Chapter 1

Introduction

1.1 General introduction

Forty-two species of mammals worldwide have suffered extinction since 1600 (IUCN 2003). Almost half of the world’s mammal extinctions in the last two hundred years have occurred in Australia, coinciding with European settlement of the continent (Short and Smith 1994). Seventeen species are extinct, 10 survive only as island populations, and a further 17 have been reduced to remnant populations of less than 10% of their range prior to European settlement.

The decline and extinction of these species has been documented by a number of early authors (e.g. Finlayson 1935, 1961; Jones 1923-25; Krefft 1866; Shortridge 1909), and has typically been associated with the impact of European settlement of Australia. Soulé (1983, p. 112) noted:

"As far as I know, no biologist has documented the extinction of a continental species of plant or animal caused solely by non-human agencies such as competition, disease or environmental perturbation in situations unaffected by man".

Possible causes for the losses in our native mammal fauna have been widely debated over the last century, yet the causal factors for the decline and extinction of individual species are rarely known (Caughley and Gunn 1996).

In many cases, the biology of a species has been so poorly known, that any threatening processes identified have been rarely more than a guess. Predation by introduced feral cats Felis catus and the European fox Vulpes vulpes, habitat modification and fragmentation (destruction by clearing for agriculture, the impacts of introduced livestock and European rabbits Oryctolagus cuniculus, changes in fire regimes), competition from introduced species, hunting pressure, pest control, pollution, and disease, or a combination of any of these factors, have commonly been implicated in the loss of mammal species in Australia (e.g. Burbidge and McKenzie 1989; Caughley and Gunn 1996; Ride and Wilson 1982; Short and Turner 1992).
For some species the threatening process or processes have been quantified. This knowledge has usually been gained by the removal of the putative threat. For example, black-footed rock-wallabies *Petrogale lateralis* were present in low numbers on granite outcrops in the wheatbelt of Western Australia. After the Department of Conservation and Land Management instigated fox control on two outcrops in the 1980s, rock-wallaby numbers increased by over 400%, while two populations without fox control declined (one to extinction) and a third population without fox control increased slightly (Kinnear, Onus and Bromilow 1988; Kinnear, Onus and Sumner 1998). The Lord Howe Island woodhen *Gallirallus sylvestris* was rescued from near-extinction by the removal of feral pigs from the island. Less than 30 woodhens were thought to remain in 1979, but with the removal of pigs from the island, the population was more than 200 by 1984 (Fullagar 1985).

However, among a handful of success stories where threatening processes have been correctly identified, there are probably many more in which threats have been diagnosed incorrectly. Few of these examples are reported in the scientific or popular literature, providing little opportunity for others to learn from misdiagnoses and mistakes. Caughley and Gunn (1996 p. 14) suggested that “Sharing knowledge of failures is as important as successes, given the urgency of problems facing species in trouble.” They listed examples where guesses at causal factors have been incorrect, and have resulted in the further decline or ultimate loss of a species. For example, Arctic foxes *Alopex lagopus* were thought to be responsible for the decline of the Aleutian Canada goose *Branta canadensis*. The foxes were eradicated from four islands, but the decline continued. Hunting pressure at other locations was then discovered to be the threatening process (Caughley and Gunn 1996).

Failures can often provide some insight into the threatening process or processes depressing a species’ numbers. For example, a reintroduction of 40 golden bandicoots *Isoodon auratus* and 40 burrowing bettongs *Bettongia lesueur* to the Gibson Desert in September 1992 failed within three months of the translocation (Christensen and Burrows 1994). Predation by foxes and changed fire regimes were thought to be the primary threatening processes in the demise of these species from mainland Australia, and as a consequence, the area was heavily baited with 1080 to control fox populations. However, in the absence of foxes, the number of feral cats increased. Cat predation was thought to be the primary cause of death of the translocated animals. Unfortunately, for
many other reintroductions, there has been a lack of experimental investigation into the causes of decline and reasons for failure, and animals are lost with little knowledge gained (Armstrong, Soderquist and Southgate 1994; Caughley 1994).

The discipline of conservation biology was established to address the issues associated with the decline and extinction of species, the subsequent loss of biological diversity, and the consequences of these losses on ecosystem function throughout the world. Historically, mammal conservation was centred around the protection of species from hunting and trade, land acquisition for nature conservation, and fauna surveys to map distribution and abundance, however recent successes have been a result of the effective control of exotic predators (Short and Smith 1994). Dickman (1996) delineated two basic approaches to halting the loss of species: identifying and preserving areas of high conservation value (Humphries, Williams and Vane-Wright 1995), or listing species (or some form of biologically or genetically recognised group) that are threatened with extinction, and attempting their recovery. These approaches have advantages and failings, and have been the subject of ongoing discussion within the scientific, wildlife management, and political arenas. The sphere of conservation biology is influenced by economics and politics. The hope is that scientists become more able to influence where money is best spent. Whatever the outcome, basic research on the ecology of species and their ecosystems is required before conservation effort can truly be effective.

1.2 The small and declining population paradigms

Caughley (1994) and Caughley and Gunn (1996 p. 3, 4) outlined two paradigms of conservation biology. “The declining-population paradigm deals with why the population is declining or has already declined to low numbers, what caused it, and what might be done to reverse the decline.” Its focus lies within the field of wildlife management: defining threatening processes and removing them or managing them in such a way as to reverse the decline. It has been regarded as a practical approach to species conservation, based on day-to-day management practices that directly assist with on-ground conservation of a species or community.

By contrast, the small population paradigm encompasses “the ideas dealing with the effect of low numbers as such upon a population’s persistence.” Demographic and
environmental stochasticity, inbreeding depression, and genetic drift are the primary factors that are regarded as influencing the size of the population. The reason why it is small in the first place is not the issue; managing the small population to maintain its viability is the main concern.

The work outlined within this thesis falls predominantly into the declining population paradigm. The future of threatened mammals on mainland Australia lies in determining the factors that have limited or are limiting their survival. While small populations may need to be managed to avoid extinction, the very nature of declining populations means that their persistence may not be ensured unless the threats to their survival are removed. If factors causing the decline cannot be removed, the only option available may be to manage the population to prevent the problems commonly associated with small population size. The ultimate aim is to increase the size of small populations and avoid the inherent problems associated with being small.

1.3 Reintroduction as a tool in conservation biology

Ride (1970) outlined three steps to address the conservation of threatened mammals in Australia:

1. Survey to acquire information on distribution, abundance and habitat;
2. Gather biological data for each species; and
3. Design management programmes for species and set aside reserves to provide for their permanent conservation.

Caughley (1994) suggested a series of actions to both assist in the diagnosis of decline, and the recovery of threatened species:

1. Confirm the species is in decline, or has previously declined;
2. Study the natural history of the species to increase knowledge of its ecology, context, and status;
3. When adequate background knowledge is available, list all conceivable agents of decline;
4. For each agent, measure its level where the species persists and where the species used to be in time or space. Any contrast may indicate an agent of decline; and
5. Test the hypothesis by experiment to confirm that the agent is causally linked to the decline, not simply associated with it. Once the threatening process or processes have been determined, the final step is to reverse the decline by removing or neutralising the agents of decline (Caughley and Gunn 1996).

After background information for threatened species has been gathered, one method of testing hypotheses about agents of decline, has been the use of reintroduction. Reintroduction is defined as “an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct” (IUCN 1995). The principal aim of any reintroduction should be to assist in the conservation of a threatened species, by establishing a viable, free-ranging wild population, with a minimum of long-term management (IUCN 1995).

In the last decade, there have been an increasing number of advocates for scientific rigour within the field of conservation biology, and in particular, the recovery of threatened species. Dickman (1996) outlined a series of steps in the planning of recovery programs, beginning with the selection of species with small or declining populations that are considered to be at risk of extinction. A national recovery plan should be produced, which often requires research and survey of remnant populations. Diagnosis of the causes of decline should be carried out using scientific methodology, by deriving a testable hypothesis about the process or processes most likely to be an agent of decline, and testing the hypothesis by experimentation. Reintroductions can be designed as tests of these hypotheses (Soderquist 1994).

There are a number of problems associated with the use of reintroductions as a conservation tool in Australia. For example, Short, Bradshaw, Giles, Prince and Wilson (1992) discussed 25 attempts to reintroduce macropods in Australia between 1905 and 1990. Only 11% of mainland reintroductions were successful, compared to 60% of introductions to islands. They attributed the failure of many of the reintroductions to cursorial predators, in particular foxes and feral cats. It is of no value to reintroduce a species without treating the cause of its decline (Caughley and Gunn 1996). For example, over 670 quokkas Setonix brachyurus were released to a reserve in Jandakot, Western Australia between 1972 and 1988. The population never successfully established due to the inadequate control of foxes and feral cats (Short et al. 1992). Other factors thought to contribute to the failure of some reintroductions included a lack
of clear objectives and lack of an appropriate experimental design. A long-term commitment to management, including the monitoring of reintroduced animals, and project evaluation, is required, as is the choice of a reintroduction site with good-quality habitat (Griffith, Scott, Carpenter and Reed 1989; Short et al. 1992). Mainland reintroductions, in particular, have to be carried out in modified habitats, as the Australian environment has been altered forever. Thus, even if a species was locally present at a reintroduction site in the past, there is still no guarantee that a reintroduced population will be able to survive in the current environment.

Despite these issues, there have been many reintroductions in the last few years that have been successful, at least in the short-term. The use of reintroduction as a tool in the conservation of threatened species is burgeoning. Short et al. (1992) pointed towards its use in understanding the decline of species, improving knowledge of their basic ecology, and improving the application of new strategies for managing agents of decline, such as introduced predators.

1.4 Decline of mammals in Australia

Reviews of the decline of Australian mammals have been produced by Allen (1983), Burbidge and McKenzie (1989), Cardillo and Bromham 2001; Dickman, Pressey, Lim and Parnaby (1993), Lunney (2001), Morton (1990), Recher and Lim (1990), Short and Smith (1994), and Smith and Quin (1996). Each review has examined patterns of decline and possible causes, and all point towards the impact of European settlement as the overriding cause of decline of our mammal fauna. One of the difficulties faced by the reviewers has been the lack of information about the relative abundance of these species at the time of European settlement (Calaby 1969). We are reliant upon anecdotal evidence of early explorers, inadequate museum specimens, and other evidence such as bone deposits in caves.

