Hypotheses arising from a population recovery of the Western Ringtail Possum *Pseudocheirus occidentalis* in fire regrowth patches in a stand of *Agonis flexuosa* trees in south-western Australia

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ABSTRACT

Published and unpublished reports about *Pseudocheirus occidentalis* (Western Ringtail Possum) in the stand of *Agonis flexuosa* (peppermint trees) at Locke (near Busselton, Western Australia) indicated that it was common in the mid 1960s, rare in the mid 1980s and abundant in the early 1990s. This local decline and recovery occurred against a background of pastoralism from the 1960s to the 1980s, patch fires in the early 1980s and an increase in the abundance of introduced foxes *Vulpes vulpes* from the 1970s onwards. There are three main hypotheses concerning the decline and recovery:

- conditions of localized, high quality browse available in an *A. flexuosa* regrowth mosaic after patch fire may encourage a female-biased sex ratio in *P. occidentalis*,
- predation by *V. vulpes* is less likely to have a significant impact on *P. occidentalis* in habitat with high continuity of the canopy,
- habitat degradation caused by pastoralism may lead to decline in *P. occidentalis*.

The disturbance processes in the last two hypotheses have little contemporary significance for *P. occidentalis* populations given the prevailing management emphasis in south-west Western Australia on controlling *V. vulpes* and excluding pastoralism from the conservation estate. However, the female-biased sex ratio in response to patch firing could potentially evolve into an important management tool for supporting recruitment in important or small populations of *P. occidentalis*.

Key words: *Pseudocheirus occidentalis, Agonis flexuosa,* fire, fox, grazing, possums

Introduction

Conservation management decisions are often made on the basis of limited information and the conservation of Australia's forest fauna is no exception to the general principle (e.g., RAC 1992, Calver *et al*. 1999, Friend and Wayne 2003). In recognition of this limitation, there is a clear need to identify and assess all relevant data, including historical records, anthropological evidence and unpublished reports as well as peer-reviewed literature to provide background for decision-making (e.g., the detailed survey of the relevant 'grey literature' in RAC 1993). While in many cases this assemblage of information will not give definitive answers, it can suggest causes for decline or mechanisms for recovery that can be tested via directed observation, experimental research or adaptive management.

The case considered here is that of the Western Ringtail Possum *Pseudocheirus occidentalis*, which is endemic to the forests and woodlands of south-western Australia (Jones 1995). The species was recognised as vulnerable by Maxwell *et al.* (1996) and is classified as rare or likely to become extinct (Schedule 1) in the Wildlife Conservation (Specially Protected Fauna) Notice 2001, Government Gazette, WA, 14 August 2001. Comparisons of the distributions in Shortridge (1909), Jones (1995) and Maxwell *et al.* (1996) show that *P. occidentalis* declined substantially during the 20th century and is now known from apparently isolated populations throughout the south-west (Jones *et al.* 1994a,b). Local declines of *P. occidentalis* occurred in different decades and local extinctions occurred as early as the 1920s and as late as the 1980s (Jones *et al.* 1994a). The species formerly occupied a wide range of vegetation types, but by the 1990s, most extant populations occurred in habitat where *Agonis flexuosa* (a myrtaceous tree or shrub locally known as peppermint) is a common or dominant tree. The stronghold of *P. occidentalis* at the end of the 20th century was around Busselton at the southern extremity of the Swan Coastal Plain, where *A. flexuosa* grows as the dominant or co-dominant tree in stands on the sandy coastal soils around the Wonnerup and Vasse floodplains. Some stands of *A. flexuosa* in this area were removed to improve pastoral values, while coastal strip development was impacting remnant stands of *A. flexuosa* in the 1990s.

Explanations for *P. occidentalis* decline across the species' range include changed fire regimes (especially wildfires – Shortridge 1909), predation by the Red Fox *Vulpes vulpes* (Maxwell *et al*. 1996), predation by feral cats *Felis catus* (Shortridge 1909), competition with the Common Brushtail

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Possum *Trichosurus vulpecula* (see speculative comments in Friend and Wayne 2003) and land clearing for both agriculture and residential development (McKay 1983, Jones 1995, Maxwell *et al*. 1996). These factors may have operated interactively and varied in importance at different times. Overall, the absence of definitive assessments of causes of decline and lack of knowledge of specific local declines and recoveries hampers decisions on the best management of remnant *P. occidentalis* populations.

