ratio dependent' functional responses, which express intake as a function of both prey and predator density, and there has been some debate over which form is the most appropriate starting point for model building (Abrams and Ginzburg 2000). The original motivation for ratio-dependent functional responses was that predator interference or predator facilitation would affect the intake of prey by predators and hence predator abundance should be taken into account. However, other mechanisms could lead to a ratio dependent functional response being appropriate.

Food is unlikely to be distributed evenly in a landscape, but when we model animal populations with non-spatial models we use spatially-averaged values. The functional response, for example, would reflect the average intake rate of the population. As food declines, we expect the average intake rate of consumers to decline, but we also expect the consumer population to decline in response to this. Those consumers that are left would likely be in areas where food is still relatively abundant and hence the average intake rate of those consumers would appear higher. Figure 5 illustrates this.

For example, for the prey-dependent functional response illustrated in Figure 6, the average intake rate of the population would be ~0.03 kg rabbit^{-1} day^{-1} at an average pasture biomass of 100 kg ha^{-1}. If we only consider a prey dependent functional response then as the rabbit population declines (say from 50 ha^{-1} to 5 ha^{-1}) intake would remain the same. At 5 rabbits ha^{-1}, however, it is likely these rabbits are in areas where pasture biomass is actually higher than 100 kg ha^{-1} even though the overall average biomass is 100 kg ha^{-1}. The average intake per rabbit would hence be higher than would be expected. This type of relationship has important consequences for the models, because it provides a mechanism in the model where animals maintain sufficient intake at low population densities so their populations do not go extinct . A ratio dependent functional response could have the form provided in equation 3 in Appendix 1.
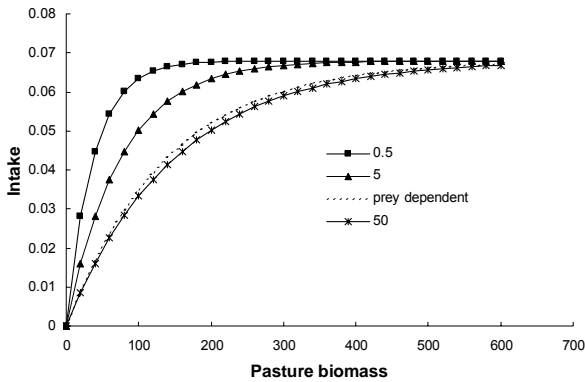
Figure 6. Prey dependent (dotted line) and ratio dependent (solid lines) functional responses.
The values 0.5, 5 and 50 indicate the abundance of the consumer.

We include the functional response of rabbits in our models to take account of their effect on their food supply. However, other herbivores in the system are often ignored (e.g. Pech and Hood 1998), which may cause serious errors if we want to properly account for pasture biomass. Other significant herbivores would be stock (in pastoral areas), kangaroos (Caughley 1987), large feral herbivores such as goats, and invertebrates.

Vegetation effect on rabbit rate of increase
In semi-arid systems rabbits begin breeding in response to rainfall (Wheeler and King 1985; Wood 1980). Pech and Hood (1998) found a relationship between rainfall, lagged three months, and the rabbit rate of increase at Yathong, consistent with this observation. They then modelled the rate of increase of rabbits as a function of standing pasture biomass three months prior, to capture this lag. The relationship used by Pech and Hood (1998) for the quarterly rate of increase of rabbits is provided in equation 4 in Appendix 1. The maximum rate of increase (5.5 - 4.6 = 0.9 per quarter) and decrease (-4.6 per quarter) were estimated by fitting the relationship to data from Yathong during a period of predator control, while the demographic efficiency (0.0045) was estimated by Choquenot (1992). This relationship could be altered to express *r* as a function of intake rather than standing biomass (see equation 5 and 6 in Appendix 1).

The resultant dynamics in a model including rainfall, vegetation and rabbits, where the intake rate is prey dependent and the numerical response is intake dependent, is shown in Figure 7a. Replacing the prey dependent intake rate with a ratio dependent intake rate stops the population from declining to very low levels and allows it to respond more rapidly to improved conditions (Figure 7b).

A more mechanistic approach would be to model rabbit rate of increase as a function of both pasture growth (rabbits respond to growing pasture by breeding), and standing biomass (standing biomass may contribute to rabbit survival), but to our knowledge this has not been attempted and data are not available. (As an example of this approach see equations 7 and 8 in Appendix 1). The behaviour of this model is shown in Figures 7c & 7d. Qualitatively this type of model appears to better reflect the abrupt changes in rabbit abundance evident in semi-arid systems (B. Cooke unpubl. data, Pech *et al.* 1992), but data are not available to parameterise this model properly.

(a)

(c)

(b)

(d)
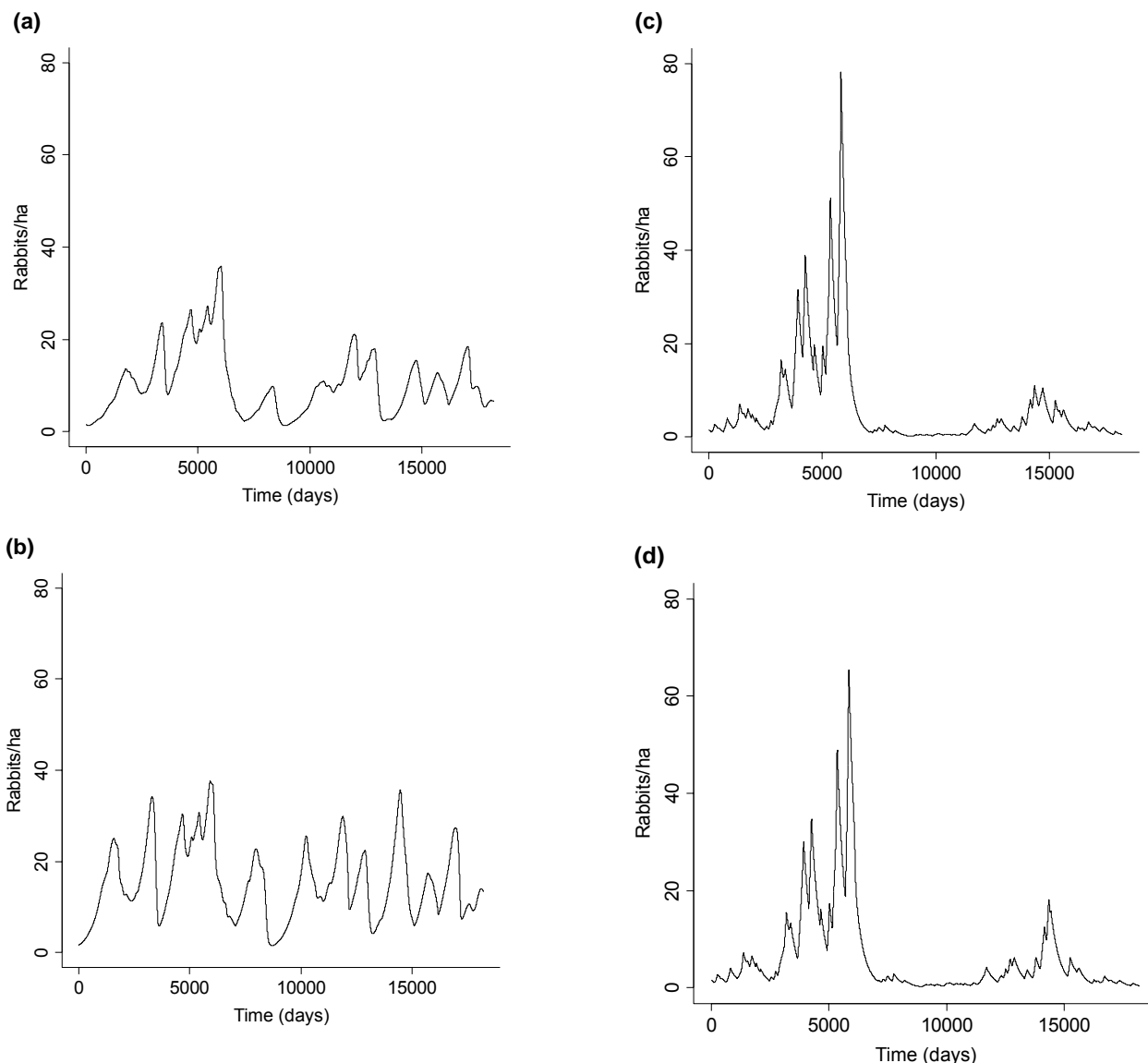
Figure 7. Rabbit vegetation models.
(a) Rabbit-vegetation model with 'prey dependent' intake and the numerical response determined by intake. (b) Rabbit-vegetation model with 'ratio dependent' intake where the numerical response is determined by intake. (c) Rabbit-vegetation model with 'prey dependent' intake, rabbit populations increase in response to pasture growth and decline as a function of intake when pasture is not growing. (d) Rabbit-vegetation model with 'ratio dependent' intake, rabbit populations increase in response to pasture growth, and decline as a function of intake when pasture is not growing.

Interaction 4

Density-dependence in rabbit populations
Interaction 4 allows for unexplained density-dependence in rabbit populations. This could come from social interactions, (see equation 9 in Appendix 1 for the numerical response function). This approach was proposed by Caughley and Krebs (1983) and has been used for possums by Bayliss and Choquenot (2002) and for ferrets and feral cats by Arthur and Norbury (unpubl. data). This has not been considered for rabbits, but there is no evidence to our knowledge that it is necessary for rabbits.

Interaction 5

Native prey effect on vegetation
Two general categories of native prey could be considered: Abundant native prey such as kangaroos, which are likely to have an impact on the vegetation (Caughley 1987); rare and threatened native prey. The latter may be herbivores, or may feed on alternative foods such as insects, but they are unlikely to have significant effects on vegetation biomass at the low densities at which they currently exist.

Effect of vegetation on native prey
The effect of vegetation on kangaroo dynamics was modelled by Caughley (1997) and Bayliss (1987). No data were provided to model the dynamics of threatened native prey in response to vegetation or rainfall in the absence of predators. Pech and Hood (1998) modelled native prey using the same numerical response to vegetation biomass as rabbits, because they were mainly interested in the effect of a different functional response of foxes to the two types of prey. Marsupials have a lower maximum birth rate than eutherian mammals of the same size (Sinclair 1997), which may suggest they have a lower maximum rate of increase than eutherian mammals of the same size. However, rate of increase is determined by both reproduction and survival (assuming closed populations), and Sinclair (1997) suggested that marsupials may have higher survival rates than eutherian mammals of the same size, which offsets lower reproduction. Hence, it is uncertain how native mammals respond to their food supply in the absence of predation. These data are required to properly model the population dynamics of threatened native Australian prey.

