

Predation Models for Primary and Secondary Prey Species

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Abstract

In Australia, the red fox (*Vulpes vulpes*) is a generalist predator of European rabbits (*Oryctolagus cuniculus*) and a range of small to medium-sized native species. The available evidence suggests that foxes are capable of regulating rabbits in semi-arid environments but their role in the population dynamics of other prey species is not clear.

A series of models, and associated experimental tests, that compare the effects of predation on primary and secondary prey species are described. The models are appropriate to the time scale of prey dynamics and differ from recent predator–prey models that focus on predator dynamics. These ideas are discussed for the fox and several of its prey species in Australia.

Introduction

Exotic predators, particularly the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*) have contributed to the decline in small to medium-sized native species in Australia, although their importance relative to that of competition from domestic and feral herbivores and from modifications to habitat is still open to debate (Morton 1990; Recher and Lim 1990; Dickman *et al.* 1993). Foxes are generalist predators relying mostly on rabbits (*Oryctolagus cuniculus*) as primary prey (Newsome *et al.* 1989). They also take a wide range of native prey species where they are available and there is compelling evidence that the population dynamics of some native prey species are strongly affected by fox predation (Kinnear *et al.* 1988; Short *et al.* 1992).

Whatever their role in the loss of native species, evidence is now emerging that the control of exotic predators is crucial in the re-establishment of some species (Kinnear *et al.* 1988; Short *et al.* 1992). While these studies have explored some aspects of the problem, a more general framework is needed for understanding the role of predation in the re-establishment and future persistence of rare and endangered native species. Attempts to re-establish native species are invariably restricted to small localised populations. But if the reintroduction is successful, some species might reach high densities over large areas. For example, the brush-tailed bettong (*Bettongia penicillata*), which is confined to a few small areas in Western Australia was formerly abundant with a continental distribution (Christensen 1983). This implies a need to consider the relative importance of predation for a wide range of prey densities. An additional factor that will be considered in some detail in this paper is the availability of existing alternative prey species such as the rabbit. Reintroduction programmes could include the control of rabbits, as well as predators, in an attempt to create suitable conditions for establishment and long-term persistence of new populations of native animals.

Holt (1977, 1984) has shown theoretically that when the abundance of primary prey increases, then an increase in predators results in a decline in the abundance of secondary prey. This has the effect of appearing like competition between prey species even when there is no

competition, and is called 'apparent competition'. An alternative approach to the interaction of species sharing a common predator was used by Armstrong (1979), who modelled the effect of different resource utilisation by prey species in the face of functionally equivalent predation. But in a review of the effect of different types of predators' functional responses, Abrams (1987) noted that, particularly with Type III functional responses, a large range of indirect effects are possible between two or more prey species.

In this paper we discuss some simple graphical models of the total response of a predator to its prey species. We recognise that a full mathematical model of a predator and two prey species may show some unexpected outcomes, depending upon, for example, the degree of refuge available to prey and the adaptive response of either predator or prey (Abrams and Matsuda 1993). The latter situation may be particularly interesting where the predator is an exotic species and the prey has not evolved responses to it. But as a simple rule of thumb the graphical models illustrate what should on average be predicted. Attention is focused on the differences between primary, or staple, prey species and other prey species that may be of secondary importance as a food source. Modifications that take into account time delays in the predator-prey system are examined and some experimental tests of the models are described.

The models we describe have general applicability. To illustrate our approach and to indicate the relevance to current management issues in Australia, the discussion will focus on the fox as a predator and on the brush-tailed bettong as an example of a native prey species, with rabbits as the main alternative prey. One reason for choosing these prey species is that rabbits and bettongs are similar-sized animals but they appear to have responded very differently to predation by foxes over the last 80–130 years.

Models for Primary and Secondary Prey Species

The interaction of a population of predators and that of a prey species can be described by a total-response function. The total response is the product of the functional response (the percentage mortality due to predation) and the numerical response (the density or the rate of increase of the predator as a function of prey density). Options for the interactions of a predator and its prey are illustrated in Fig. 1.