Burbidge and McKenzie (1989) highlighted the loss of small to medium sized terrestrial marsupials and rodents, or “critical weight range” mammals weighing between 35 and 5,500 grams. Proportionally more of these mammal extinctions have been recorded from the semi-arid and arid regions (such as central Australia and the mallee and wheatbelt regions of Western Australia) than the more mesic areas of Australia (Recher and Lim 1990; Woinarski and Braithwaite 1990). More recently,
however, Cardillo and Bromham (2001) have argued that mammal extinctions and declines in Australia were non-random with respect to body size, and that small species appeared to be the least prone to extinction. They rejected the hypothesis that intermediate size mammals have been the most prone to extinction, suggesting that their disappearance was an artefact of the body-size distribution of the continental fauna.

Despite consensus that the impact of European settlement is the fundamental cause of widespread extinctions of critical weight range mammals in Australia, there has been little consensus as to the more specific causes of decline. Scientists have offered differing opinions of the major causal factors over the last century (Table 1.1), typically based around habitat alteration, or predation by introduced species.

As early as 1836, Charles Darwin, after viewing the Bathurst region, said “...the kangaroo becomes scarce;...the English greyhound has been highly destructive. It may be long before these animals are all together exterminated, but their doom is fixed” (Ovington 1978, p. 34). Krefft (1866) also provided an early record of declining numbers of kangaroos, writing that “the low lands of the Murray have once swarmed with their numbers as they do now with cattle and sheep. At the present time, large flocks are a rare sight”. Le Souef (1923, p. 108) wrote that the “fox is by far the greatest menace that our wild animals are faced with”, and suggested that it was “responsible for clearing off practically all the small ground animals outside the coastal districts in eastern and southern Australia”. He was of the opinion that “Practically all the ground animals (outside the coastal areas) with the exception of those mentioned in eastern and southern Australia are threatened with extermination.” Glauert (1933, p. 17) wrote: “It is unavoidable that the spread of settlement and the changes it brings in its train should have a profound effect upon the native fauna, the clearing of hundred of thousands of acres in the wheatbelt has brought about astounding results.” Later, Glauert (1948) wrote: “But the need for investigation is urgent...as even the hardy supporters of the Australian coat-of-arms are threatened by the clamours of the pastoralist and the wheat farmer.”

Table 1.1: Some of the suggested causes of Australian mammal decline in the last century.

<table>
<thead>
<tr>
<th>Primary causes</th>
<th>Secondary causes</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clearing, predation (dogs, domestic cats)</td>
<td>Possibly disease</td>
<td>Shortridge (1909)</td>
</tr>
<tr>
<td>Event Description</td>
<td>Reference</td>
<td></td>
</tr>
<tr>
<td>----------------------------------------------------------------------------------</td>
<td>---------------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>Introduction of the fox, cat, rabbit</td>
<td>Le Souef (1923)</td>
<td></td>
</tr>
<tr>
<td>Clearing</td>
<td>Glauert (1933): wheatbelt</td>
<td></td>
</tr>
<tr>
<td>Fox, cat, rabbit</td>
<td>Harper (1945)</td>
<td></td>
</tr>
<tr>
<td>European settlement, introduced European animals</td>
<td>Lundelius (1957)</td>
<td></td>
</tr>
<tr>
<td>Destruction and alteration of habitat</td>
<td>Marlow (1958): NSW</td>
<td></td>
</tr>
<tr>
<td>Pastoral exploitation, introduced rabbit, fox and feral house cat</td>
<td>Finlayson (1961)</td>
<td></td>
</tr>
<tr>
<td>Fox, dingo, cat</td>
<td>Troughton (1967)</td>
<td></td>
</tr>
<tr>
<td>Habitat destruction, e.g. by sheep, rabbits, clearing</td>
<td>Calaby (1969)</td>
<td></td>
</tr>
<tr>
<td>Introduced species, clearing</td>
<td>Ride (1970)</td>
<td></td>
</tr>
<tr>
<td>Grazing by livestock</td>
<td>Newsome (1971)</td>
<td></td>
</tr>
<tr>
<td>Grazing by introduced herbivores, clearing, rabbits</td>
<td>Frith (1973)</td>
<td></td>
</tr>
<tr>
<td>Fox and rabbit</td>
<td>Jarman and Johnson (1977): NSW</td>
<td></td>
</tr>
<tr>
<td>Altered fire regimes</td>
<td>Kitchener, Chapman, Muir and Palmer (1980): WA wheatbelt</td>
<td></td>
</tr>
<tr>
<td>Predation by foxes</td>
<td>Kinnear et al. (1988)</td>
<td></td>
</tr>
<tr>
<td>Suite of environmental change by humans</td>
<td>Burbidge and McKenzie (1989)</td>
<td></td>
</tr>
<tr>
<td>Habitat alteration by pastoralism</td>
<td>Morton (1990)</td>
<td></td>
</tr>
<tr>
<td>Combination, no single cause</td>
<td>Recher and Lim (1990)</td>
<td></td>
</tr>
<tr>
<td>Grazing by stock, interference from feral mammals</td>
<td>Dickman et al. (1993): western NSW</td>
<td></td>
</tr>
<tr>
<td>Predation by foxes and feral cats</td>
<td>Short and Smith (1994)</td>
<td></td>
</tr>
<tr>
<td>Predation by cats and foxes</td>
<td>Smith and Quin (1996): conilurine rodents</td>
<td></td>
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</tbody>
</table>
Lundelius (1957), like many, referred generally to the fact that “European settlement and the introduction of European animals have resulted in the disappearance of the Australian fauna over much of its range”. Newsome (1971) suggested that overstocking and grazing by livestock depleted food resources and shelter in central Australia. This in turn, rendered native mammals more vulnerable to predation by cats and foxes.

Frith (1973; p. 145) thought that “Of all the introduced pests the Rabbit is by far the worst”. He stated that despite their abundance there are no accurate data on the effects of foxes and cats on native wildlife, though both were known to prey upon native fauna. In contrast, Kinnear et al. (1988) published the first experimental evidence that predation by foxes may have been responsible for the loss of mammal species such as rock-wallabies in the wheatbelt region of Western Australia. Morton (1990) and Recher and Lim (1990) suggested that the greatest impact of introduced predators might occur during periods of drought when populations are minimal and restricted to refugia in patches of more dense vegetation. Short and Turner (2000) ascertained that predation by foxes was the major cause of the decline of burrowing bettongs from mainland Australia, through experimental work at Heirisson Prong in Shark Bay, Western Australia where introduced predators were removed. Aitken (1979) suggested that the persistence of species on islands that are otherwise extinct on the mainland provides circumstantial evidence of the role of introduced predators in the demise of the mainland populations.

Less attention appears to have been paid to the role of the feral cat in the demise of native mammals. There is a suspicion that the cat was introduced to Australia prior to European settlement (Dickman 1993). If this is so, it may have been present for a lengthy period prior to the major loss of species. However, Gaynor (2000) and Abbott (2002) thought that the cat did not arrive in Australia until the time of European settlement. The status of the cat as a domestic pet, and its association with the earning power of the veterinary and pet product industries (Grayson, Calver and Styles 2002), is likely also to have played a role in directing attention away from the feral cat as a primary agent of decline of native mammals in Australia.

Recher and Lim (1990) maintained that the loss of species could not be attributed to a single cause. However, Short and Smith (1994) pointed out that the most significant successes in the recovery of threatened mammals have come with the control of introduced predators, rather than addressing other threatening processes such as
exotic herbivores or changes in fire regimes. The task of determining what threatening processes have caused each species or suite of species to become extinct on mainland Australia is continuing.

1.5 Decline and extinction of Peramelid bandicoots in Australia

Ride and Wilson (1982, p. 35) concluded that “Of all native mammals, the bandicoots (Peramelidae and Thylacomyidae), as a related group of species, have suffered the most.” Of ten species, only the northern brown bandicoot *Isoodon macrourus* and the long-nosed bandicoot *Perameles nasuta* remain common (Table 1.2).

Table 1.2: The current status of Australian bandicoots, listed under the Environment Protection and Biodiversity Conservation Act (1999). (-) = not listed.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Status</th>
</tr>
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<tbody>
<tr>
<td><em>Chaeropus ecaudatus</em></td>
<td>Pig-footed bandicoot</td>
<td>Extinct</td>
</tr>
<tr>
<td><em>Isoodon auratus</em></td>
<td>Golden bandicoot</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>Isoodon obesulus</em></td>
<td>Southern brown bandicoot</td>
<td>(-)</td>
</tr>
<tr>
<td><em>I. o. fusciventer</em></td>
<td>(WA subspecies)</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>I. o. nauticus</em></td>
<td>(Nuyts Archipelago subspecies)</td>
<td>(-)</td>
</tr>
<tr>
<td><em>I. o. obesulus</em></td>
<td>(NSW/SA subspecies)</td>
<td>Endangered</td>
</tr>
<tr>
<td><em>Isoodon macrourus</em></td>
<td>Northern brown bandicoot</td>
<td>(-)</td>
</tr>
<tr>
<td><em>Perameles eremiana</em></td>
<td>Desert bandicoot</td>
<td>Extinct</td>
</tr>
<tr>
<td><em>Perameles gunnii</em></td>
<td>Eastern barred bandicoot</td>
<td>(-)</td>
</tr>
<tr>
<td><em>P. g. unnamed subsp.</em></td>
<td>(Mainland subspecies)</td>
<td>Endangered</td>
</tr>
<tr>
<td><em>P. g. gunnii</em></td>
<td>(Tasmanian subspecies)</td>
<td>(-)</td>
</tr>
<tr>
<td><em>Perameles bougainville</em></td>
<td>Western barred bandicoot</td>
<td>Endangered</td>
</tr>
<tr>
<td><em>Perameles nasuta</em></td>
<td>Long-nosed bandicoot</td>
<td>(-)</td>
</tr>
<tr>
<td><em>Macrotis lagotis</em></td>
<td>Greater bilby</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>Macrotis leucura</em></td>
<td>Lesser bilby</td>
<td>Extinct</td>
</tr>
</tbody>
</table>

Jones (1924, p. 136) noted that “In general it may be said that the Peramelidae are rapidly disappearing over the whole of continental Australia…they have now disappeared from many of their old haunts, and even though they are still locally abundant in certain spots, their numbers as a whole have vastly diminished in a comparatively few years.” Of ten species, three are extinct, three are endangered, two
are vulnerable and have declined throughout much of their former range, and only two remain common (Strahan 1995).