Interaction 6

Other Regulating Factors
There are no data available to our knowledge on other factors, such as social factors, which may regulate the abundance of native prey.

Interaction 7

Competitive interactions between introduced and native species
Interaction 7 represents competitive interactions between introduced and native species that are not captured by competition for resources through the functional response (e.g. competition for shelter). To our knowledge few studies have directly addressed competition between rabbits and native species. In one study that did, no evidence was found that competition with rabbits affected burrowing bettongs (Robley *et al.* 2002).

Interaction 8

Effect of foxes on rabbits (semi-arid and arid systems)
In semi-arid systems rabbits comprise a large percentage of the fox diet, particularly when at high density (Pech and Hood 1998). Pech *et al.* (1992) estimated the functional response of foxes to rabbits at Yathong based on the weight of rabbit found in fox stomachs and an estimate of gut passage rates. They fitted a Holling Type III functional response to the data (Holling 1959).

The daily consumption of rabbits in grams per fox per day is given by equation 10 in Appendix 1.

To measure the true impact of foxes on rabbits, kill rates are required. However, these data are not available for semi-arid systems to our knowledge. If the average size of rabbits in fox stomachs is 782 g (Pech *et al.* 1992) this implies that foxes kill a maximum of 1096/782 = 1.4 rabbits day^{-1}. The average field metabolic rate of foxes in the central western tablelands of NSW in autumn was estimated as 2 328 kJ day^{-1} for male foxes (av. weight 5.6kg) and 1 681 kJ day^{-1} for female foxes (av. weight 5.4kg) (Winstanley *et al.* 2003). To yield this much energy requires ~ 435 g of mammalian prey for males and ~ 314 g of mammalian prey for females (Winstanley *et al.* 2003). This is well below the satiating intake estimated by Pech *et al.* 1992, but may provide an estimate of the sustained daily intake rate below which fox rate of increase is negative. However, applicability of these results from a temperate system to semi-arid systems is uncertain.

As with rabbits some form of ratio dependent functional response may be required to capture the likelihood that if fox populations decline in response to lower rabbit densities the average intake of rabbits by the remaining foxes may increase. Data were not available to explore this.

Effect of rabbits on fox rate of increase
The common occurrence of rabbit in the diet of foxes at high rabbit density and the low occurrence at low rabbit density, combined with the observed decline in fox populations following declines in rabbit populations in times of drought (Myers and Parker 1975a; Myers and Parker 1975b; Newsome *et al.* 1989) suggested the abundance of rabbits strongly influences the abundance of foxes. However, it is likely many other foods consumed by foxes are also reduced in abundance during drought, and confirmation of the reliance of foxes on rabbits to maintain high densities requires a reduction in rabbit density when environmental conditions are still good (i.e. times of average or above average rainfall). Before the arrival of RHD in Australia, To our knowledge there is no data for good conditions where rabbit density declined in a semi-arid system, before the arrival of RHD in Australia. The introduction of myxoma virus in the 1950s might have resulted in these conditions but only anecdotal information is available on the consequences for predator populations at that time (Newsome *et al.* 1997).

We have obtained two sets of data from semi-arid systems where fox density was monitored before and after the arrival of RHD. In one, Holden and Mutze (2002) described the response of fox populations to the large reduction in rabbit density

that occurred due to RHD in the Flinders Ranges National Park (FRNP). Rabbit populations dropped from a long-term average of ~32 km^{-1} to ~5 km^{-1} after RHD was first detected at a site that comprised part of the area where fox density was assessed. In the year following the arrival of RHD (1996) the area received average rainfall, while in 1997 it received above average rainfall. These data suggest that rabbit population density had a significant effect on fox population density in the Flinders Ranges. In the other study, at Roxby Downs (Read and Bowen 2001; WMC Olympic Dam unpubl. data), rabbit and fox populations were monitored by spotlight counts across two areas. The fox population declined prior to the arrival of RHD in early 1996, but this was during a period of above average rainfall (1992) making the relationship between rabbit population density and fox population density less certain. After the arrival of RHD the fox population remained low despite good rainfall in 1997.

We analysed the data from the Flinders Ranges in more detail by assuming rabbit density across the entire study area followed the pattern observed by Mutze *et al.* (2002) on unripped sites. The fox counts shown in Figure 3 of Holden and Mutze (2002) were taken from a number of different areas. We combined data from all of the areas to construct one time series for fox population density. The result is shown in Figure 8, and suggests that before RHD arrived in 1995, foxes had consistent dispersal peaks in late summer and consistent troughs prior to the peaks. Dispersal peaks occur in late summer and early autumn due to the seasonal nature of fox breeding, when juveniles disperse. In other words, prior to RHD the spotlight data suggested stable fox population.
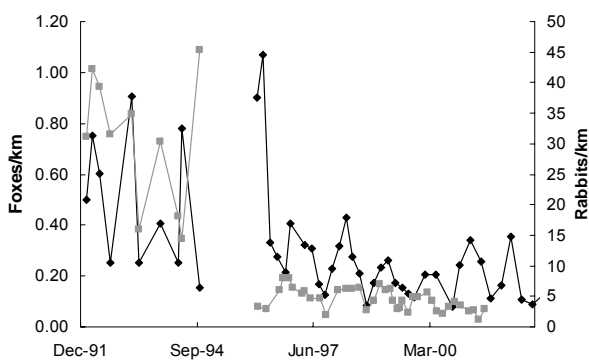
Figure 8. Fox and rabbit spotlight counts from the Flinders Ranges.
Data from a number of sites within each area were combined to generate single time series for each species. (Black line, Holden and Mutze 2002; Grey line, Mutze *et al.* 2002).

Over this three year period, the rabbit index remained high, ranging from ~16 km^{-1} up to ~45 km^{-1}. Most of that time it was over 25 km^{-1}. If the

same conversion to rabbits ha^{-1} used by Pech and Hood (1998) is applicable in this system (they assumed 40% sightability within a 150 metre wide transect) these rabbit densities (over 4 ha^{-1}) should have produced close to maximum rates of increase for foxes every year, rather than the stable population densities observed. Under their model the rate of increase of foxes is zero when rabbit density is ~0.4 ha^{-1}. This suggests either fox density was regulated by some other factor, possible social interactions (Interaction 9), or the conversion to rabbits ha^{-1} used by Pech and Hood (1998) greatly overestimated the rabbit density in this system. Another possibility is that the model of Pech and Hood (1998) greatly underestimates the rabbit density at which the fox rate of increase is zero.

No experimental control transects were monitored at the same time as the FRNP fox transect, but in February 1996, after the arrival of RHD in November 1995 on the sites used by Mutze *et al.* (2002), two additional large areas were assessed for fox abundance: an adjacent unbaited area and a distant unbaited area. Rabbit densities were low in all of these areas after the arrival of RHD (Holden unpubl. data). In April 1996 these two areas had indices of 0.79 foxes km^{-1} and 1.07 foxes km^{-1} respectively at the time of peak dispersal, again consistent with the dispersal peaks recorded by Mutze *et al.* (2002). In October 1996 the 'troughs' were 0.13 foxes km^{-1} and 0.22 foxes km^{-1} respectively, also generally consistent with the pattern pre-RHD. However, the following year the large dispersal peak did not occur in either area. If we consider the distant unbaited area as the area where fox density was not manipulated (i.e. foxes were not controlled) and combine it with the data on foxes collected by Mutze *et al.* (2002), we can compare rates of increase from the troughs to the peaks ('recruitment phase') and from the peaks to the troughs ('decline phase') in relation to rabbit density from unripped transects (Mutze *et al.* 2002). We can also compare the rates of increase from trough to trough, and from peak to peak, (i.e. different estimates of yearly rates of increase).

The rate of increase over the recruitment phase or decline phase was not related to rabbit density (Figure 9).
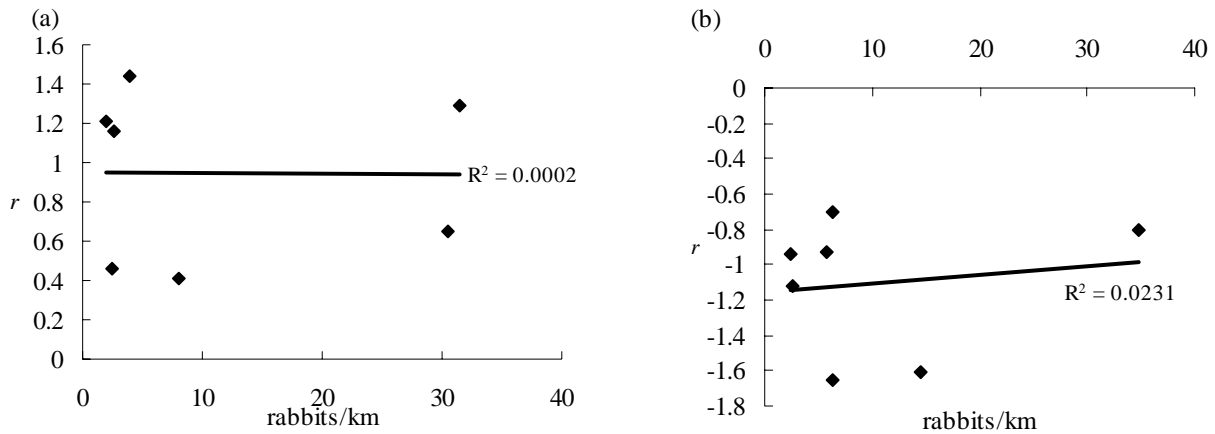
Figure 9. **Rate of increase of foxes (*r*) during (a) the recruitment phase (spring – late summer) and (b) the winter decline (late summer to spring), plotted against rabbit index of abundance.**
The recruitment rate of increase was calculated as $\ln(N_{summer}/N_{spring})$, where the spring estimate was taken as the lowest fox index in Sep-Nov, and the summer index was taken as the highest estimate in Feb-May the following year. The rabbit index was the corresponding spotlight count at the start of the recruitment phase in spring. The winter decline rate of increase was calculated as $\ln(N_{spring}/N_{summer})$, where the spring estimate was taken as the lowest fox index in Sep-Nov, and the summer index was taken as the highest estimate in Feb-May prior to the spring. The rabbit index was the corresponding spotlight count in summer.