During the 1980s and 1990s there were surveys of the distribution and abundance of *P. occidentalis* in *A. flexuosa* woodlands at Locke Nature Reserve (hereafter Locke), near Busselton that offer insights into both the species' decline and the potential for local recovery. Here, we collate both published and unpublished data from survey reports and from a population study in Locke and nearby areas that describe a local population recovery. We then use them to develop hypotheses regarding the influence of fire, pastoralism and predation by *V. vulpes* on local *P. occidentalis* populations. All these disturbance factors could be regulated by management, so predictions arising from these hypotheses could be tested by directed observation and experiment or incorporated into an adaptive management process to strengthen understanding of the decline of *P. occidentalis* and the remedial measures that can be adopted.

In developing these ideas we present a brief description of the biology of *P. occidentalis*, a description of the Locke study site and a chronology of events occurring there. The hypotheses arising from evaluation of the chronology are then presented, followed by a discussion of the implications of these hypotheses and tests of their predictions that could be made via further observation, experimentation and adaptive management.

Biology of *P. occidentalis*

P. occidentalis shares several similarities with its eastern Australian congener, the Common Ringtail Possum *P. peregrinus* (Jones 1995, McKay and Ong 1995). Both species rely heavily on the leaves of favoured myrtaceous species as food, although in parts of the Western Australian distribution where *A. flexuosa* is dominant or co-dominant it may be the major component of the diet of *P. occidentalis* (Jones 1995, McKay and Ong 1995). Tree hollows are important shelters for some populations of both species, but in suitable environments possums may also build dreys (shelters) in trees using leaves, bark and twigs. Dreys are the dominant shelter sites for most coastal populations of *P. occidentalis*, but at inland sites tree hollows may be important shelter during hot summer weather (Jones 1994b). The two species of possums also show some important differences in biology. *P. occidentalis* is slightly larger than *P. peregrinus* (ranges 900 – 1100 g and 700 – 1100 g respectively) and is less sociable (Jones 1995, McKay and Ong 1995). *P. occidentalis* tends to have a single young with estimates of the incidence of twins being approximately 10% (Ellis and Jones 1992) and 16.7% (Jones *et al*. 1994b). *P. peregrinus* commonly bears a litter of two or more (McKay and Ong 1995).

Ellis and Jones (1992) suggested that the biological differences between *P. occidentalis* and *P. peregrinus* may be driven by more dispersed habitat resources in Western Australian habitat compared to eastern Australia. In one study occurrence in *P. occidentalis* was predicted strongly by high foliar nitrogen in *A. flexuosa* leaves and continuity of the canopy, with availability of tree hollows being a weaker predictor (Jones *et al*. 1994a,b, Jones and Hillcox 1995). Furthermore, in contrast to the diverse possum fauna in eastern Australia, *P. occidentalis* and *T. vulpecula* are the only large possums in the eucalypt forests and woodlands of south-western Australia, often co-occurring in suitable habitat remnants (Jones 1995, How and Kerle 1995). The lower species richness may also be an indication of poorer quality food.

P. occidentalis has undergone a greater decline in distribution than *P. peregrinus* and it is regarded as less secure. In the late 19th century *P. occidentalis* probably occurred from the Swan River near the city of Perth south to the Kalgan River near the port of Albany and perhaps as far east as the Pallingup River, with important associations with swamps, rivers and drainage lines (Jones *et al*. 1994a). During the 20th century *P. occidentalis* has undergone patchy decline over a wide geographic area. Local extinctions have been most extensive in the north and the drier inland parts of the original range (Figure 1, Jones 1994a).