The last certain recorded specimen of a pig-footed bandicoot *Chaeropus ecaudatus* was collected near Lake Eyre in South Australia in 1907 (Aitken 1979), though Aboriginal people suggest that it disappeared from South Australia in the 1910s, and in the central desert region of Western Australia as late as the 1950s (Johnson and Burbidge 1995). It had declined throughout much of its range prior to the arrival of the fox and rabbit. Krefft (1866) stated that it was disappearing fast and likely to be dispersed by sheep and cattle.

The golden bandicoot was widely distributed through arid central Australia until as recently as the 1930s. Prior to this, it extended eastwards to the westernmost portion of Queensland, and there is also fossil evidence from western New South Wales, but it had disappeared from that state before 1870 (McKenzie, Morris and Dickman 1995). It still survives in the Prince Regent Nature Reserve in the north-west Kimberley, nearby Augustus Island, on Barrow and Middle Islands off the Pilbara coast in Western Australia, and on Marchinbar Island in the Northern Territory (Southgate, Palmer, Adams, Masters, Triggs and Woinarski 1996). The extinction of the golden bandicoot from Hermite Island (near Barrow Island) in 1912 was attributed to the feral cat (McKenzie *et al.* 1995), however reasons for its decline on the mainland remain unknown.

The southern brown bandicoot has declined in abundance and range since European settlement. It currently occurs in southern Australia, and there is one population in far north Queensland. Braithwaite (1995) attributed its decline to changes in fire regimes, land clearing, and loss of dense vegetation due to grazing by sheep and cattle.

The desert bandicoot was last recorded in 1943 from Well 35 on the Canning Stock Route (J. Friend 1990; Kitchener and Vicker 1980). The cause of its demise is uncertain, however Gordon (1995a) noted that its disappearance from the south-west portion of the Northern Territory coincided approximately with the arrival of the fox. However, its decline in the Tanami Desert to the north is thought to have occurred in the 1940s to 1960s, prior to the presence of the fox in that region. Here, changes to the fire regime adopted by Aboriginals, have been suggested as the cause of its extinction (Gordon 1995a). Newsome (1971) thought that consumption by Aborigines may have
been a causal factor in the extinction of the desert bandicoot, in addition to the impacts of livestock grazing (depleting vegetation that provided food and shelter), and introduced predators. He related a method of capture by Aborigines on Derwent Station, west of Alice Springs in the Northern Territory. Bandicoots would be flushed by horses, captured, then released again and followed to their mate's nest. The Aboriginals then put their foot on the nest, capturing two bandicoots at once and proceeding to kill and eat both. Finlayson (1961) suggested that pastoralism in central Australia may have been responsible for the decline of the desert bandicoot.

The eastern barred bandicoot is critically endangered on mainland Australia. This species used to occur across the basalt plains from Melbourne to the South Australian border (Kingston 1994), however it survives only in one remnant population at Hamilton in Victoria (Seebeck 1979). This population provided the source stock (38 founders) for numerous reintroduction attempts through the 1990s (Watson and Halley 1999). The species remains locally common and widely distributed in Tasmania where cats and rabbits are present but foxes are absent (Driessen, Mallick and Hocking 1996; Hocking 1990). The dense vegetation may offer ample cover and therefore protection from predation for bandicoots and other similar sized mammals. This cover is notably absent from mainland areas where eastern barred bandicoots once lived.

Their decline on the mainland is thought to have been caused by a combination of agricultural practices (habitat alteration which caused losses in food supply and natural vegetation cover), and predation (by introduced foxes, feral cats, domestic dogs and cats, and the native whistling kite *Haliastur sphenurus*). In more recent times and to a lesser degree road deaths, trapping, other trauma (radio-collaring, self-inflicted wounds and intraspecific aggression sustained in captivity, drowning in a swimming pool, and mishaps during transportation), toxoplasmosis or other infections, parasites, neoplasia, pesticides, poisoning, and old age (Backhouse, Clark and Reading 1994; Booth and McCracken 1994; Brown 1989; Dufty 1991, 1994c; Kingston 1994; Lenghaus, Obendorf and Wright 1990; Watson and Halley 1999). The effect of rabbits is unknown (Seebeck 1979).

Backhouse *et al.* (1994) noted that reintroductions of the eastern barred bandicoot in Victoria have demonstrated that the alleviation of predation pressure alone, with no attention to other possible causes of decline, is enough to ensure successful reestablishment. However, despite this claim, of the seven reintroduced populations,
few appear secure. The populations had all decreased in the late 1990s due to an extended period of drought, combined with the ineffective control of predators (Watson and Halley 1999).

Eastern barred bandicoots were thought to have benefited from habitat alteration in Tasmania in some instances, and to have remained common and widespread, despite the prevalence of potentially deleterious agricultural practices (Hocking 1990). However, there is some evidence of a long-term decline in numbers in Tasmania, perhaps due to clearing for agriculture and stock-grazing (Mallick, Haesler, Hocking and Driessen 1997), and more recently, an extended period of drought between 1992 and early 1995 (Mallick, Driessen and Hocking 2000). Alternatively, the loss of habitat and therefore cover due to changing land use may have increased the susceptibility of bandicoots to predation by cats. Eastern barred bandicoots tend to utilise open areas (Heinsohn 1966), and prime habitat in Tasmania includes a mosaic of pasture, scrub and bush (Driessen et al. 1996). By comparison, southern brown bandicoots in Tasmania prefer areas with a taller cover of vegetation, and are rarely seen at the edges of paddocks and scrub (Heinsohn 1966).

The western barred bandicoot formerly occurred in a broad arc across the southern half of Australia, from Western Australia through to Victoria and New South Wales. It now occurs only on two islands off the coast of Western Australia, and is described in more detail in Section 1.7.

The greater bilby *Macrotis lagotis* was once distributed widely throughout arid and semi-arid Australia, but has since declined in distribution and abundance. Factors associated with its decline include predation by foxes, habitat alteration by rabbits and pastoral activities, and possibly changed fire regimes. An extensive and rapid decline occurred between the late 1800s and 1935 (the late 1920s in Western Australia; Short 1999), and another period of decline is thought to have occurred since 1969 (Southgate 1990). Leake (1962) thought that the greater bilby persisted in the central Western Australian wheatbelt until 1929, although it had largely disappeared in the eastern wheatbelt by 1899 (Short 1999).

The lesser bilby *Macrotis leucura* formerly occurred in the deserts of north-eastern South Australia, south-eastern Northern Territory, and central Western Australia. It was last recorded in 1931 in north-eastern South Australia, though
Aboriginals of the central deserts thought that it may have survived in this region until the 1960s (Johnson 1995). Reasons for its decline and extinction are unknown.

Two species remain common and widespread throughout their former range. The northern brown bandicoot occurs in eastern and northern Australia in a band around the coast from northern New South Wales to Western Australia, preferring areas of low ground cover with tall grass and dense shrubs, and is less abundant in areas that are heavily grazed (Gordon 1995b). It occurs also in Papua New Guinea (George and Maynes 1990). The long-nosed bandicoot occurs on the east coast of Australia, from southern Victoria to Queensland, overlapping a portion of the range of the northern brown bandicoot. Its habitat ranges from rainforest to wet and dry sclerophyll woodlands (Stodart 1995). The one obvious difference between these two species and the other eight that are threatened is their occurrence in the more mesic areas of Australia. Foxes are not found in the tropical north (Jarman 1986) and in the parts of Australia where they are found, their density is lower along the more heavily timbered coast and ranges (Wilson, Dexter, O'Brien and Bomford 1992). Predation pressure by foxes on these two common species of bandicoots is non-existent in the far north and may be minimal in much of their range, presenting some supporting evidence for the role of foxes in the decline of many of the other species of bandicoot. Cats are less abundant also in more mesic areas.

There does not appear to be a single common pattern of decline of bandicoots in the arid and semi-arid regions. However, the combination of introduced predators, the fox, feral cat, or both, and habitat degradation, rendering the habitat devoid of refuge sites and dense cover to avoid predators, is a common thread to the demise of these mainland species.

1.6 Choosing a species for recovery action

International (IUCN Red List 2003) and national lists (Environment Protection and Biodiversity Conservation (EPBC) Act 1999) of threatened taxa and threatened species form the basis for choosing species that are most likely to be at risk of decline and extinction. Where more intensive management is required, target species may be chosen within a more easily accessible area, so that management is as inexpensive as possible and travel time and costs are kept to a minimum. However, it is also important
that species whose distribution occurs only in remote areas are subject to conservation actions. Recovery can involve either in-situ or ex-situ management, depending on the species, staff and resources available.

Fortunately, many threatened species that are extinct on mainland Australia survive as island populations (Table 1.3), which provide a good source for reintroductions. Bernier and Dorre Islands off the coast of Western Australia, are two such islands that are particularly important in the conservation of Australia’s threatened mammals, providing a suite of mammals for reintroductions. They are home to five of these species: the burrowing bettong *Bettongia lesueur*, banded *Lagostrophus fasciatus* and rufous hare-wallabies *Lagorchestes hirsutus*, western barred bandicoot *Perameles bougainville*, and the Shark Bay mouse *Pseudomys fieldi*.