The graphs describe predation on one prey species but the effects of alternative prey are implicit. Each graph shows the percentage recruitment of prey as a function of prey density. Net recruitment to the prey population is assumed to increase as the population increases (or, equivalently, percentage recruitment is constant) until eventually resources become limiting. When this happens recruitment declines and the prey population stabilises at the density K . The graphs also show four possible relationships between prey density and percentage mortality due to predation. These relationships are central to understanding the role of predation in the population dynamics of prey species (Sinclair and Pech 1993).

Model 1: The total response to a prey species is density dependent when this species is at low densities and inversely density dependent when it is at high densities. There is one stable state (Fig. 1a).

The relative positions of the recruitment curve and the total-response curve will determine the theoretical equilibrium density of the prey. Two possibilities, A and C , corresponding to two densities of predators, are shown in Fig. 1a: both are stable. The prey species is regulated by predators at A but not at C . In practice the density of prey is not fixed at these equilibria but is continually perturbed by changes in the environment. Populations of prey will tend to return towards A and C and should persist indefinitely.

Using foxes, rabbits and bettongs as examples, this form of the total response of foxes to bettongs could arise if, at low densities of bettongs (for example N_X in Fig. 1a), foxes subsist on rabbits. Some bettongs must be able to find a refuge from predation or, when bettongs reach low densities, alternative prey must always be sufficiently abundant to deflect predation pressure. As