Most extant populations occur in coastal or near-coastal *A. flexuosa* forest or woodland, or eucalypt forest or woodland with *A. flexuosa* understorey (Jones *et al*. 1994a). In some small parts of the species' distribution, conditions so favour *A. flexuosa* that eucalypts are excluded and these are the only sites where *P. occidentalis* is the only possum species present. This habitat type is concentrated in a small area at the southern extremity of the Swan Coastal Plain, near Busselton and is the only part of the south-west where

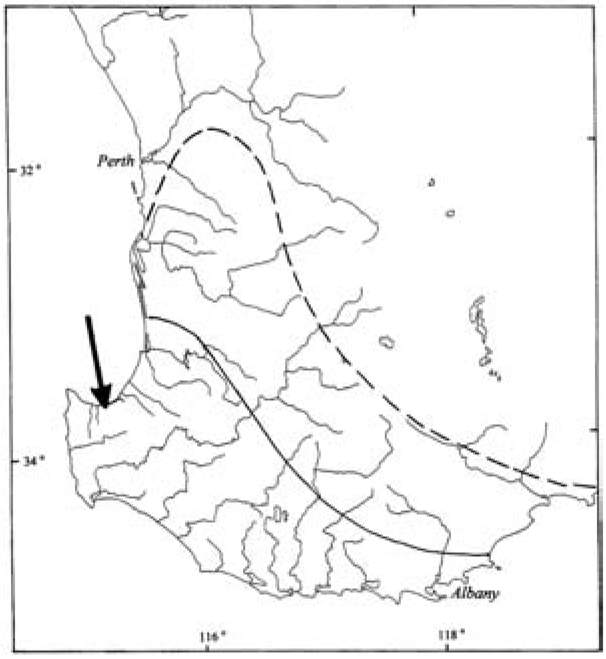

Figure 1. The location of Locke (arrowed) and approximations of the range limits of *P. occidentalis* ascertained by Shortridge (1909, dashed line) and Jones *et al.* (1994a, solid line).

P. occidentalis remained common and abundant up to the 1980s. The Busselton *A. flexuosa* stands are also the only habitat-type occupied by *P. occidentalis* where a substantial population is largely independent of the local hollow supply. Even in the summer drought the climate in these stands is mild compared to the rest of the species' current or former range. The most significant retained remnant of the Busselton *A. flexuosa* habitat type exists at Locke.

Locke

Locke is a nature conservation area of *c*. 190 ha near the coastal town of Busselton that supports a local population of *P. occidentalis* (Jones *et al*. 1994a) (Figure 1). It was originally a conservation reserve, but was reclassified as vacant Crown land in the 1960s and used as a grazing lease between 1962 and 1985. The area was later reclassified as an A-class reserve.

Locke has soils of well-drained light loams supporting woodland and forest, while richer loams including peat underlie marshlands. Lambert (1985) recognized seven vegetation types: *A. flexuosa* woodland, open flood gum *Eucalyptus rudis* woodland, marri *Corymbia callophylla* over low paperbarks *Melaleuca* spp., samphire marshland, low paperbark over shrubs and rushes, low paperbark over sedges and pasture grasses and low paperbarks over shrubs and pasture grasses.

Table 1. A chronology (1962-1992) for the Locke *P. occidentalis* population, the Locke fires, the incidence of grazing and *V. vulpes* abundance at Locke or nearby Cape Naturaliste. Blank cells indicate no data are available in those years.

Year	Possum abundance	Number of dreys	Incidence of fire (Lambert 1985, Jones unpublished)	Incidence of grazing (Lambert 1985)	Fox abundance
1992	Abundant (Jones *et al.* 1994a)	149	None reported	No grazing lease	Abundant (Jones *et al.* 1994b)
1991			None reported	No grazing lease	
1990			None reported	No grazing lease	
1989			None reported	No grazing lease	
1988			None reported	No grazing lease	
1987			None reported	No grazing lease	
1986			None reported	No grazing lease	
1985	Rare (Lambert 1985)		None reported	Grazing	
1984	Rare (Lambert 1985)	7	Patch fire	Grazing	Abundant (Lambert 1985)
1983			None reported	Grazing	
1982			None reported	Grazing	
1981			Fire	Grazing	
1980			Fire	Grazing	
1979			None reported	Grazing	
1978			None reported	Grazing	
1977			None reported	Grazing	
1976			None reported	Grazing	Abundant (at Cape Naturaliste) (King *et al.* 1981)
1975			None reported	Grazing	
1974			None reported	Grazing	
1973			None reported	Grazing	
1972			None reported	Grazing	
1971			None reported	Grazing	
1970			None reported	Grazing	Rare (at Cape Naturaliste) (King *et al*. 1981)
1969			None reported	Grazing	
1968			None reported	Grazing	
1967			None reported	Grazing	
1966			None reported	Grazing	
1965	Abundant (Lambert 1985)		None reported	Grazing	
1964			None reported	Grazing	
1963			None reported	Grazing	
1962			None reported	Grazing	