**Table 1.3:** Threatened mammals extinct on mainland Australia, but surviving on islands (including Tasmania), and their status under the Environment Protection and Biodiversity Conservation Act (1999). (-) = not listed.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dasyurus viverrinus</em></td>
<td>Eastern quoll</td>
<td>(-)</td>
</tr>
<tr>
<td><em>Pseudantechinus mimulus</em></td>
<td>Carpentarian antechinus</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>Perameles bougainville</em></td>
<td>Western barred bandicoot</td>
<td>Endangered</td>
</tr>
<tr>
<td><em>Bettongia gaimardi</em></td>
<td>Tasmanian bettong</td>
<td>(-)</td>
</tr>
<tr>
<td><em>Bettongia lesueur</em></td>
<td>Burrowing bettong</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>Lagorchestes hirsutus</em></td>
<td>Rufous hare-wallaby</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>Lagostrophus fasciatus</em></td>
<td>Banded hare-wallaby</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>Thylogale billardierii</em></td>
<td>Tasmanian pademelon</td>
<td>(-)</td>
</tr>
<tr>
<td><em>Leporillus conditor</em></td>
<td>Greater stick-nest rat</td>
<td>Vulnerable</td>
</tr>
<tr>
<td><em>Pseudomys fieldi</em></td>
<td>Shark Bay mouse</td>
<td>Vulnerable</td>
</tr>
</tbody>
</table>

One species of mammal in Australia, the bare-rumped sheathtail bat *Saccolaimus saccolaimus nudiulmiatus* is listed under the EPBC Act (1999) as 'critically endangered', 34 as 'endangered', 51 as 'vulnerable', and one as conservation-dependent. The conservation of these species is of "national environmental significance" under the EPBC Act (1999). Under Section 179 of the EPBC Act (1999) a native species is eligible to be included in the 'endangered' category if it is facing a very high risk of extinction in the wild in the near future, and in the 'vulnerable' category if it is facing a high risk of extinction in the wild in the medium-term future, as determined in
accordance with the prescribed criteria. The western barred bandicoot is classified as endangered under both the EPBC Act (1999) and IUCN (2003). Remnant populations of bandicoots on Dorre and Bernier Islands are comparatively small (c. 2200 - 4400 combined minimum population estimate for both islands) and subject to substantial fluctuations due to weather (Short, Turner, Majors and Leone 1997a; Short, Richards and Turner 1998). These two small populations are vulnerable to extinction, and recovery actions are required to increase the number of extant populations.

The western barred bandicoot was the species chosen for this study, and is representative of a suite of threatened mammals throughout Australia, including other bandicoots, and more generally, the many small to medium-sized terrestrial mammals that have declined in abundance since European settlement of Australia. Lessons learnt from a more detailed study of this species may be useful for the recovery and management of species in similar plights.

1.7 The western barred bandicoot

The western barred bandicoot (Plate 1.1) is a marsupial of the Family Peramelidae, and is one of the long-nosed bandicoots of the genus Perameles. It is the smallest extant bandicoot, with an average weight of 219 g (Short et al. 1998). It is solitary and nocturnal, sheltering during the day in concealed nests made in a small hollow amongst litter under shrubs and constructed from grasses and other vegetation. It is insectivorous and emerges at late dusk to forage by digging or hunting (Friend and Burbidge 1995).
Plate 1.1: Western barred bandicoot *Perameles bougainville*. Photo by Jeff Short, CSIRO.

1.7.1 Nomenclature

The western barred bandicoot was first described from a specimen taken at Peron Peninsula in Shark Bay by naturalists Quoy and Gaimard from the *Uranie* in 1817 (Ride and Tyndale-Biscoe 1962). Local populations of the species have been referred to by a variety of names including *P. bougainville* or *P. bougainvillei* from Shark Bay, *P. arenaria* and *P. myosura myosura* (or *P. myosurus myosurus*) from south-western Western Australia, *P. myosura*, *P. m. notina* and *P. bougainvillei fasciata* from South Australia, and *P. myosurus*, and *P. fasciata* from New South Wales (Friend 1990; Friend and Burbidge 1995; Glauert 1933; Gould 1863; Jones 1924; Krefft 1866; Richards and Short 1997; Thomas 1922; Wakefield 1963), creating some confusion in the taxonomy of the group. All these mainland forms are now extinct and few specimens exist in museums, providing little opportunity to clarify the past nomenclature. All these forms are now regarded as *P. bougainville* (Friend and Burbidge 1995).

There are currently two subspecies recognised: *P. b. bougainville* on Dorre and Bernier Islands, and *P. b. myosura* on the mainland (Maxwell, Burbidge, and Morris. 1996). A third subspecies *P. b. notina* from South Australia and south-eastern Western Australia was mentioned by Friend and Burbidge (1995), but is not recognised under
the EPBC Act (1999). No genetic studies have been carried out on the species, and limited morphological data suggest that the current classification is appropriate (Short et al. 1998).

There are three other members of the genus: the extinct desert bandicoot *P. eremiana*, last collected in 1943 from the Canning Stock Route (Gordon 1995a), the endangered eastern barred bandicoot *P. gunnii*, which has survived only in Tasmania and one localised mainland site in Hamilton in western Victoria (Seebeck, Bennett and Dufty 1990), and the long-nosed bandicoot *P. nasuta*, which is still common and widespread throughout its range in eastern Queensland, eastern New South Wales and eastern and southern Victoria (Ashby, Lunney, Robertshaw and Harden 1990; Gordon, Hall and Atherton 1990; Menkhorst and Seebeck 1990).

The first description of a bandicoot was of a southern brown bandicoot *Isoodon obesulus* from Botany Bay, then regarded as *Didelphis obesula* and provided with the common name of ‘porcupine opossum’, due to its resemblance to a miniature pig (Lyne 1990). The western barred bandicoot has been described by a variety of common names including the Aboriginal names: ‘marl’ (from the Beverley district, Western Australia) and ‘little marl’, ‘nyemmel’ (from Albany, Western Australia), ‘quoint’ (from the south-west of Western Australia), ‘thill’ (by natives of the River Murray), and ‘walilya’ or ‘walleela’ (in South Australia, though there may be some confusion with the extinct desert bandicoot), and European names: ‘zebra rats’, ‘saddle-backed bandicoot’, ‘lesser barred bandicoot’, ‘striped bandicoot’, ‘moncat’, ‘native pig’ (in the Katanning district, Western Australia) and ‘striped pouch-badgers’ (Aitken 1979; Burbidge and Fuller 1979; Copley, Kemper and Medlin 1989; Friend and Burbidge 1995; Gould 1863; Harper 1945; Haddleton 1952; Jones 1924; Krefft 1866; Ogilby 1892; Shortridge 1909; Wakefield 1966). Their distinctive barred rump and current presence only in Western Australia suggest that the common name of western barred bandicoot is suitable.

### 1.7.2 Past and present distribution

The western barred bandicoot was thought to be widely distributed across the southern mainland of Australia at the time of European settlement. It occurred in a broad arc from Onslow on the north-west coast of Western Australia, through the Western Australian wheatbelt, the Nullarbor Plain, and arid and semi-arid South
Australia, Victoria and New South Wales to the Liverpool Plains in New South Wales (Figure 1.1).

Glauert (1948) referred to comments by Waterhouse (1841) that *Perameles bougainville* occurred in Western Australia and had previously been overlooked. Shortridge (1909) reported that the species was thought to have formerly extended as far north as Shark Bay, and collected a single skull from Bernier Island. Glauert (1933) recorded *P. bougainvillei bougainvillei* as occurring on Bernier and Dorre Islands and the adjacent mainland, and *P. myosura* in the south of Western Australia near Cranbrook. Lundelius (1957) found bones in caves from Cocklebiddy Tank to Eucla.

A crew member of the “Bathurst” saw a “small opossum” on Dirk Hartog Island in January 1822, which Alexander (1915, p. 123) referred to as *Perameles bougainvillei*. Burbidge and George (1978) identified sub-fossil remains of the western barred bandicoot from the island, confirming its former presence, though the date of its demise remains unknown.

Krefft (1866) suggested that the range of *Perameles fasciata* extended from the east to west coasts of Australia. The species occurred along much of the Murray and Darling River system and was common on all parts of the Murray River. It was found also in the interior of New South Wales, the northern district of Victoria, South Australia, parts of Western Australia, and apparently in the immediate neighbourhood of Sydney (Krefft 1866). Jones (1924) detailed the distribution in South Australia from specimens in the British Museum Catalogue of 1888, including Saint Vincent’s Gulf, the Murray River, and Adelaide. Skeletal remains of unknown age were found in an owl pellet deposit in the Grampians in Victoria (Wakefield 1963).

Despite its former widespread distribution, the western barred bandicoot is now extinct on mainland Australia (Section 1.6.6), surviving only on Dorre and Bernier Islands in Shark Bay, Western Australia.
**Figure 1.1:** Shark Bay, Western Australia, showing the location of Bernier and Dorre Islands, Denham, and Heirisson Prong. Inset shows the location of Shark Bay and the former mainland range of the western barred bandicoot (shaded; from Strahan 1995). It is now found in the wild only on Bernier and Dorre Islands.
1.7.3 Habitat

The western barred bandicoot was an inhabitant of the southern semi-arid and arid areas of Australia (inset, Figure 1.1). The type specimen from Peron Peninsula was found at the foot of elevated dunes (Ride and Tyndale-Biscoe 1962). Gould (1863) described the range of *P. myosurus* in Western Australia as “inhabits the whole line of coast of the Swan River colony, but, so far as I can learn, is not found to the westward of the Darling range of hills. It resides in the densest scrub, thickets of the seedling *Casuarinae* being its favourite resort.” They lived in open saltbush, bluebush and *Acacia* plains, broken by sandhills and limestone outcrops in the western portion of central Australia (Jones 1924).

Gould (1863) described *P. fasciata* as enjoying a wide range over eastern and southern Australia. He thought that it was more common in the “interior”, in the country within the ranges, than in the area between the mountains and the sea, and in South Australia the species was found on the stony ranges and spurs, which ran down to the bend of the Murray River. Gould noted that Governor Grey said, “this animal is found in the vast open plains near the head of Saint Vincent’s Gulf”. On the western slopes of New South Wales it was recorded from the stony ridges, which branch off from the ranges towards the Darling and Namoi Rivers.

The two remaining populations on Dorre and Bernier Islands in Shark Bay have been studied on a number of occasions by scientists (Friend and Burbidge 1995; Ride and Tyndale-Biscoe 1962; Short *et al.* 1998). Friend and Burbidge (1995) reported that they are common in the scrub associated with stabilised dunes behind the beaches and also occur on the open steppe associations. At night they were commonly found in the sandhills and were seen occasionally during the day amongst low, dense scrub (Ride and Tyndale-Biscoe 1962). Trapping and spotlighting throughout the islands suggested that western barred bandicoots were widely distributed throughout the islands in all habitats, but were most likely to be found in tall scrub (Short *et al.* 1998).

1.7.4 Diet

The diet of the western barred bandicoot was thought to consist of insects and other small animals, seeds, roots, and herbs (Friend and Burbidge 1995). A recent, more comprehensive study of the diet of the western barred bandicoot at Heirisson Prong was conducted by Visser (2000). The most commonly consumed prey items
found in faecal matter were beetles, grasshoppers and crickets. Insect larvae, hemipteran bugs, spiders, earwigs, ants, millipedes, and centipedes were regularly consumed. Plant matter (seeds, berries) and skinks were also eaten (Plate 1.2). Krefft (1866, p.16) commented that “they proved as useful as cats. The *Perameles* would tumble the mice about with its fore paws, break their hind legs, and eat generally the head only. I have seen a single individual kill as many as twenty mice in a very short time, breaking their bones successively, after which is would begin to satisfy its hunger.” No evidence of the consumption of mice has been recorded since.