The rate of increase from peak to peak (and trough to trough) was not related to rabbit density (Figure 10).
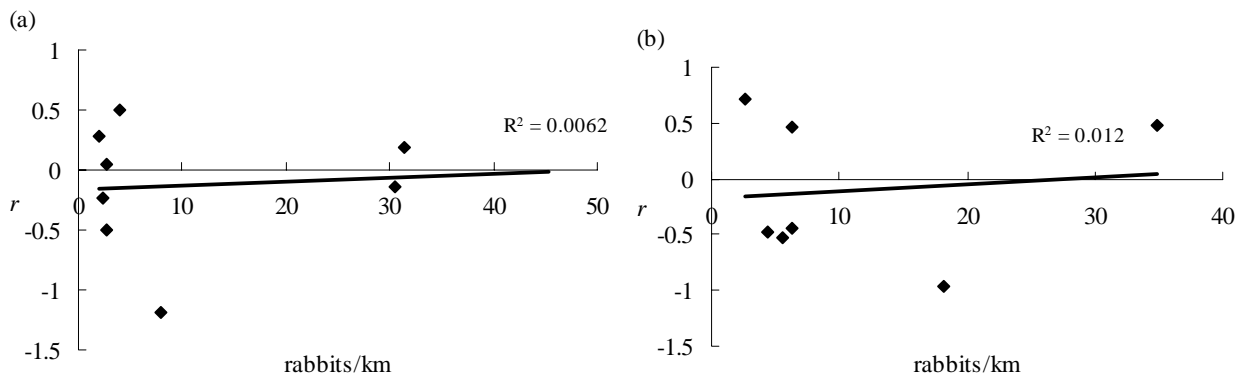
Figure 10. Fox rate of increase from (a) peak to peak and from (b) trough to trough plotted against the rabbit index mid-way between the peaks or troughs.

Despite no apparent relationship between fox population rate of increase and rabbit density, fox density appeared to decline following the arrival of RHD if we consider either peak or trough indices of foxes (Figure 8). At the distant site the post-RHD peak fox index was ~36% of the pre-RHD peak index, while the post-RHD trough fox index was ~50% of the pre-RHD trough index (Holden and Mutze 2002).

If shooting foxes had little impact on the fox index, the FRNP data suggest fox density was limited by some factor other than rabbit density when rabbit density and fox density was high, but following the decline in rabbit density post RHD, fox density may have been limited by rabbit density.

At Roxby Downs the fox population declined prior to the arrival of RHD in 1995 (Figure 11). Unfortunately we do not know whether rabbit density was high prior to April 1989, this could explain the initially high fox density. If the same conversion to rabbits/ha used by Pech and Hood (1998) is applicable in this system rabbit densities during the period when foxes declined should have produced positive rates of increase for foxes every year, rather than the observed decline.
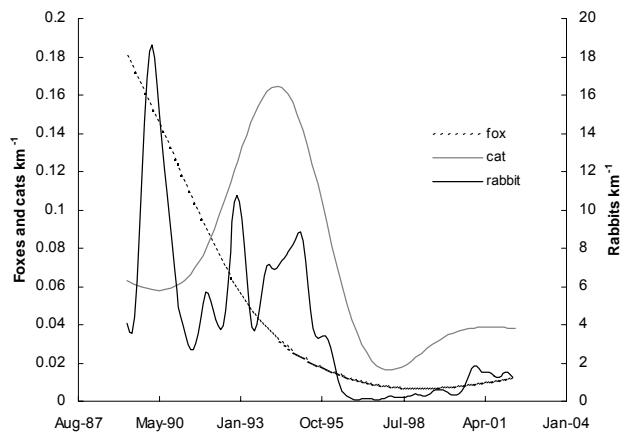
Figure 11. Rabbit, cat and fox indices of abundance at Roxby Downs.
Read and Bowen 2001 and Read and Bowen, unpubl. data. To simplify the data, which were noisy, we fitted smoothed splines.

This highlights one of the problems we have in developing quantitative models for these systems; the data are usually not collected in an appropriate way. Rabbit abundance indices are usually expressed as rabbits per spotlight km, and it is unclear whether an observed number per spotlight km in one study is equivalent to the same number per spotlight km in another study. In the Flinders Ranges study the peak rabbit density in April 1992 averaged ~40 km^{-1}, while in the Roxby Downs area it averaged ~5 km^{-1}. Was there an eight-fold difference or were the apparent different densities due to partly to measurement protocols or site-dependent factors such as sightability? It is also unclear whether the temporal sequence of observations within sites really reflects true densities because of the influence of changing vegetation on spotlight counts. The numerical response of foxes to rabbits is expressed in equation 11 in Appendix 1 and is from Pech and Hood (1998).

The model was based on: the allometric estimate of maximum rate of increase, an observed maximum rate of decline during the drought at Yathong, and a value for demographic efficiency obtained by trial and error, to produce an overall model that showed qualitatively reasonable behaviour in terms of rabbit population dynamics.

A more mechanistic approach would express the fox rate of increase in terms of food intake, and would also break the year into recruitment and decline (non-recruitment) periods, but whether this is feasible requires future investigation. Our initial intention was to at least express rate of increase over the recruitment period and the decline period in terms of rabbit availability, as has been done for predators in New Zealand (Arthur and Norbury, unpubl. data), and for foxes in temperate areas

where lagged rainfall was used as an index of food availability (Pech *et al.* 1997), but data were not available. An example of the approach is described in equations 12 and 13 in Appendix 1.

Interaction 9

Density-dependence in fox populations
Interaction 9 allows for unexplained density-dependence in fox populations. There is some evidence from the Flinders Ranges this may occur, based on the observations that fox density remained relatively stable prior to the release of RHD despite high rabbit densities, although tenuous (see above). Foxes are highly territorial, and probably exist as a family group with one male, one female and cubs prior to cub dispersal. Family groups with more than one adult vixen have been observed outside Australia, although it is highly unlikely in semi-arid and arid environments (Saunders *et al.*1995) and adult females with overlapping home ranges have been recorded in eastern Australia (Saunders *et al.* 2002), but these tend to occur in areas with abundant resources such as urban environments. Hence, fox density may be regulated by social interactions.

Density dependence could be included by adding a term to the Pech and Hood (1998) model for fox numerical response, (equation 14 in Appendix 1), or by adding a density dependent term to either the decline phase or increase phase in the more detailed model but is not warranted on the available data.

Interaction 10

The effect of feral cats on rabbits
In semi-arid systems rabbits comprise a large percentage of the diet of feral cats (Holden and Mutze 2002; Read and Bowen 2001; Olympic Dam unpubl. data; Risbey *et al.* 1999). Based on the data presented in Holden and Mutze (2002) and rabbit spotlight counts from (Mutze *et al.* 2002), feral cats have a type II functional response to rabbits, and have higher predation rates on rabbits at lower densities compared to foxes (Figure. 12). As with the Yathong data (Pech *et al.* 1992) foxes appear to have a type III functional response to rabbits. The fitted model for feral cats is a Holling type II functional response, (see equation 15 in Appendix 1).

To establish a cat functional response to rabbits we have assumed that occurrence in stomachs reflects actual intake. To properly model the offtake rate of feral cats on rabbits we need to express the equation in terms of biomass of rabbit rather than percentage occurrence in the diet. To measure the true impact of feral cats on rabbits, as for foxes, we actually require kill rates but these data are not available for semi-arid

systems. If we assume percentage occurrence in the diet reflects actual intake of rabbit by feral cats then we require an estimate of satiating intake. As a first estimate of this we apply fox satiating intake (see equation 10 in Appendix 1), scaled to reflect average body size of feral cats and foxes in semi-arid areas (based on data from Roxby Downs (Read and Bowen 2001). This gives an estimate of (3.4[average weight of feral cats]$^{0.75}$/4.6[average weight of foxes]$^{0.75}$) x 1096 = 874g. To express the functional response in terms of a rabbit density we also need to convert rabbits per spotlight km to rabbit ha^{-1}.
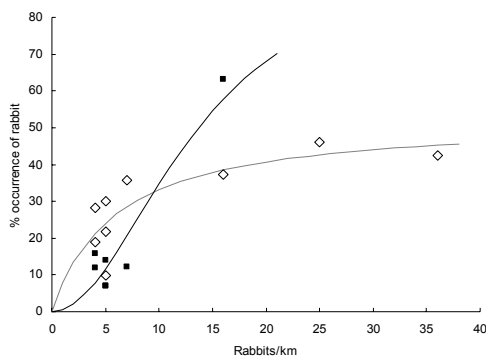
Figure 12. Cat (open diamonds) and fox (closed squares) functional responses to rabbits in the Flinders Ranges.
Data on occurrence of items in stomachs are from Holden and Mutze (2002). Rabbit abundance indices are from unripped transects of Mutze *et al.* (2002).

While not from a semi-arid system, data from Burrendong Dam in NSW provides some evidence that feral cats continue to prey on rabbits at lower densities than foxes (Davey *et al.* In Prep; Molsher 1999).

The effect of rabbits on cat rate of increase
The common occurrence of rabbit in the diet of feral cats at high rabbit density, combined with the observed decline in cat populations following declines in rabbit populations in times of drought (Newsome *et al.* 1989), suggests cat rate of increase could depend on the abundance of rabbits. However, the availability of alternative food is also likely to decrease during droughts. If we consider the functional response of feral cats to rabbits relative to the functional response of foxes to rabbits we could make contrasting predictions about how we expect these predators to respond to a reduction in the density of rabbits. One possibility is that feral cats continue to exploit rabbits at lower densities than foxes because they are better able to catch rabbits than foxes. Then we would hence predict that when rabbit densities drop foxes are disadvantaged and decline, while feral cats can continue to exploit rabbits and can maintain their population density. Alternatively, the continued presence of rabbit in the diet at low

rabbit density could mean that feral cats are not as capable of accessing alternative prey as foxes are, and hence when rabbit numbers decline foxes are still able to maintain their population density, while feral cats decline.