The *A. flexuosa* woodlands comprise *c*. 40 ha of the site and at varying times have supported large numbers of *P. occidentalis* (Jones *et al*. 1994a). The contemporary remnants of the coastal Busselton *A. flexuosa* stands have been estimated to total about 350 ha in 2002 (unpublished data, B. Jones and K. Williams). Most significant remnants are small patches (2-5 ha) and about half will probably be affected by development during the first decade of the 21st century.

Chronology of *P. occidentalis* decline and recovery at Locke and associated events

Overview of events

Between 1960 and 1995, Locke was subject to fire, *V. vulpes* predation and pastoralism, all acknowledged as potential factors in the decline of native mammal populations in Australia (e.g., Maxwell *et al*. 1996, Calver and Dell 1998). It is therefore instructive to examine the incidence of these factors against fluctuations in the population of *P. occidentalis*. A chronology of events at the site is shown in Table 1, drawn from comments in a range of published and unpublished reports.

P. occidentalis at Locke

Lambert (1985) reported that *P. occidentalis* was abundant in *A. flexuosa* woodlands at Locke in the mid 1960s and that a colleague found the same in 1973. However, in a single night survey in 1984 Lambert (1985) reported only one *P. occidentalis* in the western section of the *A. flexuosa* woodlands and none in the eastern section. His further daylight surveys located seven unoccupied dreys in the western section and none in the eastern section. He commented that: 'The Western Ringtail Possum has virtually disappeared from the estate's woodlands, once noted in the district for it's (sic) large population of this species' (Lambert 1985, p. 122). This status was corroborated by other researchers who reported few possums in the *A. flexuosa* woodlands at Locke in 1985 (pers. comm. from R. A. How and J. Dell, Western Australian Museum). However, by 1990 – 1992 *P. occidentalis* numbers were high in the eastern section of the *A. flexuosa* woodlands and lower in the western section (see map of drey locations in Figure 2a). The number of dreys observed during the 1990 – 1992 study totalled 149, considerably higher than the seven noted by Lambert (1985). A capture-recapture study estimated the population size in 1990 - 1992 as 95 – 105 adults (Jones *et al*. 1994b). Dreys were the predominant shelter sites used by this population (Jones *et al*. 1994a). The locations of the dreys observed in 1990 – 1992 were plotted in a series of 1 ha grids, indicating the distribution of possum activity within the *A. flexuosa* woodlands (Figure 2b). The substantial increase in the number of *P. occidentalis* at Locke between the mid-1980s and early 1990s could have included local recruitment, local immigration and some releases of possums from urban Busselton.

An unusual demographic was evident in the Locke *P. occidentalis* population from 1990-1992, with the sex ratio being female-biased. Sixty nine percent of the 104 adults and juveniles handled during the 1990 - 1992 capture-recapture study were female and this pattern of female