1.7.5 *Aboriginal knowledge*

Neither Burbidge and Fuller (1979) nor Finlayson (1961) obtained any evidence of the western barred bandicoot from interviews with Aboriginal people in the Warburton region of Western Australia and central Australia, despite extensive enquiries. They thought it unlikely that the species’ distribution reached these areas. Meagher (1974) reported that Aboriginals ate bandicoots in the south-west of Western Australia; probably the western barred bandicoot and southern brown bandicoot. Nind (1831, p. 37) noted that “girls, after eleven or twelve years of age, seldom eat bandicoots, such food being considered a preventive to breeding”. Early naturalists and explorers have reported a variety of common names for the species (Section 1.6.1), yet there is little other information recorded in the literature about Aboriginal knowledge of the species.
Plate 1.2: Western barred bandicoot consuming a spider on Heirisson Prong. Photo by Jiri Lochman, Lochman Transparencies.

1.7.6 Decline and extinction on mainland Australia

At the time of the collection of the first specimen at Peron Peninsula in Shark Bay, the western barred bandicoot was regarded as “common” (Quoy and Gaimard 1824 in Ride and Tyndale-Biscoe 1962).

Quoy and Gaimard, aboard the French ship “Astrolabe”, may have collected young *Perameles* from King George Sound in October 1826 (Alexander 1915, p. 128), although Glauert (1948) later referred to the specimens as the southern brown bandicoot. George Masters collected 20 adults and young, two skins and seven skulls of *Perameles myosurus* between September 1868 and April 1869 from “King George’s Sound and Salt River” (between King George’s Sound and the Pallinup River; Glauert 1948). Haddleton (1952) mentioned western barred bandicoots in the Katanning district of Western Australia in 1864, but they had completely disappeared at the time of writing his book *Katanning Pioneer*. Shortridge (1909) collected one specimen from east of Pingelly (Woyaline Wells) and one from Kojonup (Darton) in the south-west during his expedition of 1904-1907. He regarded them as being “not plentiful in the South-west”, although they were reported by Aboriginal informants to be fairly numerous in the “Salt River district” (Kellerberrin - Tammin area 200 km east of Perth).
Glauert (1933) mentioned that no specimens had been lodged in the “Museum” (British Museum of Natural History) since 1900 and he therefore assumed the species to be extinct. John Gilbert collected four *Perameles* during time spent at the Swan River Colony and while accompanying James Drummond on collecting trips, possibly to “Guangan” (thought to be the Wongan Hills District). He sent these specimens to England in December 1843 (Glauert 1948).

The last specimens collected in New South Wales were from the junction of the Darling and Namoi Rivers in 1840, Liverpool Plains in 1841, the Murray River in 1857 and near the Murray-Darling River junction in 1867 (Marlow 1958). Marlow regarded the species as extinct in New South Wales but still to be found occasionally in Victoria. Jones (1924) indicated that “it remains only in the wastes of the Western portion of the Centre” of South Australia, living on the open plains.

The last records of the species on mainland Australia were thought to be from Onslow, Eucla Pass and Rawlinna in Western Australia in 1910, 1914 and 1929 respectively, and at Ooldea in South Australia in 1922 (J. Friend 1990; Kitchener and Vicker 1981). However, the South Australian Museum has three additional specimens that were collected from south of Mt Crombie (south of the Musgrave and Mann Range in north-western South Australia) in 1931 (Copley et al. 1989). In 1931, surveyor H.L. Paine and Government geologist F.C. Forman journeyed from Western Australia to the South Australian border, and collected a “most interesting little bandicoot, unfortunately immature, of the genus *Perameles*” (Glauert 1948) at the Gahnda Rock Hole near Warburton in Western Australia (Kitchener and Vicker 1981). This animal resembled a young western barred bandicoot from Dorre Island, with longer, softer fur, brighter colouration, and longer ears, however Burbidge and Fuller (1979) believed the specimen to be *P. eremiana*.

A. J. Carlisle, a former resident of the western Nullarbor Plain in Western Australia, reported sighting plentiful numbers of “zebra rats” (most likely western barred bandicoots) between 1928 and 1936, but these were last seen in 1938 (Brooker 1977). Barrett (1930) wrote that bandicoots were inhabitants of the Nullarbor, and he had “heard, for instance, of a striped marsupial, a bandicoot whose description doesn’t tally with any given in the books on Australian mammals”. This may have been a western barred bandicoot. Troughton (1967) mentioned that the South Australian form had disappeared from the more populated areas and was “restricted to the sub-desert
western area of the state” at the time of writing *Furred Animals of Australia* in 1941. The date of their final demise is therefore unclear, but they are likely to have disappeared some time in the 1930s. There have been no reports of the species on mainland Australia since that time.

The reasons for the decline of the western barred bandicoot on mainland Australia have been regarded as unknown or unclear. Many earlier authors suggested a combination of predation by cats and foxes, habitat alteration and changes in vegetation caused by grazing by rabbits and livestock, clearing for crops, and the impact of feral goats and pigs in some areas (Anonymous, 1979; Aitken 1979; Ovington 1978). In Joan Dixon’s facsimile edition of *Gould's Australian Marsupials and Monotremes* (Gould 1974), it is suggested that the decline of the western barred bandicoot in the eastern states may have been caused by fox predation and habitat destruction by rabbits. It was also suggested that the species may have been in decline prior to the European settlement of Australia.

Maxwell *et al.* (1996) proposed predation by cats and foxes, modification of vegetation by rabbits and stock, and possibly changes in fire regimes in parts of its former range, as reasons for the decline to extinction of the western barred bandicoot on mainland Australia. Short (1995) regarded predation by cats and foxes as the major factor in their decline, with the impacts of rabbits, fire, habitat degradation and clearing, as additional possibilities. The IUCN (2003) regarded the major threats to be introduced competitors and predators, the clearing of natural vegetation and habitat modification, and accidental poisoning by rabbit control efforts.

There is little information about the decline of the western barred bandicoot on mainland Australia. The last specimen collected in New South Wales in 1867 (Marlow 1958) was at least 25 years prior to the arrival of the fox (Jarman 1986) and the rabbit (Stodart and Parer 1988). Collecting effort continued in New South Wales after this period (Dickman *et al.* 1993), and as Krefft (1866) had noted that it was “common on all parts of the Murray River”, it is likely that the species had indeed disappeared from this area. Menkhorst and Seebeck (1990) thought that the western barred bandicoot was widespread in north-western Victoria until the mid to late 1800s, when pastoral and agricultural settlement had spread though this region. Causes of the species’ decline are thought to include: decreases in vegetation cover and diversity from grazing by rabbits, sheep and cattle; changes in fire regimes; predation by introduced foxes and cats; and
later, clearing for agriculture (Menkhorst and Seebeck 1990). However, as their disappearance was prior to the arrival of rabbits and foxes, and after the commencement of pastoralism, it is possible that the feral cat played a more important role in their demise, as suggested by Dickman et al. (1993).

By the 1920s the western barred bandicoot had probably disappeared from the southeastern portion of South Australia (Jones 1924), although specimens were collected in the Ooldea area in the early 1920s (Kemper 1990). If A. J. Carlisle’s comments about plentiful “zebra rats” in the 1920s and early 1930s is accurate, and the species referred to was *P. bougainville*, the decline of the western barred bandicoot across the Nullarbor Plain coincided with the spread of the European fox, which was reported at Eucla in 1913, and 160 km west of the Western Australian/South Australian border in 1915 (Long 1988). While pastoralism had become established in the area by the 1870s (Short 1999), much of the region has never been occupied for pastoralism (Copley 1999). Brooker (1977) suggested that lengthy periods of drought during 1933 and 1935, combined with the impact of rabbits and the recently arrived European fox, were responsible for the demise of bandicoots, bettongs and greater stick nest rats from the Nullarbor Plain.

There is debate as to the timing of arrival of feral cats in Australia. Many authors have suggested that they were already present prior to European settlement (e.g. Burbidge, Johnson, Fuller, and Southgate 1988; Dickman 1993; Rolls 1969), based on anecdotal evidence from Aborigines. However, after a comprehensive search of a variety of historical sources, Gaynor (2000) and Abbott (2002) found no evidence that the cat was present on the mainland prior to European settlement. He suggested that cats spread from multiple coastal introductions in the period 1824-1886, colonising the majority of the continent by 1890. Short (1999) suggested that cats may have been present in northern Australia, but are less likely to have been present in southern Australia prior to European settlement in 1788.

Mason (1897) reported sightings of cats on the Nullarbor Plain in the 1890s, former resident Amy Crocker, said that “wild cats were here a good 30 years before foxes came” (hence, about 1885 as foxes arrived in 1917; Richards and Short 1996), and cats are known to have been released at Eucla in Western Australia in 1899 (Short 1999). Therefore, cats are likely to have co-existed with bandicoots for at least 30 - 40 years on the Nullarbor Plain. Rabbits arrived in the region in the 1890s (Stodart and
Parer 1988), thus it is likely that bandicoots and rabbits also coexisted for 30 - 40 years. It would therefore appear that the presence of cats and rabbits did not play a primary role in the decline of the western barred bandicoot across the Nullarbor. Rather, their demise occurred only five to ten years after the arrival of the fox.

From this background information, it appears that the western barred bandicoot declined in the path of pastoralism and settlement in eastern Australia, prior to the arrival of the fox and rabbit, but after the arrival of the feral cat. My hypothesis for its decline is that the depletion of vegetation cover reduced the habitat available for refuge from predators, rendering it increasingly more susceptible to predation by the feral cat. The demise of the species from the more arid areas appears to coincide with the arrival of the fox. Either the fox is a more efficient predator of bandicoots than the feral cat, or a similar depletion of vegetation cover though grazing by livestock, rendered the bandicoots more vulnerable to the combined predation by both foxes and feral cats.