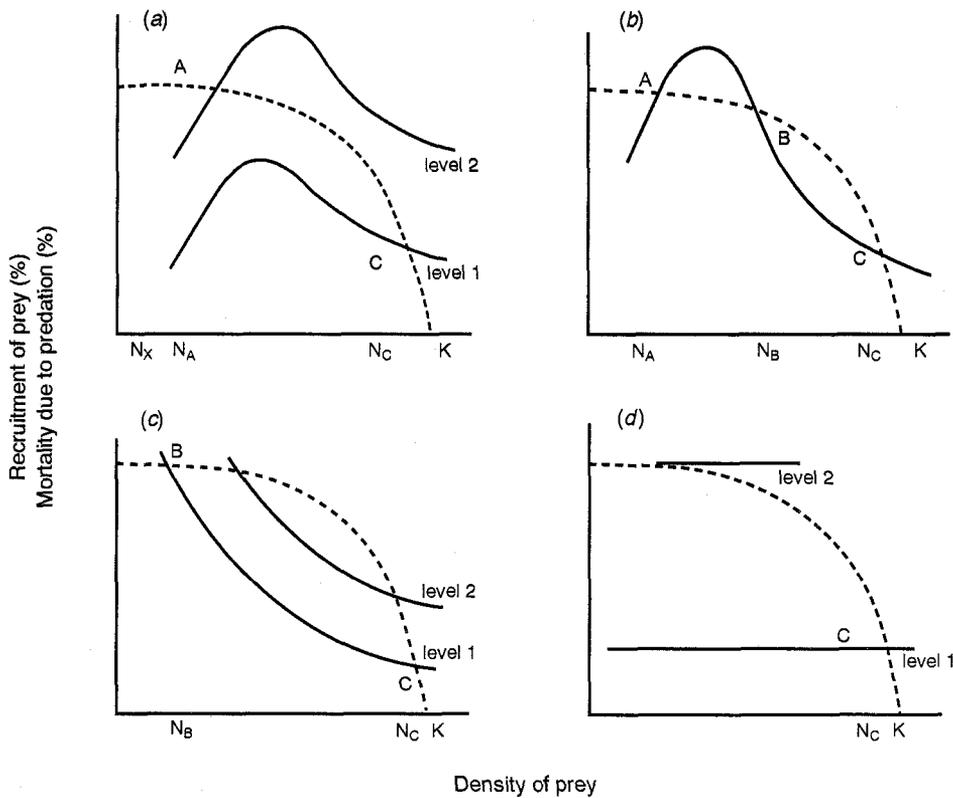


Fig. 1. Predator-prey dynamics. (a) A density-dependent total response and single stable state. The equilibria where percentage recruitment of prey (-----) balances percentage mortality due to predation (——) are indicated by A for high predator abundance (level 2) and C for low predator abundance (level 1). The corresponding densities of prey are N_A and N_C . N_X is an arbitrary density less than N_A and K is the carrying capacity of the environment in the absence of predation. (b) A density-dependent total response and two stable states. Particular levels of percentage recruitment of prey (-----) and percentage mortality due to predation (——) can result in stable equilibria at A and C, with corresponding densities of prey at N_A and N_C , separated by a boundary at B. (c) An inverse density-dependent total response. An unstable equilibrium, or boundary, at B and a stable equilibrium at C occur where percentage mortality due to predation (——) balances percentage recruitment of prey (-----). High predator abundance (level 2) or low predator abundance (level 1) can alter the values of the prey densities N_B and N_C corresponding to B and C. (d) A density-independent total response. The percentage mortality due to predation (——) is shown for high (level 2) and low (level 1) predator abundance. A stable equilibrium at C, with corresponding prey density N_C , occurs where percentage recruitment of prey (-----) balances a low level of predation.

the density of bettongs increases, mortality due to predation increases. This can occur most rapidly through a density-dependent functional response. Bettongs become the primary prey for foxes and, at high densities of bettongs, the total response is inversely density-dependent as foxes are satiated. Although in principle a density-dependent numerical response could produce the same effect, this might be obscured by the time-lag between recruitment or mortality of foxes and the relatively rapid changes in the density of many of their prey species. This is discussed in more detail below.

Model 2: The total response is density dependent at low prey densities and inversely density dependent at high prey densities. There are two stable states because of the special configuration of recruitment and total-response curves (Fig. 1b).

Model 2 is a special case of Model 1 but has some quite different properties. The relative positions of the recruitment and total-response curves result in two stable states at *A* and *C* separated by a boundary at *B*. The low density state, *A*, is regulated by predators whereas the high density state, *C*, occurs when the prey escapes predator regulation. The range of densities between N_A (corresponding to *A*) and N_B (corresponding to *B*) is the so-called 'predator pit'. If the density of the prey species is greater than N_A but less than N_B , it will be driven by predation towards *A*. If the density of prey is greater than N_B (for example, after a temporary reduction in predator density) then it should increase up to N_C . As with State *C* in Fig. 1a, the high density state for the prey should be quite robust (that is, relatively insensitive to small-to-moderate changes in predator density). It is important to establish whether remnant populations of a prey species are at State *A* or State *C* in Fig. 1b. If they are at *A*, the possibility exists for a dramatic increase in their density if the abundance of predators is reduced.

Model 3: The total response is inversely density dependent for all densities of a prey species (Fig. 1c).

Two possibilities for the relative positions of the recruitment curve and the total-response curve are shown in Fig. 1c. The state corresponding to intersection *C* is stable but *B* is unstable and marks the lower bound for prey densities. If, for some reason, the density of prey should fall below N_B , predation will drive them to extinction. Changes in the abundance of predators and hence the density N_B will be determined mainly by other prey species.

For foxes and bettongs, Model 3 could apply if foxes depend primarily on alternative prey and bettongs are essentially a small consistent by-catch. Then the percentage predation on bettongs will be greatest at low bettong densities but will decrease as bettong density increases. If the density of foxes increases (Level 2 in Fig. 1c) or recruitment of bettongs decreases, intersections *B* and *C* move closer together increasing the probability of a crash in the abundance of bettongs. The key difference between Model 3 and Model 1 or 2 is the action at low prey densities. This difference strongly influences the likelihood of successful reintroductions, and the long-term prospects for survival, of bettong populations.

Model 4: The total response is independent of the density of a prey species (Fig. 1d).

Model 4 is essentially a variant of Model 3 and has identical results at low predator densities (Level 1). The difference is that now predators are assumed to take a constant (rather than declining) proportion of a particular prey species. The dynamics of Models 3 and 4 are similar even though the boundary point *B* (Fig. 1d) no longer exists. As predator densities increase to Level 2 the prey population could switch suddenly from a stable state to extinction.