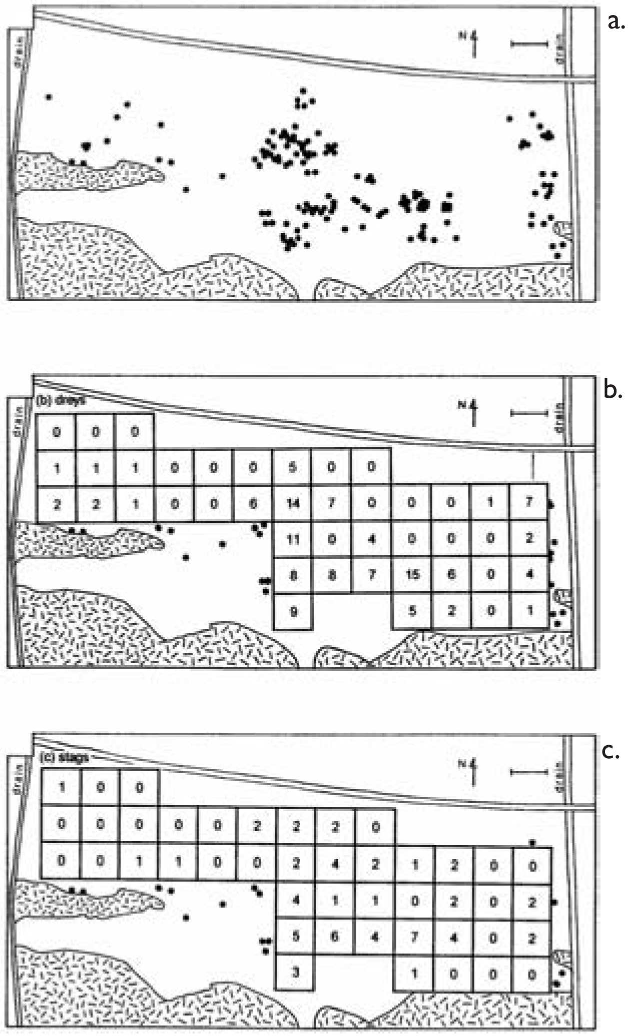

Figure 2. The *A. flexuosa* stand at Locke: (a) the map of drey locations presented as Fig. 3c in Jones *et al*. 1994b, and below, the grids showing the number of (b) dreys and (c) stags in the 44 cells.

predominance was statistically significant in both adult and dependent young age classes (see Table 2 in Jones *et al.* 1994b). This was a substantial deviation from the gender parity in another nearby *P. occidentalis* population (at Abba River, 18 km distant, in Jones *et al.* (1994b), or for populations of *P. peregrinus* studied in southeastern Australia (Hughes *et al*. 1965, How *et al*. 1984, Pahl 1987). Locke females captured during the early 1990s between them carried 20 pouch young and only six of these were male. Another nine post-emergent, but unweaned, young were caught and only three of these were male (see Table 2 in Jones *et al*. 1994b). The gender ratio was not the only population parameter that seemed to differ between the Locke and Abba River *P. occidentalis* samples of the early 1990s. Limited data in Jones *et al.* (1994b) suggested Locke young grew faster (Locke: 6.5-7.5 g/month, Abba 2.5-4.5 g/month) and Locke twinning rates were higher.

During the 1970s and 1980s Locke was one of two main sites recommended by local wildlife officers when asked where to release *P. occidentalis* picked up or trapped in urban Busselton. De Tores *et al*. (1998) noted that five *P. occidentalis* were fitted with radio-collars and released at Locke in 1991. Four were dead within six weeks, with wounds on the carcasses being suggestive of fox predation.

Fire

Lambert (1985, p.4) recorded known fires in Locke in 1980 ('Eastern section: burnt autumn 1980'), 1981 ('Western section: burnt autumn 1981') and 1984 ('Eastern section: .... patch burnt in autumn 1984'). It is unlikely that there were substantial fires since then, because the wattle *Acacia* spp. understorey which predominates after fire was much more prevalent in the mid 1980s (Lambert 1985) than by the early 1990s (B. A. Jones, unpublished data). Furthermore, review of aerial photographs of the Locke *A. flexuosa* stand in 1983, 1984, 1986 and 1989 indicated that any fires which may have occurred after those of 1983/1984 did not have a detectable impact on the *A. flexuosa* canopy. There has been no further recorded fire in the Locke *A. flexuosa* stand between 1990 and 2003.

Fire damage in the *A. flexuosa* woodlands that are important to *P. occidentalis* was evident from the growth form of the trees. Some trees carried all their foliage on a high crown above a single trunk, while others appeared to have numerous smaller stems springing from a single rootstock (main trunk absent, presumably burnt out). Still others had the main trunk standing with or without some foliage, but regrowth had also shot from the rootstock. Furthermore, a spatial pattern of fire can be deduced from the presence of stags (large dead *A. flexuosa* trees) killed by the fires. Stags in each one-hectare cell on the 1988 1:2000 aerial photograph of Locke were marked onto a grid map (only larger stags could be reliably identified). Stags were predominantly recognisable as *A. flexuosa* trees, but some may have been *Melaleuca* trees (which grew in small parts of the Locke stand). The spatial pattern of fire damage in *A. flexuosa* woodlands was then scored for a grid of 44 cells of one hectare each, corresponding to the plots of drey distributions for *P. occidentalis* (Figure 2).