The results from South Australia suggested that cat density was affected by rabbit density, but whether feral cats continue to maintain higher rates of increase than foxes at some rabbit densities was equivocal. In the Flinders Ranges cat density declined and feral cats were in poor condition following the reduction in rabbit density despite good environmental conditions (Holden and Mutze 2002). At Roxby Downs, cat density also declined following the arrival of RHD, but when rabbit density was intermediate between the initial high density and the low density that occurred after RHD arrived, there was some evidence the cat population increased while the fox population declined (Figure 11).

Establishing a numerical response for feral cats
It has been reported that feral cats preferentially prey on juvenile rabbits (Catling 1988; Jones 1977) and this may explain the slow population recovery observed in Victoria following a cull of feral cats when few young rabbits were available (Jones and Coman 1981). If feral cats respond to the availability of juvenile rabbits rather than the total abundance of rabbits, then it may be necessary to express the numerical response of feral cats in terms of availability of juvenile rabbits. To our knowledge data are not available to parameterise a model of this form. One possibility may be to model the numerical response of feral cats, as a function of the numerical response of rabbits, assuming those juvenile rabbits are available when the rate of increase of rabbits is positive.

If we use a functional form based on the abundance of rabbits as for foxes (e.g. like eqn 11, Appendix 1), the maximum rate of increase of feral cats based on an average body size of 2.8 kg is 0.99 per year (0.25 per quarter). The maximum rate of decrease is unknown, and difficult to estimate because of the difficulty in assessing the abundance of feral cats. The demographic efficiency is unknown, but if feral cats can increase when rabbit densities are low (*cf.* foxes) their demographic efficiency would be larger than foxes. The effect of demographic efficiency on resultant dynamics is explored below.

Interaction 11

Density-dependence in cat populations
Interaction 11 allows for unexplained density-dependence in the dynamics of cat populations. Whether some form of social regulation affects the abundance of feral cats is unknown.

Interaction 12

Interactions between foxes and cats not captured by competition
Interaction 12 represents interactions between foxes and feral cats not captured by competition for resources through the functional response. This could be interference competition or direct predation. The effect of foxes on feral cats and *vice versa* is unknown. Possible increases in cat abundance in response to a reduction in fox populations through poisoning at Herrison Prong (Risbey *et al.* 2000) and to a natural reduction in the fox population at Roxbury Downs (Read and Bowen 2001) suggested that foxes may reduce cat abundance. However, large-scale control of foxes in the Flinders Ranges undertaken while rabbit populations were still high did not result in an increase in the cat population (Holden and Mutze 2002).

One way to model these interactions is by reducing the numerical response of one predator species in response to the presence of the other (equation 16 in Appendix 1). Data are not available to parameterise this relationship.

Interaction 13

Effect of foxes on native prey
The functional response of foxes to native prey is unknown, but foxes have been implicated in the decline and extinction of many native species in the critical weight range (Burbidge and McKenzie 1989). Pech and Hood (1998) modelled a generic type II functional response, which is capable of driving prey to extinction (Sinclair *et al.* 1998). To properly quantify the impact of foxes on native prey we ideally need kill rates of native prey by foxes as a function of both native prey abundance and rabbit abundance. The latter factor is required to deal with any preference foxes might have for different prey. In particular, it is essential to know whether kill rates of native prey are high because native prey are intrinsically vulnerable to foxes, because this changes the structure of the model required for this part of the system.

Effect of native prey on rate of increase of foxes
Threatened native species are unlikely to contribute significantly to the rate of increase of foxes, but many other relatively abundant native prey sources might be important. Foxes have a diverse diet, for example insects are often eaten in summer, but data are not available to properly quantify the contribution of each prey type to the rate of increase of foxes.

Interaction 14

Effect of feral cats on native prey
The functional response of feral cats to native prey is unknown, but feral cats have been implicated in the decline and extinction of a number of native species (Dickman 1996; Risbey *et al.* 2000). To properly quantify the impact of feral cats on native prey we ideally need kill rates of native prey by feral cats as a function of both native prey abundance and rabbit abundance. As for foxes it is essential to know whether kill rates of native prey by feral cats are high because native prey are intrinsically vulnerable to feral cats.

Effect of native prey on the rate of increase of feral cats
Threatened native species are unlikely to contribute significantly to the rate of increase of feral cats, but the contribution of more abundant native prey is unknown.

Interaction 15

Disease in rabbit populations
RHD had a large impact on rabbit populations in semi-arid systems when it was first introduced, and it appears to be still effectively limiting the abundance of rabbits at Roxby Downs (Read and Bowen 2001) and in the Flinders Ranges (Mutze *et al.* 2002) and elsewhere (Sandell and Start 1999). The longer-term effectiveness of RHD at limiting rabbit populations is uncertain. The effect of myxomatosis on rabbit population dynamics since the release of the arid-adapted rabbit flea is also uncertain.

A simple model for preliminary exploration

The discussion above has identified many gaps in our understanding of the relationships identified in Figure 5. There are far too many permutations and combinations to simulate the effects of varying all the different parameters. Below we present a simple model that builds on the Pech and Hood (1998) model. We explore the consequences of adding density dependence in fox population dynamics and extend the model by adding feral cats and ignoring any effects of RHD on rabbit populations. The model is simulated using 120 years of actual rainfall from a semi-arid area of Australia (annual mean 321 mm, sd 110 mm). For vegetation we use equation 1 with the V^* term removed; for the rabbit functional response we use equation 2; for the rabbit numerical response we use equation 4; for the fox functional response we use equation 10; for the fox numerical response we use equation 14; for the cat functional response we use a modified form of equation 15 (see equation 17 in Appendix 1). For the cat numerical response we use

equation 16, with a = 0.56 (the same as foxes), and c-a = 0.25 (i.e. the intrinsic rate of increase r_m = c-a is estimated using the allometric relationship of Sinclair (1996) and an average body weight of 2.8 kg for adult females). We vary the demographic efficiency d and the effect of foxes on feral cats h. In the absence of any other information we set the minimum density of feral cats the same as foxes (0.1 km^{-2}).

The effect of density dependence on fox–rabbit interactions
Figure 13 shows simulations from a vegetation-rabbit-fox model with density dependence in the numerical response for foxes (g > 0 in equation 14) and without (a & without density dependence g = 0 in equation 14). Density dependence restricts fox population growth and allows rabbit populations to achieve higher densities.

As mentioned above, whether these dynamics properly reflect fox population dynamics is uncertain, and the sensitivity of the model to changes in rainfall raises some concerns. The rainfall data used for the simulation are actual rainfall data from a semi-arid area in Australia, and there is a slight upward trend in the yearly rainfall. This slight upward trend had a significant effect on fox population dynamics, with fox populations at higher densities in the last 50 years of the simulation compared with the first 50 years. (See also Davis *et al.* 2003 for a discussion of the effect of changing either the mean or the variance of rainfall distribution in the model used by Pech and Hood 1998).

(a)

(b)

(c)

(d)
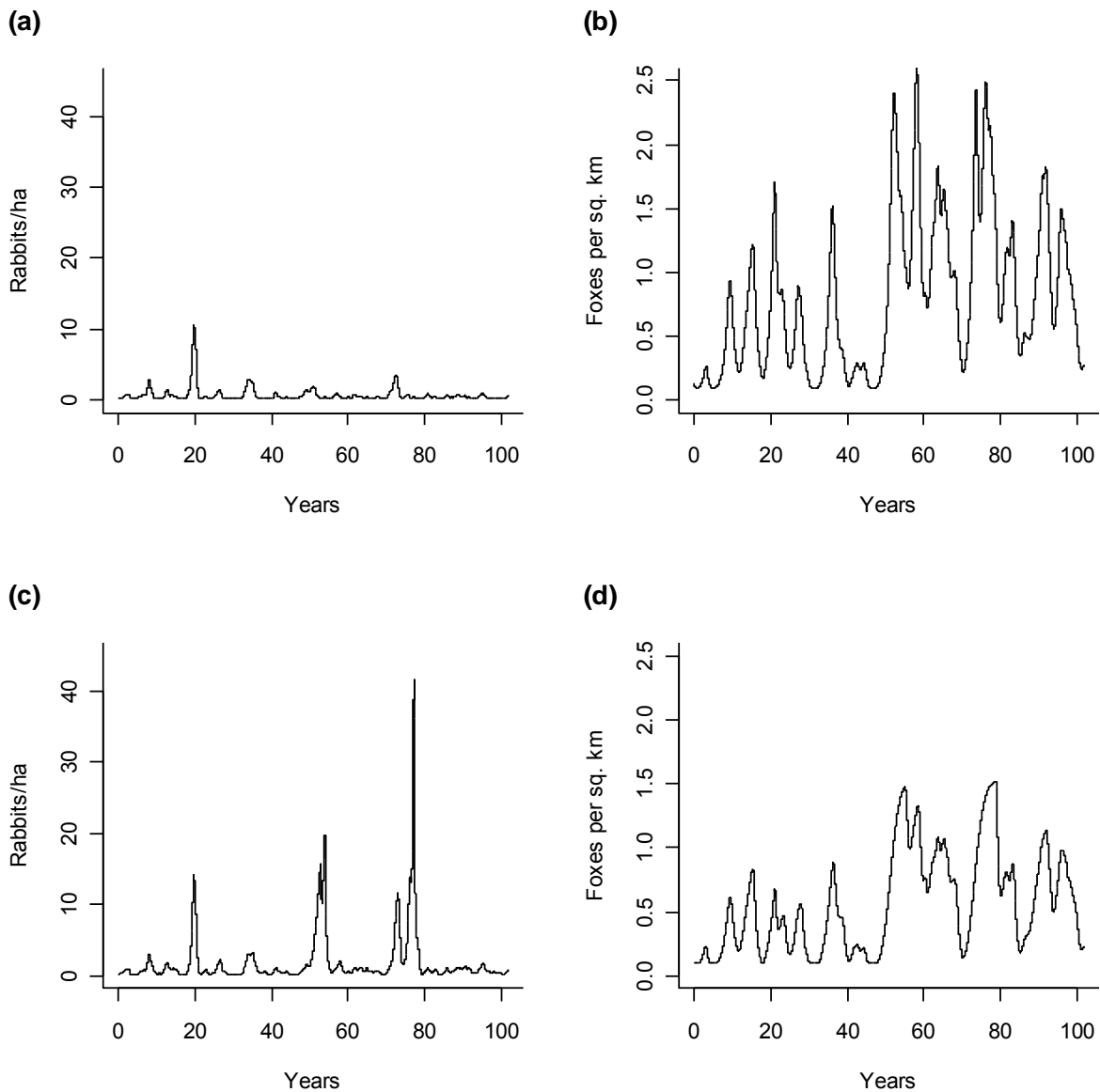
Figure 13. Simulated population trajectories without additional density dependence in fox population dynamics (i.e. the original Pech and Hood 1998) model (a & b), with density dependence added (c & d, *g* = 0.0015).