Time Delays

Models 1–4 are based on possible alternatives for the total-response function. However, there are problems with the concept of a total response in the case of a predator whose population dynamics operate on a different time scale to that of its prey.

The functional response can be a major factor in the population dynamics of the prey — it directly, and immediately, affects their mortality rate on a time scale of days to weeks. In contrast the feedback from the prey on the predator is firstly through its supply of food for maintenance and secondly through food availability over an extended breeding season leading to the recruitment of new predators. In addition, for a generalist predator the feedback is complicated by the availability of alternative prey items. Oksanen *et al.* (1992) have pointed out the logical inconsistency of combining processes operating at different time scales in a single set of equations to describe the population dynamics of a predator–prey system. This argument

applies equally well to the graphical presentation of a total-response function. If a total response is to be calculated it should use a consistent time scale when combining mortality and recruitment processes. Oksanen *et al.* (1992) propose a solution for describing the dynamics of the system at a time scale appropriate to the dynamics of the predator. They do this to compare the result with an alternative ratio-dependent theory proposed by Arditi and Ginzburg (1989). What both approaches indicate is the difficulty in constructing suitable models of predator-prey systems in which the population dynamics of predators and prey operate at different time scales.

A simple approach to the time-scale problem is to decouple slow and fast processes. Then, at the short time scale of prey dynamics, the predator population can be treated as constant or slowly varying. This can be illustrated, for example, with foxes, rabbits and bettongs. Rabbits are polyoestrus and can increase from low density to very high density within one spring-to-summer breeding season (Gilbert *et al.* 1987). Bettongs breed continuously. The young of *B. penicillata* leave the pouch after about 98 days but the quiescent blastocyst responds to intermittent lactation by implanting so that the birth of the next pouch young follows 17 days later (Smith 1989). In contrast to rabbits and bettongs, foxes are monoestrus. They mate in winter, with the annual pulse of cubs entering the population in spring (McIntosh 1963). For the remainder of the annual cycle, fox density changes through mortality but, in broad terms, each year the upper limit to the density of foxes is set at, or prior to, the onset of the rabbit breeding season. Therefore, as rabbits, bettongs and other small to medium-sized prey change in abundance, there will be relatively slow changes in fox density, and the dominant impact of fox predation on prey dynamics will be through the functional response. For example, Pech *et al.* (1992) found that most, if not all, of the variation in the total response of foxes to rabbits was due to the functional response. Models 1–4 can still be used but the curves for mortality will be dominated by the functional response.

For comparison with the approaches of Oksanen *et al.* (1992), or Arditi and Ginzburg (1989), this view of prey dynamics is represented by the isoclines in Fig. 2. The prey isoclines from Rosenzweig and MacArthur (1963) are the conventional humped curve (Fig. 2a) and the curve with a prey refuge (Fig. 2b), which is equivalent to a Type III functional response. The predator 'isoclines' are simply horizontal bands corresponding to a predator density set independently of current prey density. In the case of foxes, rabbits and bettongs, each isocline is appropriate for a time frame of up to one year and a 'poor', 'average' or 'good' year corresponds to a prey isocline at a different level. Even if there is a general decline in fox density after the end of the breeding season, on a time scale of weeks during which there may be large changes in prey density, the functional response may change but there will be little or no change in fox numbers. The position of the predator isocline is determined by the recent history of the system and is not just the environmental ceiling on predator density suggested by

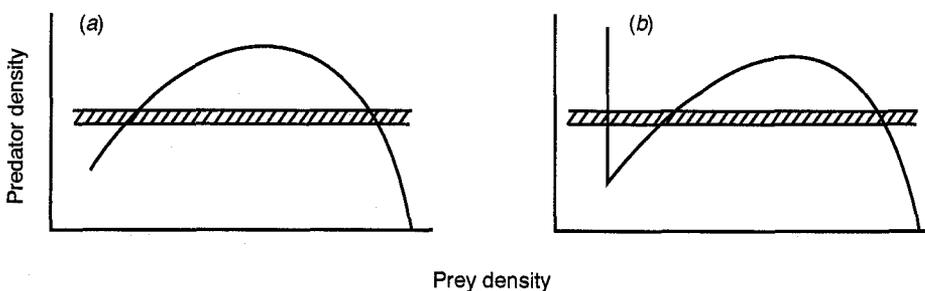


Fig. 2. Isoclines for predators and prey on the short time scale of prey dynamics. The prey isocline (—) in (a) is the single-humped model of Rosenzweig and MacArthur (1963), and in (b) includes a refuge for prey at low prey densities (Rosenzweig and MacArthur 1963). The predator 'isocline' (indicated with the horizontal shaded band) is independent of prey density.