Vulpes vulpes

Survey work by King *et al*. (1981) at their Cape Naturaliste study area (about 20 km west of Locke) showed that *V. vulpes* was rare in 1968, 1969 and 1970, but much more common between 1974 and 1978. They also noted that the increase in *V. vulpes* abundance they observed at Cape Naturaliste (and at Chidlow, to the north near Perth), corresponded with a decline of rabbit poisoning (1080) in the Busselton area during the 1970s. On the basis of the rise in *V. vulpes* abundance at Cape Naturaliste in the 1970s it would seem that when the 1980-1981 fires occurred at Locke, the abundance of *V. vulpes* was high in the area. In 1984, Lambert (1985) considered *V. vulpes* abundance at Locke to be high, and in 1991-1992, *V. vulpes* scats were noticeably more abundant at Locke than at two other nearby possum study sites (Jones *et al*. 1994b). During the late 1980s and early 1990s Locke was baited for *V. vulpes* in the spring of some years using buried eggs containing the toxin 1080. From the mid-1990s it was baited more intensively using dried meat baits containing 1080.

Pastoralism

Lambert (1985) noted that the area was grazed by cattle between 1962 and 1985. This contributed to replacement of understorey with pasture grasses, ringbarking of some *Melaleuca* spp., trampling of vegetation and increases in erosion, especially in marshlands and sandy rises. Lambert (1985) noted that the *A. flexuosa* woodlands, which were the best possum habitat, were least damaged, but he nevertheless speculated that cattle grazing may have been a factor in *P. occidentalis* decline in the 1980s.

The hypotheses arising from the chronology of observations

Hypothesis 1 – Fire and population ecology of *P. occidentalis*

Although there is a growing literature on mammalian responses to fire in south-western Western Australia, published accounts of the fire ecology of *P. occidentalis* are incidental to studies of other species. Indeed, Friend and Wayne's (2003) review discussed relevant papers as part of their coverage of *T. vulpecula*, concluding that the very limited data available suggest that *P. occidentalis* and *T. vulpecula* show a similar response to fire. There were only minimal impacts on both species from low intensity fires, whereas high intensity fires reduced numbers of both species heavily followed by a recovery, probably including an influx of animals to feed on regrowth foliage. Regrowth after fire often shows high levels of foliar nutrients, which are attractive to phytophagous arthropods (Radho-Toly *et al.* 2001) and presumably to folivorous mammals as well. Given the established connections between foliar nutrients and the distributions of arboreal marsupials (e.g., Kavanagh and Lambert 1990, Hume *et al.* 1996), many species appear able to detect and respond to this factor.

The observations at Locke conform to this general picture, with *P. occidentalis* numbers apparently declining post-fire but recovering within a decade. The distribution of dreys showed a significant rank correlation with the frequency of stags ($R_{s(42)} = 0.49$, $p < 0.001$), indicating that *P. occidentalis* activity was associated with fire regrowth in the *A. flexuosa* woodlands. However, there was an important twist in terms of the female-biased sex ratios observed in the recovering *P. occidentalis* population. They occurred in both adults and dependent young, indicating that they do not arise from differences in catchability or dispersal, but from sex allocation before birth or differential survival early in the life history. Sex ratio theory indicates that individuals may increase their long-term reproductive success, measured as the number of grandoffspring produced, by such manipulation of the sex ratio of their offspring under varying conditions of mate competition, maternal condition and competition for local resources (e.g., Emlen 1997 and included references). This is already established in a range of marsupials including dasyurids and phalangerids, as Johnson and Ritchie (2002, p. 655) observed:

> The fact that biased sex ratios are established before birth in both of the known cases of adaptive adjustment of population sex ratios in marsupials, representing two orders, together with the high incidence of biased sex ratios of offspring in marsupial species … , suggests that the capacity to adjust sex ratios at conception might be widespread amongst marsupials.