Figure 14 shows the effect of controlling rabbits on fox population density. Controlling rabbits to less than 1 ha^{-1} has little effect on fox population dynamics. Controlling rabbits to 0.5 ha^{-1} has a large effect on fox populations during the first 50 years of the simulation, but fox populations are relatively high during the last 50 years, showing the sensitivity of the model to an increase in rainfall. When rabbits are controlled below ~0.4 ha^{-1} the fox population must decline to its minimum allowable density under this model (this is the value below which the demographic efficiency of foxes results in fox rate of increase being negative).
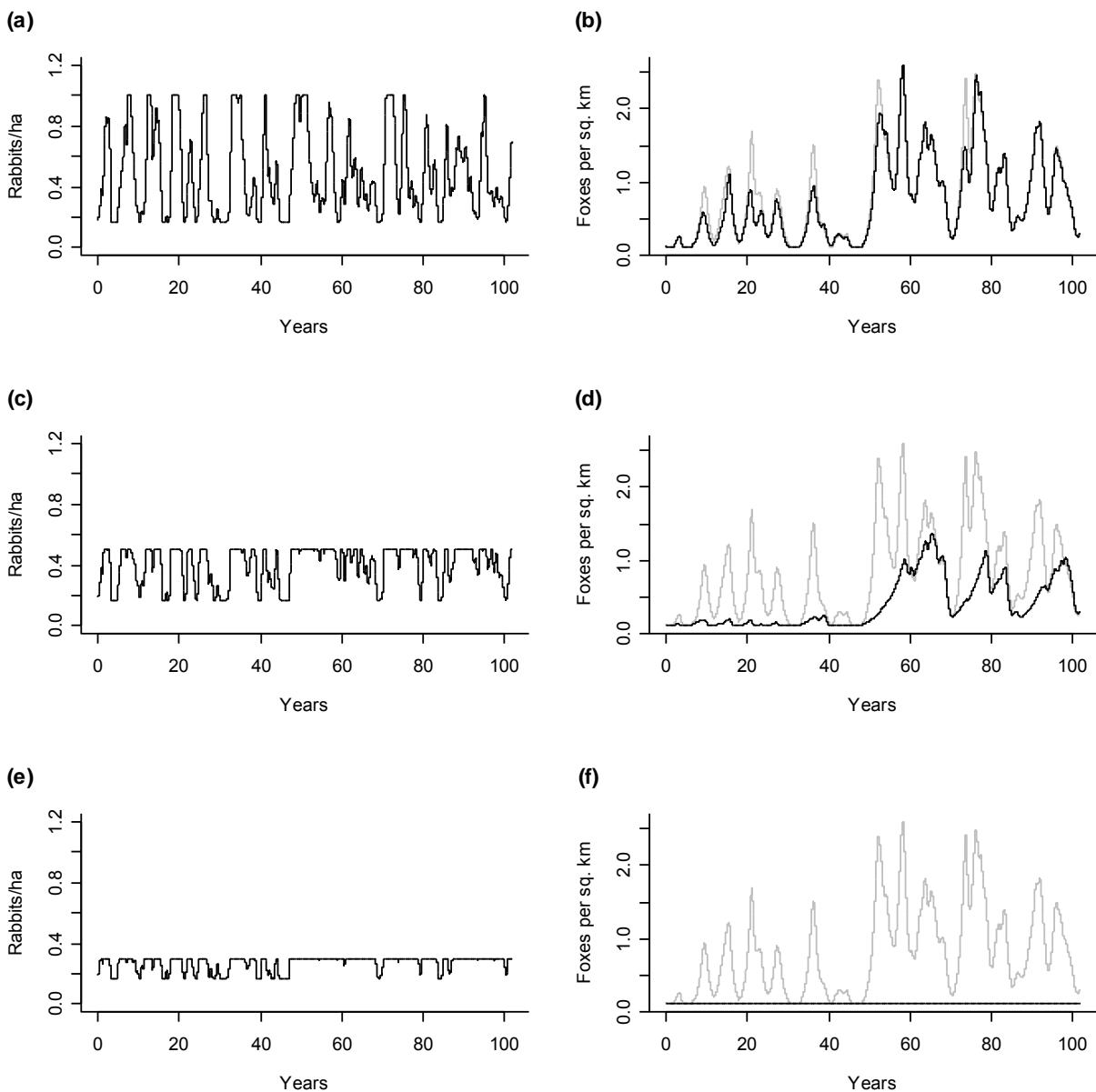
Figure 14. Effects of rabbit control on fox population dynamics.
The density dependent factor, *g* in equation 14, is zero for all the simulations. The figures on the left show the level to which rabbit density is controlled (1 ha^{-1}, 0.5 ha^{-1}, 0.3 ha^{-1}). The grey line in the figures on the right shows the fox density when rabbit density is not controlled. The black line shows the response of fox density to rabbit control.

The effect of adding feral cats
Adding feral cats to the model (with parameter *h* = 0 in equation 16) reduces the abundance of rabbits through predation, and reduces the number of foxes through competition for rabbits (compare Figure 14 a & b with Figure 15). The strength of the effect is determined by the demographic efficiency of feral cats (Figure 15). It is evident from this formulation of the model that all species are often at their defined minimum values. This indicates that a much better understanding of the relationships between the species (and the importance of prey items other than rabbits for maintaining predator populations)

is required to properly model their dynamics. If a negative effect of foxes on feral cats is added, the cat population decreases and the fox population increases (Figure 16). The problem remains that rabbits and foxes are often at their defined minimum values.
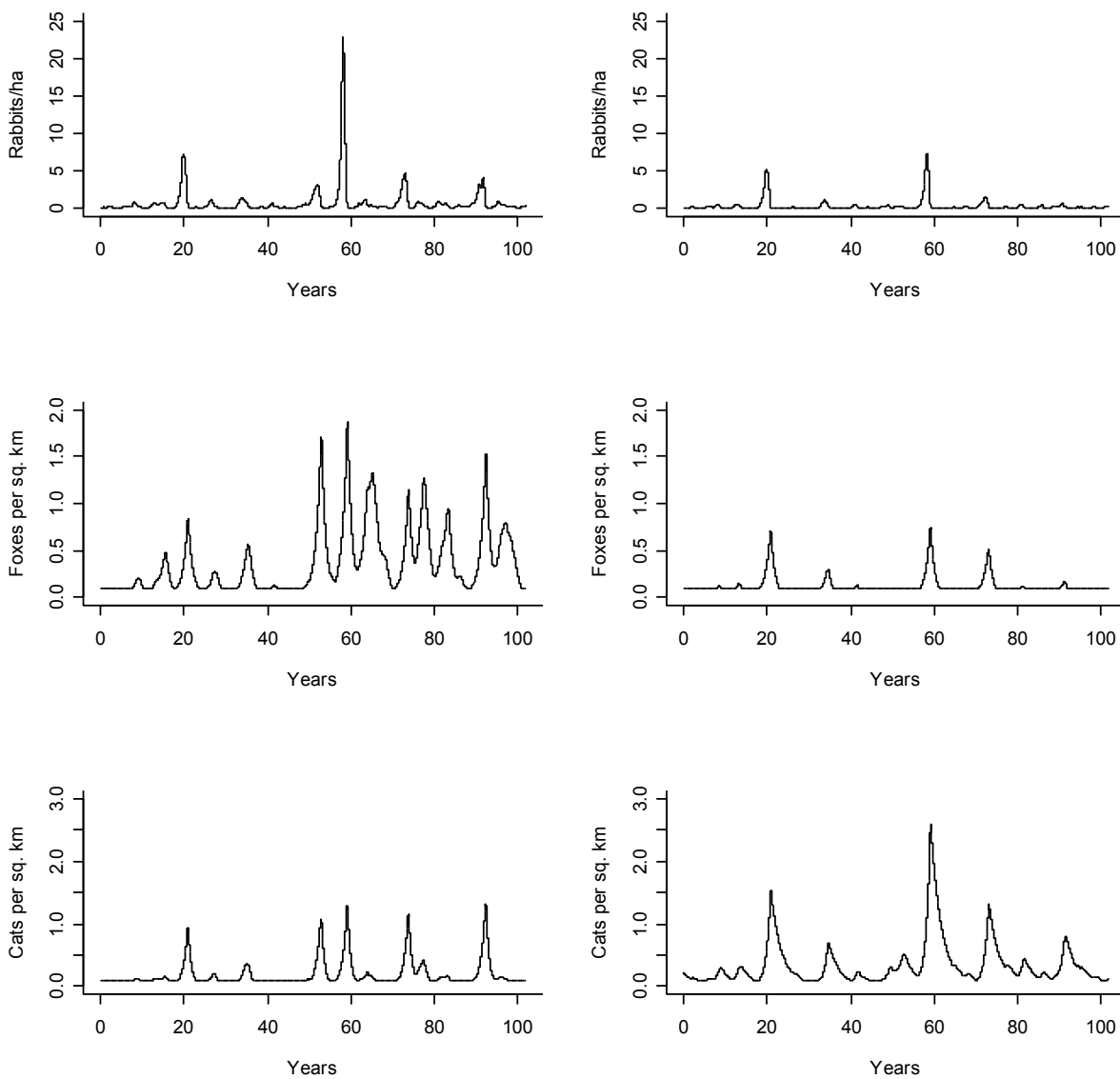
Figure 15. Simulated population dynamics using the Pech and Hood (1998) model with feral cats added.
A comparison between the figures on the left and those on the right shows the effect of changing the demographic efficiency of feral cats from 2 to 5: feral cats become more competitive, their population increases, the rabbit population is generally kept lower, and the fox population is reduced.
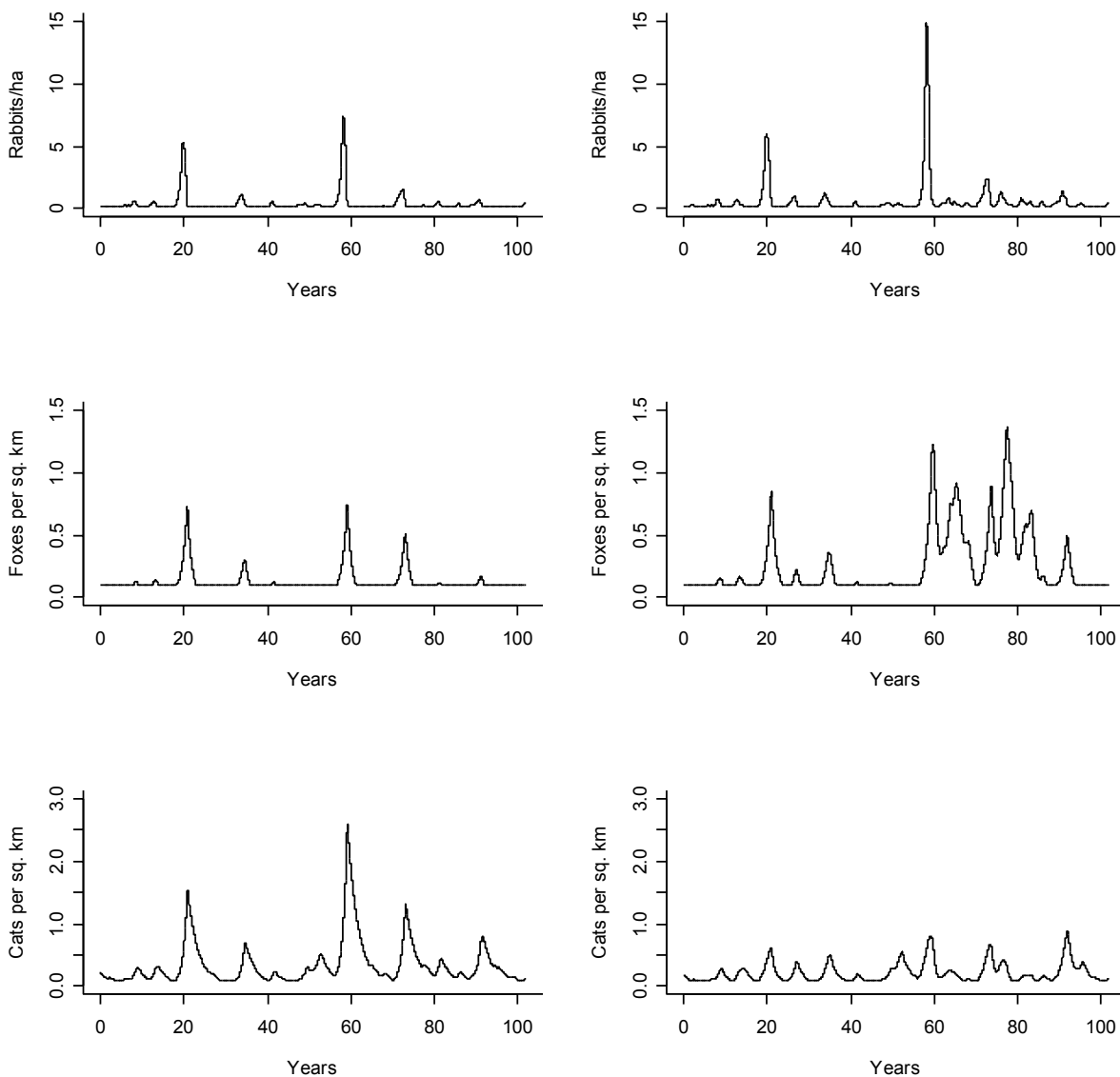
Figure 16. Simulated population dynamics using the Pech and Hood (1998) model with feral cats added.
The demographic efficiency of feral cats was set at 5. A comparison between the figures on the left and those on the right shows the effect of adding a negative effect of foxes on feral cats (h=0.003, eqn 16). Feral cats average lower densities, foxes average higher densities and rabbit density increases also as the more efficient predator is suppressed.