Rosenzweig and MacArthur (1963). But on the short time scale of prey dynamics, it is irrelevant whether the predator isocline is a vertical line (Rosenzweig and MacArthur 1963), or has a positive (Arditi and Ginzburg 1989) or negative (Oksanen *et al.* 1992) slope. The relative positions of the predator and prey isoclines in Fig. 2 determine the possible states of the system in a way exactly equivalent to that in Fig. 1.

In semi-arid and arid Australia (i.e. about 70% of the continent), the appropriate model for rabbit population dynamics at longer time scales will include a number of factors such as climatic variability and sporadic outbreaks of myxomatosis (Fenner and Ratcliffe 1965), which could override any long-term effects of predation. As far as rabbits are concerned, the system is often and unpredictably reset by limiting factors. This is the essence of the extended version of the concept of Newsome *et al.* (1989), of 'Environmentally Modulated Predation' (described in Pech *et al.* 1992).

The population dynamics of foxes will operate at a longer time scale than that of many, if not all, of their small to medium-sized prey. For a generalist predator, recruitment and survivorship are likely to be related to total food supply, not just the density of one particular prey species. Therefore, the appropriate equation for fox dynamics should include a sum of the intake from all food species, each of which is integrated over the immediate past history. In terms of isocline diagrams, the prey isocline ought to be an amalgam of contributions from all prey species and an analysis based on a single prey species is likely to be misleading except in unrealistically simple fox-prey systems.

Experimental Tests for the Models

There are a number of ways to distinguish between Models 1–4. However, in the context of conserving rare native species, new colonies of animals will usually be small and it may be unacceptable to expose rare species to apparently 'unnecessary' levels of predation in order to test models of predation. Alternatively, a risk-averse approach to managing rare native species must be balanced against the potential for extremely valuable insights into their population dynamics, which can be gained from experimental studies (Walters and Holling 1990). Several methods could be used to test the models but the most productive approach is likely to be through perturbation experiments (Sinclair 1989).

Measure the Total Response of the Predator

The models are based on alternative forms of the total-response function and could, in principle, be distinguished by measuring the total response of a predator to each of its prey species. This requires techniques for estimating the density of predators and prey, and for measuring mortality due to predation as the prey density is varied. Predation could be measured directly, for example with mortality sensors on the prey, or indirectly by analysis of stomach contents of predators. It may not be necessary to measure the functional response at all prey densities but instead focus on critical intervals in the total range of prey densities. For example, small populations of a prey species persisting in the presence of a predator could be at State A or C in Figs 1a and 1b. The states could be distinguished by means of small perturbations in prey density to determine the slope of the total response. In State A, the slope of the total response is positive; in State C it is negative. For Models 3 and 4, the slope of the total-response function is never positive.

The problems with this approach can include a lack of prey populations over a suitable range of densities, an inability to manipulate prey density, 'noise' in the data due to other factors such as environmental fluctuations (but see Sinclair and Pech 1993), extreme variability in the abundance of alternative prey species and the effects of time delays in the numerical response of predators.

Measure Attributes of the Prey

It may be possible to infer, from indirect measurements, whether predation is regulating a prey population. If a prey species is at State *A* in Figs 1*a* and 1*b*, then a small reduction in predator density should allow an immediate increase in prey density. As Kinnear *et al.* (1988) found for the rock-wallaby (*Petrogale lateralis*) in Western Australia and Messier and Crête (1984) for moose (*Alces alces*) in Québec, condition indices of individual prey should indicate that the population still has the capacity to increase. Alternatively, if food resources are limiting the prey population, it is at State *C* in Fig. 1. This may be apparent in indices of body condition or reproductive condition (see, for example, Newsome 1965) and even a large reduction in predator density should produce a minimal increase in prey density.