We hypothesize that the conditions of localized, high quality browse available in a regrowth mosaic arising after patch fire may encourage a female-biased sex ratio in *P. occidentalis* that enables rapid expansion of the local population. If these sex ratios could be encouraged through particular fire regimes, then rapid recovery of small populations might be possible. The potential to use limited patch fire to regulate population structure and stimulate rapid recovery makes this a very important hypothesis for management.

The primary test of the hypothesis would be determination of sex ratios of dependent young from several sites which show a patch-fired regrowth mosaic of 5-10 years post-fire. Finding sites with suitable mosaics and not limited by another resource constraint such as availability of hollows is the most significant challenge to this approach. In view of the extensive fires in eastern Australia in the summer of 2002-2003 and the probability that *P. peregrinus* has a similar level of reproductive flexibility to *P. occidentalis*, eastern Australian studies may be more feasible if sites with appropriate burning could be found (see Russell *et al*. 2003 for an example where the fire appears to have been too severe). Reliable testing of the hypothesis using a series of experimental patch fires would need to be a decade long process.

Hypothesis 2 – V. vulpes predation and population trends in P. occidentalis

Both circumstantial and experimental evidence implicate *V. vulpes* predation in population declines of a range of marsupial species (Kinnear *et al*. 2002 and included references, see Russell *et al*. 2003 for data relevant to *P. peregrinus*). However, the impact of predation is also known to vary in relation to shelter in the habitat, which in turn is influenced by fire frequency (Friend and Wayne 2003 and included references). The Locke study is of interest because the decline and recovery of the *P. occidentalis* population occurred despite estimates of substantial *V. vulpes* numbers in the vicinity. This, coupled with the observation that continuity of the canopy is an important predictor of occurrence of *P. occidentalis*, leads to the hypothesis that predation by *V. vulpes* only contributes to declines in *P. occidentalis* when canopy continuity is low (although this may not apply in the case of translocated animals during the period of their orientation to new surroundings).

We do not regard testing this hypothesis as significant for contemporary management in south-western Western Australia, because broad scale control of *V. vulpes* is part of conservation of marsupial communities. Indeed, de Tores *et al*. (1998) concluded that effective fox control is essential for successful establishment of translocated *P. occidentalis* in the south-west.

Hypothesis 3 – Grazing impacts and population trends in P. occidentalis

Damage caused by grazing stock is documented in many habitats across Australia, so the impacts noted by Lambert (1985) at Locke are unremarkable. Although he speculated that habitat changes caused by grazing may have contributed to the initial decline of *P. occidentalis*, testing this hypothesis has low priority because the other impacts associated with pastoralism are sufficient reason to exclude grazing from conservation areas.

Discussion

This compilation of observations on the *P. occidentalis* population at Locke and relevant published and unpublished literature illustrates both the problems and the potential of combining a range of sources to study population trends. On the one hand, observations over time were conducted with different techniques and intensities and there were no controls over a range of variables potentially interactive in their impacts on the *P. occidentalis* population. Consequently, it is difficult to establish quantitatively the extent of population fluctuations and the distribution and intensity of the 1980s fires, distinguish between the contributions of natural increase and migration in the recovery, or to separate the possible effects of fire, pastoralism or predation by *V. vulpes*. Furthermore, at this site *T. vulpecula* was not present so there were no potential competitive interactions with that species. These complications preclude drawing any definite conclusions. However, the observations do suggest three hypotheses regarding trends in *P. occidentalis* populations:

- conditions of localized, high quality browse available in a regrowth mosaic arising after patch fire may encourage a female-biased sex ratio,
- predation by *V. vulpes* on *P. occidentalis* is less likely to have a significant impact at sites where high continuity of the canopy is maintained,
- habitat degradation caused by pastoralism may lead to decline in *P. occidentalis*.

While the processes outlined in the last two hypotheses have little significance for *P. occidentalis* under current management practices, the first offers potential to manipulate habitat and thereby sex ratios to maximize recruitment in *P. occidentalis* populations. It is possible to test this hypothesis through collection of targeted observations or before/after studies in association with planned burns of *P. occidentalis* habitat. Such hypothesis generation is a major benefit that can arise from overviews of extended natural history observations of populations at a single site.

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