Summary

The preliminary simulation models explore the potential interactions between rabbits, foxes and feral cats, but they are based mainly on hypothesised relationships. The sensitivity of the model to small changes in rainfall suggests a more detailed understanding of the relationships is required. The tendency of the model to reach the lower defined minimum for all species when both predators are present also suggests a much better understanding of the relationships is required. Refinements to the model such as the utilisation of ratio-dependent functional responses may partly address issues of stability at lower resource densities. More specifically, there is a clear need to properly quantify the relationship between rabbits and the two predators. Numerical responses for the two predators should be determined in relation to both the abundance of rabbits (or juvenile rabbits) and simultaneously the abundance of alternative food sources. Based on diet studies both foxes and feral cats consume many prey species other than rabbits, but to our knowledge no quantitative information currently exists to build this into the predators' numerical responses. Ideally, numerical responses would be

based on intake rates, but whether this is feasible is currently unknown. Foxes and feral cats have clearly defined breeding seasons, and future investigation of the relationships should focus on these characteristics. The pulsed dynamics resulting from breeding and non-breeding seasons will affect model behaviour and are likely to generate predictions that are substantially different to the continuous models we have used above. This is an important topic for future research. The effect of foxes and feral cats on the rate of increase of each other through interference competition, competition for resources or predation is essentially unknown.

To properly quantify and model the impact of foxes and feral cats on both rabbits and native prey requires kill rates of these prey, assessed in relation to the availability of all prey types. This is particularly important for native prey and we currently have no data on this. At the same time it is essential to develop an understanding of the population dynamics of native Australian prey and the population dynamics of rabbits using data obtained since the arrival of RHD, and in the absence of predation from introduced predators.

Temperate systems
There are no interactive models currently available for temperate systems that include foxes. We have explored data sets from Burrendong Dam (A. Newsome unpubl. Data; Davey *et al.* in prep.), the ACT region (Don Fletcher *et al.* unpubl. data) andfrom the central western slopes of NSW (G. Saunders unpubl. data). The data sets are characterised by short spotlight transects (range 4.1km – 30 km, with most <10 km). Short transects result in highly variable counts of foxes. This is because foxes have large home ranges and are generally shy and cryptic in their behaviour.   With one exception, none of the data sets show the clear seasonal recruitment peaks that could be anticipated for foxes. Nonetheless, spotlight transect lengths of 16.2 km, 6.2 km and 4.2 km were sufficient to detect the effects of poison baiting on fox populations at Burrendong (A. Newsome unpubl. data; Davey *et al.* in prep.).

However, we found no evidence from any of the data from temperate systems that the reduction in rabbit density due to RHD had any effect on fox abundance. Using a composite plot, which assumes that spotlight indices were comparable between all temperate areas for which data were available, we found no relationship between rabbit abundance and fox abundance (Figure. 17).
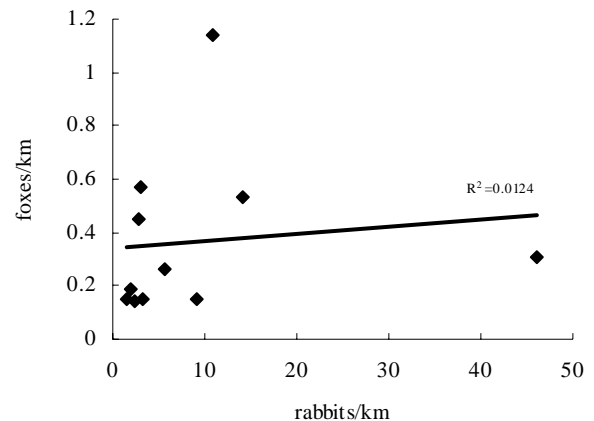
Figure 17. Rabbit and fox abundance relationship in temperate systems.
Composite plot using spotlight data from Burrendong (A. Newsome unpubl. data; Davey *et al.* in prep.), the ACT (Don Fletcher *et al.* unpubl. data) and the central western slopes of NSW (Glen Saunders unpubl. data).

Because of likely differences in sightability, the continued use of spotlight counts makes it difficult to produce quantitative models using data from different areas. However, initial interpretation suggests it may not be appropriate to link fox dynamics to rabbit dynamics in temperate systems. Alternatively, despite some reductions in rabbit abundance due to RHD, rabbit populations may still not have reached the low densities required to reduce fox density below the current partially controlled or socially regulated level in agricultural landscapes. This requires further exploration. Certainly, the functional response of foxes to rabbits estimated before and after the arrival of RHD at Burrendong suggests foxes have a diverse diet (Davey *et al.* in prep) and may not be reliant on rabbits.

Feral cats
Feral cats are rarely seen in spotlight counts in temperate systems and no quantitative numerical relationships can be established from the available data. Dietary data indicate rabbits are important prey for feral cats even at low rabbit population densities (Davey *et al.* in prep). Molsher (1999) suggested feral cats showed a behavioural response to the removal of foxes at Burrendong, indicating potential competition between these species, but no numerical response was evident. However, appropriate data to assess whether cat populations increased in response to the reduction in foxes were not available, and a way of quantifying cat abundance is needed for future studies.

Summary – temperate systems
The few data available for temperate systems suggested fox population dynamics may not be linked as strongly to rabbit dynamics as they appear to be in semi-arid systems. Alternative models are likely to be required for temperate systems (e.g. Pech *et al.* 1997). Almost certainly these models will require data on the interactions of predators and a wide variety of foods, including foods associated with human activity.

At this stage there is no evidence that interactive population models can be transferred directly between ecosystems in different climatic zones. Research to fill knowledge gaps will need to be applied separately in temperate and arid areas of Australia. In addition, no information is available to test whether or not the models, or the existing demographic data, are applicable to areas such as northern Australia (where the range of foxes and rabbits may be expanding); or to areas such as Tasmania, where there are substantial differences in the abundance of native predators and the availability of native prey species for foxes (should they ever establish).

6 Implications for Integrated control

The general principals and strategies of integrated control are outlined in Braysher (1993). Williams *et al.* (1995) and Saunders *et al.* (1995) provided guidelines for the application of these principals and strategies to rabbits and foxes, respectively.

The general principals set out by Braysher (1993) included defining the problem, clearly stating the objectives and setting out the criteria of success and failure, evaluating various management options, implementing actions; monitoring and evaluating the outcomes against the objectives.

Being able to clearly state the objectives of an integrated control program requires an understanding of the impacts of feral cats, foxes and rabbits, or a combination of these species, on native fauna. This review highlights the general lack of knowledge on the impacts of these species and the interactions between species.