Manipulate Prey Species

It may be possible to experimentally manipulate the density and the recruitment rate of the prey population.

(i) *Reintroductions.* For an experimental reintroduction of a prey species, the size of the founder population may determine its future dynamics. Since newly establishing populations are likely to be small, the distinction between Model 1 or 2 and Model 3 may be critical. If Model 1 is appropriate then a reintroduction of the prey species into a suitable habitat should result in it increasing towards a stable state such as *A* or *C* (depending on the density of the predators) and persisting indefinitely. If Model 2 applies, then a small reintroduction of the prey species should result in an increase in their density towards a stable state at *A* but they will not be able to reach high densities without some predator control. In contrast to Model 1 (or 2), for Model 3 a small reintroduction ($<N_B$ in Fig. 1*c*) will fail but a large reintroduction may be successful if fluctuations in the density of predators are damped to ensure that a predation rate above Level 2 (Fig. 1*c*) is not reached. For Model 4, the outcome of reintroducing a prey species does not depend on the size of the initial population but is highly sensitive to the level of predation. Below Level 2 (for example, at Level 1) in Fig. 1*d* it will succeed, but above Level 2 it will fail.

(ii) *Existing prey at low density.* It may be possible to manipulate the rate of increase of prey populations at low density, for example by altering their food supply. For Model 1, changes in the prey's rate of increase should produce immediate and reversible changes in the density of the prey for all initial densities. For Model 2, state transitions that may be a mechanism for the formation of plagues are possible [see, for example, Newsome and Corbett (1975) and Pech *et al.* (1992)].

(iii) *Alternative prey.* The experimental manipulation of an alternative prey species may be feasible, especially when it is a pest species as the rabbit is in Australia. For example, if the density of rabbits is reduced, then no change in fox predation on other prey, such as bettongs, implies that they (bettongs) are the primary prey for the common predator. This supports Models 1 and 2 for bettongs. Alternatively, a long-term increase in bettongs may imply that fox density has declined because their primary prey (rabbits) is now less abundant. Therefore, predation on bettongs is less likely to be density dependent and Model 3 (or 4) is supported. However, because of time delays in the numerical response of the predator to a reduction in its primary prey, there may be an immediate increase in predation of secondary prey resulting in a short-term decrease in their density.

Manipulate Predators

The removal of predators should produce an immediate response in each population of prey species. If, for example, following the removal of foxes there is a large increase in the density of rabbits but minimal change in bettong density then bettongs are minor prey and Models 3 and 4 are more likely. However, some increase in bettongs following the removal of predators would be expected for all models.

Models 1 and 2 can be distinguished with a two-stage experiment (Sinclair 1989; Pech *et al.* 1992). In the first stage, the density of predators is reduced allowing a large increase in the prey

to N_C . In Stage 2, predators are reintroduced. According to Model 1, the density of prey will decline to N_A (Fig. 1a) during Stage 2. For Model 2 a small decline in the density of prey may occur but during Stage 2 they will persist at a density greater than N_B (Fig. 1b). If Model 3 or 4 applies, an experimental manipulation of this kind applied for long enough could ultimately result in the extinction of the secondary prey species.

Discussion

Over the last century, the decline of small to medium-sized native mammals in Australia, particularly in arid and semi-arid areas, has coincided with the establishment and persistence of the rabbit (Morton 1990; Recher and Lim 1990; Dickman *et al.* 1993). The models and associated experiments described in this paper are proposed as a framework for understanding, at a population level, the role of predation in the dynamics of different types of prey species. The most important distinction between Model 1 or 2 and Model 3 or 4 depends on the ability of prey species at low densities to avoid predation. This may require suitable habitat for a refuge, but can also result from differences in predator-avoidance behaviour producing a relatively invulnerable class of animals.