1.7.7 Status of existing populations

Shortridge (1909) suggested that the western barred bandicoot was rare on Bernier Island, probably due to the introduction of a number of cats to the island. At the time, the only evidence obtained of the presence of western barred bandicoots was a damaged skull. However, Lipfert (1910) collected 12 good specimens in 1910 and Glauert (1933) reported that it was subsequently found to be fairly common, as did Ride and Tyndale-Biscoe (1962). Short et al. (1997a) estimated a combined minimum population of c. 2,200 - 4,400 animals on Bernier and Dorre Islands.

Maxwell et al. (1996) recommended translocation to at least three mainland sites, to ensure the species suffered no further decline. The first mainland population was established by CSIRO, Shark Bay Salt Joint Venture and the Useless Loop community at Heirisson Prong in Western Australia (this thesis) in 1995. A second mainland population was established by the Arid Recovery Project at Roxby Downs, South Australia, in 2001. A papilloma-like virus found in the Bernier Island population in 2001 has raised some concern about the health of the wild populations, and further proposed translocations to Roxby Downs in South Australia and Faure Island in Shark Bay have been postponed pending research into the nature of the virus (Friend 2002).
1.8  Study sites

1.8.1  Heirisson Prong

Heirisson Prong (26°4' S, 113°18' E; Figure 1.1) is a long, narrow peninsula that juts into Shark Bay, Western Australia. The peninsula is 880 km north of Perth and 450 km and 370 km by road from the nearest major towns of Geraldton and Carnarvon respectively. The peninsula is part of the Carrarang Pastoral Station, which covers an area of 600 km². The area is leased by the mining company, Shark Bay Salt Joint Venture, which runs a salt harvesting operation immediately to the south of the research site. The site was selected for the reintroduction of a suite of endangered mammals for a number of reasons (Short, Turner, Parker and Twiss 1994; Short and Turner 2000):

1) It had never been grazed due to the lack of free water for stock;
2) Its proximity to nearby remnant populations of threatened mammals on Dorre and Bernier Islands 90 km to the north;
3) Similar vegetation, climate and geology to these islands;
4) The long, narrow peninsula facilitated fencing a large area for the control of introduced predators at a low cost; and
5) Accessibility for ease of management and infrastructure support.

The mining town of Useless Loop is located 4 km south-east of the study site.

In 1989, community members from Useless Loop employed a consultant to investigate the possibility of forming a sanctuary for threatened species on their doorstep. A number of government bodies were approached, and in 1990, staff from CSIRO Sustainable Ecosystems (then CSIRO Wildlife and Ecology) recognised the potential of the site for experimentation in reintroduction biology, and the recovery of threatened mammals. Heirisson Prong presented an opportunity to establish a medium-scale site for reintroductions. Ocean on three sides of the tip of the peninsula, plus a short predator-proof fence at a narrow isthmus, produced a secure area of 12 km² for conservation purposes. The protected area is approximately 12 km long and 2 km at its widest point (Figure 1.2).

The fenced tip of the peninsula provided a ‘core zone’ of natural vegetation to keep threatened species in, and attempt to keep introduced predators (foxes and cats) out. The area had been baited monthly for foxes with ‘1080’ (sodium monofluoroacetate) poisoned meat baits since 1990, and up to four times a year with mouse carcasses impregnated with 1080 for cats, since 1995. Rabbit control was
conducted in the core zone by baiting using 1080 poisoned oats from 1990. This baiting was discontinued in 1995 with the reintroduction of western barred bandicoots, due to the risk of poisoning bandicoots as well as rabbits. South of the core conservation zone, a 200 km$^2$ ‘buffer zone’ was created. Introduced foxes were controlled by biannual aerial baiting with 1080 meat baits and trapping, and feral cats, which tend not to scavenge meat baits, were controlled by trapping. This area includes a salt harvesting operation, a pastoral lease with extensive sheep grazing, and coastal areas utilised for recreation.

The predator-proof barrier fence is 1.6 m high and 2.9 km long. It stretches across a narrow isthmus of the peninsula. The barrier fence is not bandicoot-proof. A community group from the small mining town of Useless Loop is responsible for the day-to-day management of the site (fence maintenance and predator control).

The dominant landforms are a series of sand dunes that run across the peninsula in a south-east to north-westerly direction. The dunes are separated by a number of small valleys and flat sandplains. Details of topography, soil type, vegetation and climate are provided in Short et al. (1994). Vegetation associations include heath dominated by plants less than one metre high, such as *Melaleuca cardiophylla* and *Thryptomene baeckeacea* (Plate 1.3); and heath with emergent shrubs up to two metres high, dominated by *Acacia ligulata*, *A. tetragonophylla*, *Pimelea microcephala*, species of *Atriplex*, *Rhagodia*, and *Scaevola*, and with other species such as *Alectryon oleifolius*, *Diplolaena dampieri*, *Exocarpus aphyllus*, *Nitraria billardierei*, *Pittosporum phylliraoides*, *Stylobasium spathulatum* and species of *Eremophila*, *Santalum*, and *Solanum*. 
Plate 1.3: Heath vegetation association at Heirisson Prong, dominated by *Melaleuca cardiophylla* and *Thryptomene baeckeacea*.

Heirisson Prong has a dry, warm, Mediterranean climate. It is semi-arid with an average rainfall of 228 mm per annum, recorded at Denham Station 6044 by the Bureau of Meteorology, 20 km to the north-east of Heirisson Prong and 120 km south south-east of Dorre Island. Most rain falls in winter. During the period of study between 1995 and 1999 rainfall varied from 57 mm below the average in 1995 to 75 mm above the average in 1996 (Figure 2.1a). The long-term fire history is unknown, but there has been no record of fire in the region since the 1960s.

A predator refuge is situated in the central portion of Heirisson Prong (Figure 1.2), enclosing 17 hectares of natural vegetation dominated by *Acacia tetragonophylla* shrubland, and *Melaleuca cardiophylla* and *Thryptomene baeckeacea* heath. Other common species present include *Acacia ligulata*, *Alectryon oleifolium*, *Rhagodia eremiana*, *Scaevola spinescens* and *Atriplex bunburyana*. The predator refuge was fenced with a fine wire mesh 1.8 m high, with an internal and external mesh skirt to prevent animals digging in or out, a 300 mm internal mesh overhang 400 mm high to prevent bandicoots climbing out, and was electrified (Section 2.2).
Figure 1.2: Map of Heirisson Prong, detailing the core conservation zone where predators are excluded, buffer zone where predators are controlled, and proximity to Useless Loop town site.
In November 1995 translocated bandicoots were housed in a single yard of nine hectares, which was subsequently divided into two yards each of 4.5 hectares in February 1999. In May 1998, the area of captive breeding yards was increased to include four smaller yards of two hectares each, which had previously been used to house burrowing bettongs since May 1992 (Short et al. 1994). Hence, the total area of captive breeding yards was 17 hectares in May 1998. Just over a year later, in August 1999, most bandicoots were removed from the captive yards in preparation for the arrival of the greater stick-nest rat *Leporillus conditor*.

Climate, soils, landforms and vegetation within the predator refuge are similar to those of the surrounding area on Heirisson Prong. The refuge lies within the centre of a large valley in the middle of the peninsula, and is surrounded by low sand dunes to the north, east and west.

The Shark Bay mainland was home to 31 species of native mammal prior to European settlement, but this number has since declined to 12 species (Baynes 1990). Heirisson Prong supports five species of native terrestrial mammal, including the euro *Macropus robustus*, the ash grey mouse *Pseudomys albocinereus*, the sandy inland mouse *P. hermannsburgensis*, the little long-tailed dunnart *Sminthopsis dolichura*, and the pale field rat *Rattus tunneyi*. Introduced mammal species include: the European red fox, feral cat, European rabbit and the house mouse *Mus musculus*. The area also supports a wide range of bird, reptile and aquatic fauna. A number of potential predators of smaller mammals reside in the area, including wedge-tailed eagles *Aquila audax*, the southern boobook owl *Ninox novaeseelandiae*, Gould’s monitor *Varanus gouldii*, and the king brown snake *Pseudechis australis*.

The general aims of the Heirisson Prong project were to develop guidelines for the management of threatened species by improving the control of feral animals, developing knowledge of the ecology of threatened mammals, and refining reintroduction techniques (Short and Turner 1992). Studies of the western barred bandicoot reported in this thesis contribute to the latter two project aims.

In the two years following the construction of the predator-proof barrier fence, predators were controlled on the peninsula, and a captive breeding colony of the burrowing bettong was established on Heirisson Prong in 1992 (Short and Turner 2000). Animals were released to range freely on the 12 km² peninsula between 1993
and 1998, which resulted in the establishment of a free-range population on the peninsula (Short and Turner 2000).

In late 1994, the Western Australian Department of Conservation and Land Management (CALM), conducted a release of the endangered Shark Bay mouse to Heirisson Prong (Morris, Speldewinde and Orell 2000). This reintroduction was not a success, with no evidence of mice remaining one year after the reintroduction (P. Boglio pers. comm.), and little idea of the cause of the failure. In 1995, a third species was reintroduced - the endangered western barred bandicoot *Perameles bougainville* (Richards and Short 1997, 2003), which is the subject of this thesis. This was followed by the greater stick-nest rat in 1999 (Richards, Copley and Morris 2001).

### 1.8.2 Dorre and Bernier Islands

Dorre (53 km²) and Bernier (44 km²) Islands are ‘A’ Class Reserves that form the seaward margin of the Shark Bay World Heritage Area in Western Australia, about 60 km west of the coastal town of Carnarvon (Figure 1.1). They are both arid, uninhabited, and waterless, with vegetation dominated by low heath and scrub. Detailed descriptions of climate, landforms, vegetation, fauna, and history of Dorre and Bernier Islands are given by Ride, Mees, Douglas, Royce and Tyndale-Biscoe (1962) and Short and Turner (1992).
1.9 Research aims

The aims of the research described in this thesis were:

- To establish a free-ranging mainland population of western barred bandicoots at a site where introduced predators are controlled to assist in the conservation of this species;
- To test the hypothesis that reintroduced western barred bandicoots will expand their range and increase in number if foxes and feral cats are maintained at low densities or excluded;
- To describe techniques that contribute to the successful reintroduction of western barred bandicoots to mainland sites;
- To increase knowledge of the basic biology of the species;
- To compare the survival and ecology of the reintroduced population on Heirisson Prong with that of the source population on Dorre Island, in order to assist in determining the likelihood of persistence of the reintroduced population;
- To assess the impact of rabbits on the survival, condition, reproduction and nest construction of western barred bandicoots on Heirisson Prong; and
- To provide information relevant to other planned reintroductions of the western barred bandicoot in Western Australia and South Australia, and the eastern barred bandicoot in Victoria.