A risk adverse approach would be to undertake integrated control wherever feral cats, foxes and rabbits co-occur. However, this may not be practical or possible due to limitations on resources.

There appears to be a link between feral cats and rabbit abundance and fox and rabbit abundance in semi-arid and arid areas. A reduction in rabbits, under the right circumstances, can lead to a lagged reduction in both fox and feral cat abundance. In situations were there are small populations of native species that are at risk from predation, and where rabbits are the primary prey of foxes and/or feral cats, it may be beneficial to undertake integrated control. In areas where rabbits are not the primary prey of feral cats or foxes, integrated control may not be necessary, and targeted predator control may be a better investment of limited resources.

Assuming that reliable information on the impacts of feral cats, foxes and rabbits can be obtained for a particular area, setting the criteria of success or failure is currently hindered by the available techniques to assess changes in abundance of feral cats and in small populations of rare native species.

Currently, there is an array of control techniques and strategies used for rabbits and foxes, and only limited strategic approaches and tactical tools for the control of feral cats (Algar *et al.* 1999). To our knowledge, few studies have investigated the efficiencies and effectiveness of these control strategies, in terms of the target prey species and

the resource it threatens, or the relative costs and benefits of integrated control techniques for a combination of predators and rabbits, and native species.

Implementing an integrated control program is therefore limited by the above constraints. Monitoring and evaluating control programs is limited by the lack of reliable techniques to monitor changes in the abundance of feral cats and many populations of native species, and to a lesser extent changes in fox abundance.

7 Gaps in Knowledge

The aim of this review was to synthesise the current state of knowledge on the interactions between feral cats, foxes, rabbits (their control) and their impacts on native species, including native herbivore and predator species.

A number of studies have provided valuable insights into the impacts that changes in prey abundance (via control or natural events) can have on populations of introduced predators, and how predators can influence the abundance of prey species. The interactions between foxes (and to a lesser extent feral cats) and native species have also been studied through both field experimentation and theoretical modelling.

Despite these important studies, there are many aspects of predator–prey interactions that lack reliable information. Therefore, managers charged with controlling these species for agricultural and environmental benefits must make decisions based on unreliable knowledge and are faced with the uncertainty that their actions may not reliably result in the desired outcome.

In this section we highlight the key areas where further investigation would improve our understanding of the impacts feral cats, foxes and rabbits, and the control of combinations of these species have on native species.

7.1 Priorities in current gaps in our understanding

We believe that all of the knowledge gaps presented below are vital to improving our understanding of the interactions between feral cats, foxes, rabbits and native species. However, we have prioritised these gaps in order of importance in regard to the potential level of benefit for managers.

We provide basic design scenarios and suggestions for the general location where these investigations might be conducted. This should not be viewed as an exhaustive description of experimental design, but rather a guide.

At present very few control operations concurrently target feral cats, foxes and rabbits. There is no information that we are aware of on the costs and benefits of integrated control. Before this type of analysis can be properly undertaken the identified gaps in our current level of understanding need to be addressed.

Set out below are the four key areas that we consider need the most urgent attention. Following on from these are a series of subset areas that also require investigation:

1. *How to effectively monitor changes in abundance of introduced predators, particularly feral cats.*

Currently, there are no robust methods for assessing changes in predator abundance in Australia, particularly for feral cats. Thus, there are no means of assessing the effectiveness of control operations at reducing predator abundance. This is the highest priority, as the remaining knowledge gaps all require accurate assessment of changes in predator abundance as a result of pest control operations. A review of monitoring techniques for feral cats is currently being undertaken by the Arthur Rylah Research Institute for Environmental Research.

2. *The impact of predator control operations on the population dynamics and social organisation of sympatric predators and the impacts on native species and communities.*

While there is some evidence that both fox and cat abundance is related to rabbit abundance in arid and semi-arid areas, we have little information on the potential for feral cats to increase in abundance or to alter their foraging behaviour following the removal/reduction of a higher order predator. We also know little about the impact of changes in predator communities on the persistence of native species. However, the limitations of techniques for estimating predator abundance, particularly feral cats, restrict our ability to identify if feral cats do increase in abundance and/or impact on native wildlife.

3. *The role of rabbits in temperate systems in supporting elevated numbers of foxes and feral cats.*

The little data available suggests fox population dynamics may not be related to rabbit abundance in temperate systems in Australia. There is no evidence either way for feral cats. Investigations into these interactions and the effects on native species will require studies covering a wide range of foods as rabbits are unlikely to be the primary prey of these predators in these areas.

4. The effects of disease (RHD and myxomatosis), particularly in temperate environments, on the interactions between predators and their prey.

Much of the information we have on the interactions between feral cats, foxes and rabbits has been gained either prior to or at the time of the arrival of RHD. We have little information on the effects of combinations of RHD and predation, and the flow-on effects to native prey species.

7.1.1   Further information requirements

The following gaps in the knowledge are in some instances a subset of the broader areas of investigation highlighted above; many arise through the model development process described in Section 5. We provide these as a guide to a more targeted research approach that will help parameterise the models and reduce the gaps in our understanding.

- What factors regulate populations of native species?

There is currently no information on how native species respond to changes in food supply in the absence of predation, or how social factors may influence population dynamics. This information is needed to properly develop models for the population dynamics of native prey in the absence of predation.

This will require identification of key resources, and quantification of rates of increase in relation to the availability of these resources. This type of study should fit within broad scale predator removal undertaken for management as a more detailed exploration of the response of threatened prey to predator removal.

- What factors regulate predator populations?

It is possible that there are density dependent regulatory mechanisms that act to regulate populations of both feral cats and foxes. There is some evidence for this for foxes in semi-arid systems in South Australia, but nothing is known of this for feral cats.

- *What is the functional response of foxes and feral cats to changes in the abundance of native species at risk from predation?*

 While these predators have been implicated in the decline and extinction of a range of native species, many still persist. To properly understand the impact of feral cats and foxes on native species we need to quantify the rate of predator-induced mortality as a function of changes in native prey abundance. Quantification of kill rates for native prey (and rabbits) in relation to the abundance of *all* food sources in an area and in relation to the abundance of predators.

- What are the potential costs of releasing rabbits from predator induced regulation, both ecologically and economically?

The damage rabbits cause to flora and soils is well documented, but the flow-on effects to native fauna species are less well understood. We currently have little reliable information on the potential impacts of increases in rabbit abundance as a result of a release in regulation.

- What are the interactions between dingoes, foxes, feral cats and quoll species, and how do changes in rabbit abundance affect these?

We currently know very little about the impact of introduced predators and predator control on the long-term persistence of populations of native predators, in particular quoll species, or how changes in rabbit abundance might influence these interactions. To fill this gap requires experimental evidence of the changes in rates of increase (or relevant demographic parameters) of one predator in relation to manipulation in the density of the other predator and / or their primary prey.

Assessing demographic parameters would allow a better understanding of the mechanism of interaction.

- Quantification of rates of increase of foxes and feral cats (or relevant demographic parameters such as reproduction and survival) in relation to availability of resources including rabbits (or juvenile rabbits), native prey and other foods.

Rates of increase should be divided into a recruitment phase and a decline phase. This research will require better ways of quantifying the abundance of the predators and their prey, and/or techniques to assess survival and reproduction. The use of DNA technology to estimate population abundance is one example of a method that may improve monitoring techniques.

8   Filling the gaps

To gain reliable knowledge on the most effective and efficient combination of pest management strategies that would bring about gains in biodiversity, we could apply the basic principals of investigative science. That is, undertake large-scale manipulative experiments that are replicated, randomised and controlled. These three tenets of the scientific method underpin the acquisition of reliable knowledge. However, large-scale manipulative experiments are difficult to implement in the field and require long-term support and investment from management agencies. Financial and logistical constraints have the effect of reducing the temporal scale over which studies are able to operate. This is a major limitation as patterns and processes often take many years to emerge. It is often the case that large management-scale experiments must sacrifice one or more of the components of experimental design.

Our ability to impose reductions of specified levels on feral cats and foxes is limited. The techniques available are essentially blunt instruments, able only to impose changes at a coarse level. This limits our capacity to fine-tune our understanding of many of the interactions between management actions (control), predators, their prey and native species. It is also difficult to plan for outbreaks of disease such as myxomatosis or RHD that may confound experimental manipulations.

These limitations can have the effect of restricting the generality of the outcomes or reducing the strength of the inferences that can be drawn. However in some instances manipulative experimentation, at the scale of management or at least at the scale of the predators, is the only way to improve our knowledge.

A combination of management scale experimentation and smaller scale research targeted at specific questions, such as those listed in the previous section, will lead to increased levels of reliable knowledge that can also be used to optimise the modelling processes. Based on improvements in knowledge, management actions may then be altered to optimise benefits of pest control. Continual updating of system models decreases the amount of time it takes to improve the reliability of management decisions.

Experimental Design

This review does not provide detailed designs for each identified gap in current knowledge as this would require knowledge of site specific features, history of control, infrastructure, limitations on access, community and State Government support, and legislative requirements.

However, we do provide some guidelines as to the general design features for studies to fill the gaps in our knowledge.

Community and Institutional Support

It is likely that community engagement will be essential, as control operations will probably be undertaken across tenure due to the distribution of the species and the scale at which experiments are likely to be undertaken. Accordingly, the implementation and long-term success of large-scale projects will in part rely on community support. Institutional support is also vital, providing the resources to implement projects.

It is important that in the development stage of these projects the expectations of the timing and magnitude of results are kept realistic. Failure to deliver on unrealistic expectations can lead to a withdrawal of community and institutional support, resulting in premature cessation of projects.

Legislative Requirements

A vital component to any experiment is the use of non-treatment sites. However, the control of pest animals is often legislated and is obligatory for State Government and other land managers. Not controlling pest species may contravene local legislation.

Scale

It is important that manipulative experiments are conducted at the appropriate scale. For example, for an experiment investigating the impact of changes in rabbit abundance on fox population dynamics, it would be necessary to have at least two experimental units and one control unit that each encompasses the home range of several fox groups. Similarly, experiments on competition between rabbits and medium-sized native herbivores would be at the scale of the herbivores.

The scale of the monitoring program also needs to be appropriate for the species investigated. For example, spotlight transects that monitor changes in rabbit abundance are typically shorter (< 5 km) than those required to assess changes in fox abundance (> 10 km).

Duration

One of the major limitations on many of the studies to date has been the limited duration of the experiments. If the experiment was investigating changes in survival rates, the study needs to be able to account for the natural variation in these rates. This may take several years.