Rabbits and native species such as bettongs are likely to be of similar value as food items for foxes. One animal constitutes a meal of about 1 kg, which is a stomachful for one fox (Lloyd 1980), and can probably be caught by a fox hunting alone. But the relative ability of rabbits and bettongs to avoid predators is not known. Most rabbits appear susceptible to foxes but predation may not be equally spread across all age classes. Catling (1988) found that foxes ate mainly older rabbits, although in areas with sandy soils foxes can dig up warrens for young rabbits (Wood 1980). For comparison, brush-tailed bettongs nest above the ground and probably use shrub thickets for shelter. In Western Australia these thickets can include *Gastrolobium bilobum*, which contains the poison monosodium fluoroacetate (1080), and bettongs may benefit through secondary poisoning of susceptible predators like foxes (Short *et al.* 1992).

One strategy for ensuring a prey species' survival is to swamp either the predators' functional or numerical response by bursts of high reproductive activity [see, for example, Newsome and Corbett (1975), Sinclair *et al.* (1990), and Pech *et al.* (1992)]. This may also provide an opportunity for prey species to recolonise 'sink' habitats in the way suggested by Morton (1990). The strategy is most likely to succeed for those prey species that take advantage of unseasonably good conditions because foxes are locked into synchronised, monoestrus breeding. Rabbits may extend their breeding season and are capable of breeding at any time of the year. Like most Macropodoidea, all species of *Bettongia* are continuous breeders (Tyndale-Biscoe 1989) and should be able to take advantage of the characteristically variable climate of arid and semi-arid Australia. In an analogous predator-prey system, Corbett and Newsome (1987) observed a switch by dingoes (*Canis familiaris dingo*) onto red kangaroos (*Macropus rufus*) during a drought. Red kangaroos were driven virtually to local extinction, with the data (fig. 4e in Corbett and Newsome 1987) suggesting the inverse density-dependent response of Model 3. Nevertheless, red kangaroos can respond immediately to favourable conditions, including through the mechanism of embryonic diapause (Newsome 1965), and are generally widespread and common in central Australia. The difference between the long-term survival of red kangaroos and brush-tailed bettongs in the face of predation may be due to the red kangaroo's mobility and ability to persist in areas beyond the reach of dingoes, which must drink frequently, and every day in summer (A. E. Newsome and L. K. Corbett, unpublished data).

The importance, for a prey species' persistence, of responding to predation on a vulnerable age class is illustrated in an experimental study by Robertshaw and Harden (1985) of dingo predation on the swamp wallaby (*Wallabia bicolor*). The relative numbers of dingoes and wallabies were manipulated, partly through a 'wild dog' control programme and partly by removing wallabies at one site, so that the numbers of predators relative to those of prey were

different between two sites. The effect of high levels of predation was to shift the breeding of swamp wallabies from a strongly seasonal pattern to continuous breeding throughout the year. The mechanism for the disruption of the breeding cycle was either direct predation of young-at-foot or interruption of lactation in females forced to abandon their young when harassed by dingoes. Although it appears that the change in breeding pattern was a consequence of dingo predation, the outcome was a reduced level of predation on young, dependent wallabies. The proportion of dependent to independent wallabies in dingo scats was 1:1.48 in the seasonally breeding population and 1:3.6 in the continuous breeders. This difference may be sufficient to increase the survival of young wallabies in a low-density population allowing it to persist in a predator-regulated state.

In Australia, the management of exotic predators such as foxes has focused on the use of intensive lethal control methods to reduce, or completely remove, their impact on native species. But the successful re-establishment of native prey species under conditions of high or complete predator removal may give little indication of their future if the management of predators is changed and predation pressure is increased. Also, once a primary prey species such as the rabbit is established, the opportunity exists for a predator to severely deplete secondary species as by-catch. As a result, some secondary species may persist only in refugia such as off-shore islands or in small areas with an artificially reduced predator density. In the long term, it may be possible to develop successful management strategies for native species, foxes and rabbits based on the models described in this paper. The application of such strategies outside small reserves will depend on the development of broad-scale biological control methods for foxes that employ either immuno-contraceptive (Tyndale-Biscoe 1993) and/or lethal agents.

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