1.10 Structure of thesis

Chapter One provides a general outline of the field of conservation biology, and the use of reintroductions as a technique to assist in the recovery of threatened species. It introduces the study animal, the western barred bandicoot, and discusses possible reasons for its decline and extinction from mainland Australia, and those of similar mammals. An outline of the study sites and background of the research project at Heirisson Prong in Shark Bay, is provided.

Chapter Two details the reintroduction of the western barred bandicoot to Heirisson Prong, including site preparation, the translocation of animals from Dorre
Island to a predator refuge on Heirisson Prong, their subsequent release to free-range, movements, survival, and population establishment.

Chapter Three details the biology of the reintroduced western barred bandicoot on Heirisson Prong, providing a comparison with the remnant wild populations on Bernier and Dorre Islands, and other species of bandicoot.

Chapter Four describes the nesting biology of the western barred bandicoot at Heirisson Prong during high and low densities of rabbits.

Chapter Five examines the impact of rabbits on the three shrub species most commonly used by the western barred bandicoot for nest sites. The potential impact of rabbits on the persistence of reintroduced bandicoots at Heirisson Prong is discussed.

Chapter Six examines future options for the management of the western barred bandicoot through population viability analysis using VORTEX software, and Chapter Seven provides a general discussion of the results of the reintroduction of the western barred bandicoot from Dorre Island to Heirisson Prong, with recommendations for future management and research.
Chapter 2

Reintroduction and establishment of the western barred bandicoot on mainland Australia

2.1 Introduction

Reintroductions of threatened mammals to the arid and semi-arid regions of mainland Australia have met with almost universal failure due to a combination of predation from the feral cat and European red fox, and dispersal of animals upon release (Christensen and Burrows 1994; Gibson, Johnson, Langford, Cole, Clarke and Willowra Community 1994a; Gibson, Lundie-Jenkins, Langford, Cole, Clarke and Johnson 1994b; Short et al. 1992; Southgate 1994; Southgate and Possingham 1995). Due to the problem of introduced predators, less attention has been paid to the problems associated with dispersal of released animals. In part, this has been due to the overriding problem of loss of reintroduced animals to predators.

Problems with dispersal have been encountered during reintroductions of golden bandicoots to the Gibson Desert Nature Reserve (Christensen and Burrows 1994), brush-tailed phascogales *Phascogale tapoatafa* to Gippsland and central and southern Victoria (Soderquist 1994), burrowing bettongs to Heirisson Prong in Shark Bay (Short and Turner 2000), and chuditch *Dasyurus geoffroii* to Cape Arid National Park in Western Australia (K. Morris *pers. comm.*). Males, in particular, often dispersed away from the release site and contributed little or nothing to population establishment. In the majority of these reintroductions, there were no barriers to movements.

In fenced areas set aside for the conservation of endangered mammals such as Karakamia Sanctuary in Western Australia, or the Arid Recovery Reserve at Roxby Downs, and Yookamurra and Warrawong Sanctuaries in South Australia, dispersal may be less of a problem, as a fence acts as a barrier to long-distance movements, at least for medium-sized mammals. However, for smaller mammals such as the western barred bandicoot, fences may not act as barriers, and with the increasing effectiveness of fox control, particularly in the south-west of Western Australia, the potential for non-fenced reintroductions has increased. In both these situations techniques to minimise dispersal of reintroduced animals are likely to be important to aid in the successful establishment of populations.
Predators had been controlled at Heirisson Prong prior to the initiation of this study (Short et al. 1994; Short and Turner 2000), but dispersal was still a potential problem. While the barrier fence had the potential to halt the movements of bettongs, the fence was not bandicoot-proof. To establish a population of bandicoots on Heirisson Prong, it was therefore considered that dispersal of reintroduced animals had to be kept to a minimum to allow contact between individuals and create ongoing opportunities for breeding.

The objectives of the reintroduction described in this chapter were to establish a free-range population of western barred bandicoots, to establish efficient techniques for successful reintroductions of the western barred bandicoot by controlling predators and minimising the dispersal of released animals, and to gain an insight into the relative importance of threatening factors implicated in their extinction from mainland Australia. A variety of options for limiting dispersal were discussed. These included:

(a) Release to a familiar or unfamiliar site;
(b) “Soft” or “hard” release (with or without temporary enclosures to restrict movements over the first few days after release);
(c) Release of animals with an established social group captured with contiguous or overlapping home ranges or animals chosen at random from the captive population; and
(d) Release in an area already colonized by bandicoots or to an area several kilometres from an existing bandicoot population.

The first method of release to a familiar and unfamiliar site was trialled at Heirisson Prong, with the latter three methods available for trial if the first was unsuccessful.

The reintroduction was preceded by studies of distribution, abundance and ecology of the species at Dorre and Bernier Islands (Short et al. 1997a; Short et al. 1998). This chapter describes the first attempt to reintroduce the western barred bandicoot to mainland Australia.

### 2.2 Methods

The reintroduction of the western barred bandicoot was carried out following similar methods used for burrowing bettongs at the same reintroduction site (Short and Turner 2000). These were based upon the IUCN guidelines for translocations (IUCN...
Chapter 2: Reintroduction

1987). The most important issues were the control of introduced predators, efficient transfer of animals, limiting dispersal during the reintroduction phase, and ongoing monitoring of the population. The majority of the site preparation before this study had already been performed for the reintroduction of burrowing bettongs at the same site (Section 1.8; Short et al. 1994; Short and Turner 2000). Data used in this thesis was collected between 1995 and 1999. The collection of data continued, but was generally not used in the thesis due to changes in the manner in which data was collected.

The 17 hectare predator refuge was used for the initial containment of the translocated animals and to provide a refuge from any mammalian predators breaching the barrier fence (Figure 1.2). The area was fenced with fine wire mesh, with an internal overhang to minimise dispersal of adult bandicoots to the greater 12 km² peninsula, and a skirt at ground level to prevent rabbits from digging underneath. Supplementary food (cat kibble) and water were provided for the first year. Rabbit and Gould's monitor numbers were controlled within the predator refuge by trapping. Two monitors and 280 rabbits were removed from the predator refuge between September 1993 and May 1998.

2.2.1 Monitoring of introduced species

Foxes were eliminated from the core conservation zone in 1991 and feral cats in 1995 (Short and Turner 2000). Over the following four years to 1999, occasional incursions by predators occurred, but the invaders were usually successfully baited within 1-2 months of gaining entry. Predator incursions were monitored by spotlighting at 3-monthly intervals, monthly mapping of predator tracks, and opportunistic sightings. Fox incursions occurred in July 1996 and July 1997 (Short, Kinnear and Robley 2002).

Cat tracks or sightings were recorded intermittently and at low levels between July 1996 and March 1998, suggesting occasional forays across the fence (Figure 2.1b). Monitoring of tracks suggested that these cats were either poisoned or left the area within 1–2 months. However, from July 1998, one or two cats were routinely sighted, suggesting that they had taken up residence on the peninsula.
Figure 2.1: (a) monthly rainfall for Denham from 1995 - 1999 (grey) and long-term median rainfall for Denham 1893 - 2000 (black); (b) number of bandicoots in the predator refuge (black) and free-range population (grey) over time. Numbers estimated as minimum known to be alive (KTBA; see explanation in Section 2.2.5). Estimates include recaptures to May 2000. Long arrows denote known fox incursions, short arrows denote cat incursions, and ‘C’ denotes removal of a cat by poisoning or trapping; and (c) rabbit sightings per kilometre ± SE on Heirisson Prong, between April 1995 and October 1999 (Robley, Short and Bradley 2002; Short 1999).
While considerable effort was made to maintain the barrier fence as predator-proof as possible, corrosion, wave action, storm damage, an irregular maintenance schedule, and an inadequate original design meant that it was not an absolute defence against predator invasion. Regular poisoning using mice carcasses impregnated with 1080 was conducted in response to sightings of cats or their sign within the core conservation zone.

Rabbits were controlled using 1080 poisoned oats until 1995, but were not controlled thereafter to avoid the risk of poisoning to bandicoots. Their numbers were estimated by spotlight counts following the methods outlined in Short et al. (1994). Rabbit numbers fluctuated, from a very high peak of 13 rabbits per spotlight kilometre (38/ha estimated by warren entrance counts) over the late spring and summer of 1997/8, to lows of less than one rabbit per spotlight kilometre (5/ha, which is still regarded as a high density of rabbits according to Williams, Parer, Coman, Burley and Braysher 1995) between July 1998 and August 1999 (Figure 2.1c; Robley et al. 2002; Short 1999).

### 2.2.2 Translocations

Western barred bandicoots were trapped at White Beach on Dorre Island using cage traps baited with peanut paste, rolled oats and sardines, in November 1995. Two hundred and thirty trap nights were conducted over three nights, for the capture of 30 bandicoots. Traps were placed in two lines spaced 50 m apart, within a radius of 1.5 km from White Beach. They were checked in the late evening and prior to dawn. Animals were sexed, weighed, and measured (hind foot, head length) and their reproductive status assessed (presence and size of pouch young or lactating nipples). Each individual was marked with a metal ear tag. Bandicoots were selected based on a desired sex ratio of 1 male:3 females and a preference for sexually mature individuals, to both increase the likelihood of offspring being produced, and to promote the commencement of breeding as quickly as possible. Each of the 12 animals selected were housed in a black calico bag in a cool, dark and quiet location prior to transport. They were fed daily with live mealworms and freshly chopped apple. Bandicoots were transported to the release site by boat and car in calico bags inside pet paks, with two bags per pet pack, partitioned centrally. Travel time from Dorre Island to Heirisson Prong was eight hours.
Ten of the 12 bandicoots were radio-collared prior to release. Radio collars were constructed with both a brass loop antennae and 12 cm whip aerial, allowing collars to be located if broken. They included a single-stage Model LT1 transmitter and two 1.4 volt batteries, housed in dental acrylic and heat shrink tubing. Collars weighed 8 g and were constructed by Titley Electronics (Ballina, New South Wales). Battery life was approximately six months. Bandicoots were released at dusk into straw-filled PVC tubing in the predator refuge on Heirisson Prong 1-3 days after initial capture.