Experimental Control

The use of non-treatment (experimental controls) sites is often the best approach and a basic feature of experimental design. These areas are often difficult to incorporate at the scale of management, or managers are very reluctant to 'do nothing'. It is important that pre-manipulation assessments of both treatment and non-treatment sites are undertaken to ensure that the sites are comparable and that underlying differences are not influencing species abundance prior to beginning the study. Pre-manipulation assessment may need to account for seasonal or yearly variations in population demography.

It may not be possible to find areas that have not had some management intervention; however, it may be possible to cease management in some areas and compare changes in the system to areas where control is maintained.

Randomisation

In order to make statements about the generality of the outcomes from experiments, treatments need to be allocated randomly. This is to avoid underlying patterns and bias. In large-scale experiments this is not always possible. Without randomisation results from large-scale experiments are specific to that area in which they are conducted. It is not possible to transfer the knowledge gained in one area to another.

Location

There are a number of large-scale management programs currently underway across a range of biogeographic regions in Australia. In Victoria, Southern Ark is a large-scale fox control program that operates over 1 million hectares of south-eastern Victoria. While this program is focused on fox control it offers an opportunity to incorporate integrated control options, including substantial areas set aside as non-treatment sites (6 x 20 000 ha). In the north-west of Victoria there are several large (> 100 000 ha) parks that also have the potential to undertake management scale research in a semi-arid setting and which all contain feral cats, foxes and rabbits. Victoria also has a number of fox free islands that have established feral cat and rabbit populations.

The New South Wales fox threat abatement plan is being implemented across a wide rage of habitat types specifically aimed at protecting a suite of native species.

Also in NSW is Lake Burrendong, a temperate grazing area that has the advantage of having had research undertaken in the past on feral cats, foxes and rabbits, although Lake Burrendong is no longer an active research site.

In South Australia, project Bounce Back and the Arid Recovery Program operate in semi-arid and arid environments, and have established infrastructure.

In Western Australia there are a number of large-scale predator control projects that have been underway for a number of years. These projects focus on the control of foxes, and to a lesser extent, feral cats, and cover a wide range of biogeographic areas from temperate forest to semi-arid coast.

All these areas have a range of species that are considered threatened by predation or potential competition from rabbits.

It is recommended that at the completion of each investigation the information be used to update models of the systems and its predictions.

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10 Acknowledgments

11 Appendices

Appendix 1. Predictive model of pest species interactions in Australia.

Interactions 1 and 2

The effect of climate on vegetation biomass and growth in Australia in semi-arid systems was quantified by Robertson (1987). In Australia most published interactive models for semi-arid systems (Caughley 1987; Choquenot 1998; Pech and Hood 1998) have used Caughley's modification of Robertson's (1987) pasture growth model (Caughley 1987), where the quarterly change in pasture biomass is given by:

$$\Delta V = -55.12 - 0.0153V - 0.00056V^2 + 2.5R + V^* \qquad \text{eqn 1}$$

Pasture biomass V is in units of kg ha^{-1}, R is the quarterly total rainfall in mm and V^* is drawn from a normal distribution with the mean equal to the estimate from the regression equation and a standard deviation of 52 kg ha^{-1} (Caughley 1987).

Interaction 3

Rabbits effect on vegetation
The effect of rabbits on vegetation was measured by Short (1987) using an intensive grazing trial in Kinchega National Park. The daily per capita consumption of pasture by rabbits, adjusted for body weight and expressed as kg animal^{-1} day^{-1} was:

$$g_R = 0.068(1 - e^{-V/138})(w^{0.75}) \qquad \text{eqn 2}$$

where V is the pasture biomass in kg ha^{-1} and w is the weight of a rabbit in kg. The satiating intake is $0.068w^{0.75}$. This is an Ivlev form of a type II prey dependent functional response.

A ratio dependent functional response could have the form:

$$g_R = 0.068(1 - e^{\frac{xV}{R^y}})(w^{0.75}) \qquad \text{eqn 3}$$

where the parameters x and y determine the shape of the relationship.

Vegetation effect on rabbit rate of increase

The relationship used by Pech and Hood (1998) for the quarterly rate of increase of rabbits was:

$$r = -4.6 + 5.5(1 - e^{-0.0045V}) \qquad \text{eqn 4}$$

where V was the pasture biomass in the previous quarter.

This relationship could be altered to express r as a function of intake rather than standing biomass. For example:

$$r = -a + c(1 - e^{-dI}) \qquad \text{eqn 5}$$

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where a is the maximum rate of decrease, c-a is the maximum rate of increase, d is the demographic efficiency, and I is the intake. d is related to the proportion p of satiating intake $sw^{0.75}$ below which the population declines by:

$$d = \frac{-\ln(1 - a/c)}{s.p.w^{0.75}}$$

eqn 6

A more mechanistic approach would be to model rabbit rate of increase as a function of both pasture growth (rabbits respond to growing pasture by breeding), and standing biomass (standing biomass may contribute to rabbit survival), but to our knowledge this has not been attempted and data are not available. As an example of this approach rabbit dynamics could be divided into periods where rabbits breed and periods where breeding ceases and populations decline. Breeding could be determined as a function of a threshold biomass (i.e. breeding only occurs when a certain biomass of vegetation is present) combined with an Ivlev numerical response of the form:

$$r = r_m (1 - e^{-d\Delta V})$$ when V > threshold

eqn 7

where r_m is the maximum rate of increase, d determines the shape of the relationship between growth and rate of increase and ΔV is the growth. When the vegetation is not growing rabbits do not breed and the population declines depending on available biomass (or intake):

$$r = -a + c(1 - e^{-dV})$$

eqn 8

where a in this case reflects the maximum rate of decrease, $c = ln$(maximum finite survival rate in non-breeding period), d is the demographic efficiency and V is the biomass.

Interaction 4

Interaction 4 allows for unexplained density-dependence in rabbit populations. This could come from social interactions for example, and is modelled by a numerical response function of the form:

$$r = -a + c(1 - e^{-dV}) - jR$$

eqn 9

where j defines the density dependence.

Interaction 8

Effect of foxes on rabbits

In semi-arid systems rabbits comprise a large percentage of the fox diet, particularly when at high density (Pech and Hood 1998). Pech *et al.* (1992) estimated the functional response of foxes to rabbits at Yathong based on the weight of rabbit found in fox stomachs and an estimate of gut passage rates. They fitted a Holling type III functional response to the data (Holling 1959). The daily consumption of rabbits in grams per fox per day was:

$$g_F(R) = 1096R^2 / [(1.32)^2 + R^2]$$

eqn 10

where R is the number of rabbits ha^{-1} (Pech and Hood 1998).

Effect of rabbits on fox rate of increase

Pech and Hood (1998) expressed the numerical response of foxes to rabbits as:

$$r_F = -0.56 + 0.77(1 - e^{-3.2R})$$ eqn 11

where R is the number of rabbits ha^{-1}. For computer simulations they defined a minimum fox density of 0.1 km^{-2} to prevent fox populations from reaching unrealistically low densities and/or going extinct.

A more mechanistic approach would express fox rate of increase in terms of food intake, and would also break the year into recruitment periods and decline (non-recruitment) periods, but whether this is feasible requires future investigation. As an example of the approach, recruitment could be considered a point event (say weaning) and modelled as a function of intake integrated over a preceding period (or average intake for simplicity):

$$r_F(recruits) = c(1 - e^{-d(i-T)}) \quad \text{for } i \geq T$$ eqn 12a

$$r_F(recruits) = 0 \qquad \text{for } i < T$$ eqn 12b

where c is the maximum recruitment rate, d is the demographic efficiency, i is the averaged intake over a defined period, and T is a threshold intake below which recruitment is not possible. The maximum intake rate is defined by the maximum number of females produced per female per recruitment period $c = ln(1+\text{max. females produced})$. After the recruitment peak the population declines until the next recruitment phase at a rate according to the equation:

$$r_F(decline) = -a + c(1 - e^{-d'I})$$ eqn 13

where a is the maximum rate of decline, $c-a$ is the minimum rate of decline, d' is the demographic efficiency based on intake and I is the intake. As an example of estimating $c-a$, if litters of four cubs, with two females and two males is a reasonable approximation of the maximum recruitment of foxes, and an r_{max} of 0.84 per year is a reasonable approximation of the maximum rate of increase of foxes, then the maximum finite yearly survival rate ($c-a$) is about $e^{0.84}/3 = 77\%$.

Interaction 9

Interaction 9 allows for unexplained density-dependence in fox populations. Density dependence could be added by adding a term to the Pech and Hood model for fox numerical response:

$$r_F = -0.56 + 0.77(1 - e^{-3.2R}) - jF$$ eqn 14

or by adding a density dependent term to either the decline phase or increase phase in the more detailed model.

Interaction 10

The effect of feral cats on rabbits

The fitted model for feral cats is a Holling type II functional response (Figure 12):

$$g_C(R) = 52.6R/(5.9 + R)$$ eqn 15

where R is the number of rabbits km^{-1}, and the intake rate is expressed as a percentage occurrence in the diet per unit time.

Interaction 12

Interaction 12 is added to represent interactions between foxes and feral cats not captured by competition for resources through the functional response. This could be interference competition or direct predation.

One way to model these interactions is by reducing the numerical response of one predator species in response to the presence of the other. For example, the cat numerical response could be expressed as:

$$r_C = -a + c(1 - e^{-dR}) - hF \qquad\qquad \text{eqn 16}$$

where R is the abundance of rabbits (or juvenile rabbits), and F is the abundance of foxes.

A simple model for preliminary exploration

For cat functional response we use a modified form of equation 15 (i.e. the satiating intake re-scaled from the value for foxes, and rabbit abundance converted from a spotlight count to an estimate per unit area):

$$g_C(R) = 0.874R/(0.5 + R) \qquad\qquad \text{eqn 17}$$

where R is the density of rabbits ha^{-1}. For the cat numerical response we use equation 16, with a = 0.56 (the same as foxes), and c-a = 0.25 (i.e. the intrinsic rate of increase r_m = c-a is estimated using the allometric relationship of Sinclair (1996) and an average body weight of 2.8 kg for adult females). We vary the demographic efficiency d and the effect of foxes on feral cats h. In the absence of any other information we set the minimum density of feral cats the same as foxes (0.1 km^{-2}).