2.2.3 Release to free-range

Two sites were chosen for the initial release of bandicoots from the predator refuge to free-range on Heirisson Prong in May 1997. The sites represented a ‘familiar’ and ‘unfamiliar’ location, chosen to examine the effect of proximity of an established population of bandicoots on dispersal by released animals. The familiar site was adjacent to the predator refuge and the unfamiliar site was 2.5 kilometres to the north (Figure 2.2). Both sites were chosen to locate animals a substantial distance from the barrier fence (the fence was not bandicoot-proof), and to be as similar in landform and vegetation type as possible.

Western barred bandicoots occupy a substantially different niche to that of burrowing bettongs (recently re-established at the site; Short and Turner 2000), and the two species were once broadly sympatric, so negative interactions between the two species were not anticipated. In particular, western barred bandicoots are omnivorous, predominantly consuming invertebrates and nest on the surface under shrubs, while burrowing bettongs are predominantly herbivorous and nest in warrens.

All bandicoots were radio-collared. Radio collars were modified from those used in the predator refuge to include a two-stage model GP1 Microlite transmitter and two lithium batteries. Collars were again constructed by Titley Electronics, with a battery life of approximately four weeks.

Bandicoots were released at dusk into straw-filled PVC tubing and allowed to exit at will. A radio-telemetry station was erected on a low hill at each release site. Bandicoots were located every hour from dusk till after dawn (20:00 h to 06:00 h) for the first three nights. The direction and intensity of each signal were recorded, to monitor any large movements away from the release sites. Animals were radio-tracked
daily to their diurnal nest site for periods of eight to 11 days. Locations were mapped using a Geographic Positioning System (GPS) or reference to prominent landmarks.

Bandicoots in subsequent releases to free-range were not radio-collared, and were released adjacent to the predator refuge. No further trials to limit dispersal were conducted, due to the success of the initial release.

### 2.2.4 Monitoring of bandicoots

Radio-collared bandicoots were trapped in the weeks after translocation and release to free-range to check their weight and condition. Collars were removed at the end of each monitoring session or if there was some cause for concern regarding a bandicoot's welfare.

Ongoing monitoring of bandicoots was carried out by trapping at three-monthly intervals. Elliott traps (30 x 10 x 10 cm collapsible aluminium box traps, Elliott Scientific, Upwey, Victoria) were set on a 50 m grid throughout the predator refuge and trapped for two to four nights. Grid locations were marked permanently with a tomato stake, reflective tape and flagging tape. There were a total of 49 trap locations in yards 7 and 8, reduced to 45 in June 1999. Trapping methods varied within yards 1 to 4, but usually involved a row of ten trap locations down the centre of each yard running east to west and spaced 20 metres apart, or two rows of five trap locations down each perimeter fence spaced 50 metres apart. A trapping grid that mirrored the grid in yards 7 and 8 was placed in yards 1 to 4 in June 1999, with a total of 45 trap locations within the four combined yards. Elliott traps were rarely used in the summer months as trapped animals were prone to ant attack. Cage traps were used during these periods.

Cage traps were also set at 100 m intervals along approximately 40 km of track system throughout Heirisson Prong to capture free-range bandicoots. Each location was trapped for two nights. This provided a means of comparing trap success over time, monitoring the dispersal of bandicoots from the release sites, and allowed estimations of population size. Trap locations were not fixed between field trips.

Young bandicoots were able to disperse from the predator refuge through the wire mesh. Intensive trapping was carried out in the vicinity of the predator refuge in June 1996 and early May 1997 to check for such dispersal prior to the deliberate release later in May 1997. Trapping was conducted outside the core conservation area to the south of the barrier fence in May and July 1997, July 1998 and February 1999 to check for the
dispersal of bandicoots into the buffer zone where predators were still present (cats plentiful, foxes in low numbers).

Bandicoots translocated from Dorre Island were identified individually by ear tagging. Those born on Heirisson Prong were identified by ear punching, and in later years, by passive implant transponders (PIT) tagging (Microchips Australia, Keysborough, Victoria) under the skin at the base of the neck.

2.2.5 Data analysis

The number of bandicoots was assessed from the minimum number known to be alive (KTBA), calculated as the total number of bandicoots captured during a monitoring period at time $t$, plus those individuals previously marked that were trapped on any subsequent monitoring period after time $t$ (Krebs 1966). The final estimate (October 1999) included all animals caught in October 1999 plus animals marked prior to that date and subsequently recaptured during surveys in February and May 2000.

Population size was estimated also from trapping data by mark-recapture between trapping periods using a Jolly-Seber estimate. This assumes equal probability of capture and equal probability of survival between trapping sessions for all individuals, that no marks were lost, and that sampling time is negligible in relation to intervals between samples (Krebs 1999). These assumptions appeared to be satisfied in this study.

The rate of population increase was estimated from the observed rate of increase of KTBA bandicoots (Caughley 1977; Short et al. 1998). The doubling time of the bandicoot population was calculated as $0.6931/r$ (Caughley 1977). One-factor ANOVAs were used for comparison of movements between the sexes.

2.2.6 Short-term criteria for successful establishment

Criteria for the successful establishment of western barred bandicoots on Heirisson Prong were adopted prior to the reintroduction. The first four criteria were those that Backhouse et al. (1994) set for the reintroduction of the eastern barred bandicoot *Perameles gunnii* in Victoria, and the fifth to address the issue of population persistence beyond the first two years of population establishment:

1. $\geq 50\%$ survival of translocated bandicoots after one month;
2. $\geq 10\%$ survival of translocated bandicoots after 6 months;
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(3) Reproduction in the wild within 6 months of translocation;
(4) Wild-bred bandicoots reproducing in the wild within two years; and
(5) Population persistence and increase over the subsequent two years after successful reproduction in the wild, with no requirement for additional translocations.

2.3 Results

2.3.1 Translocations from Dorre Island

Fifty bandicoots were planned for the translocation. However, as only nine females were captured near White Beach on Dorre Island in November 1995, all were taken, along with three males. An additional two bandicoots (both female) were captured in August 1996. They were transferred to Heirisson Prong and released to the predator refuge. Five of the 11 females carried pouch young.

2.3.2 Refuge from mammalian predators

Bandicoots released in 1995 were radio-collared and were monitored after release by radio-tracking and trapping. The two animals released in 1996 were monitored solely by trapping. All bandicoots released in 1995 survived the first days after release. No pouch young were lost during the translocation, or the first days after release. Two weeks after release three radio-collared animals were found dead (one with a broken leg, one with the collar caught on a branch, and one from unknown causes) and four radio-collared animals were missing. Of the missing animals, two were females and each was carrying two pouch young. The remaining five animals (3 males, 2 females, no pouch young) survived from three to forty months post-release. Four of these animals had fur loss on the rump and/or were missing a portion of their tail in the two months following their arrival in the predator refuge, suggesting intraspecific aggression.

One of the two females released in 1996 was not recaptured after release. The other was trapped two days after her release at the perimeter of the predator refuge. Six months post-release she was captured with no tail and a broken toe on her hind foot, but survived for at least 11 months post-release. These injuries and the presumed death of the other female may have been a result of intraspecific aggression resulting from their release into an established bandicoot population.
Only one of the females carrying pouch young was known to have survived to contribute young to the reintroduced population, but another three females carrying pouch young but missing after their release, may have contributed pouch young to the fledgling population. Hence, the population at Heirisson Prong is derived from a minimum of seven and a maximum of 15 animals: two females (no pouch young) and three males from the first translocation and one female (with pouch young) and a sire from the second translocation are known to have survived, and four females (two with pouch young) and two sires from the first translocation and one female (with pouch young) and a sire from the second translocation that were not recaptured after their release to Heirisson Prong.

There was no evidence that bandicoots had approached the water and little evidence that they had eaten any of the supplementary food provided in the first year after translocation. Both were discontinued, with no change detected in bandicoot condition or reproduction.

The first recruit was a female captured in July 1996, weighing 191 g. By May 1997, the colony within the predator refuge had grown to 20 bandicoots (twelve male, eight female), providing ten animals for an initial release to free-range. Bandicoots continued to be captured with portions of their tail missing or scarring on their rump after the translocations. There was no evidence that tail loss was a result of Elliott trapping, due to careful examination of bandicoots upon capture and no signs of recent trauma. Free-range animals were also found to suffer from similar injuries in the absence of the use of Elliott traps. These injuries may have been a result of ongoing intraspecific aggression. The colony in the predator refuge was disbanded in mid-1999 with the successful establishment of the free-range population. Remaining animals were released to free-range.

2.3.3 Release to free-range, post-release movements and survival

Fifty-one bandicoots were released to free-range on Heirisson Prong in five separate releases in 1997 and 1999 (Table 2.1). All were hard releases, with no supplementary food or temporary holding at the release site.

Table 2.1: Western barred bandicoots released to free-range on Heirisson Prong from the predator refuge. Note: (-1) represents bandicoots that were returned to the predator refuge.
Ten bandicoots were released from the predator refuge in May 1997. Five were released at the familiar site adjacent to the predator refuge (three male, two female), and five to an unfamiliar site 2.5 km to the north (three male, two female). The majority of bandicoots remained in close proximity to their release sites (Figure 2.2). Two males ventured 850 m and 700 m from the familiar and unfamiliar release sites respectively, in the first ten days after release but returned on subsequent nights. One male moved 2.8 km from the unfamiliar to the familiar release site during the first two nights after its release, then proceeded south over the following eight nights to a distance of 4.0 km from the release site. To prevent loss of this bandicoot from the core conservation zone, it was captured and returned to the predator refuge. One female and one male lost condition (losses of $\geq 20\%$ of body weight) during the week following their release at the familiar site and were also returned to the predator refuge.

The greatest distance moved from the release site by a female within the first ten days of release was 260 m. The median distance moved per day (between diurnal nest sites) by male bandicoots in the first ten days of release was 136 m ($178 \pm 65$ m, mean $\pm$ standard error (SE)), while for females the median daily movement was 28 m ($28 \pm 6$ m, mean $\pm$ SE). The difference in movements between the sexes was not significantly different due to high within-sex variance ($F_{1,8} = 3.39, P = 0.10$). The median distance moved from the release site by a male in the first ten days was 184 m ($801 \pm 650$ m, mean $\pm$ SE), and the median distance for a female was 140 m ($143 \pm 47$ m, mean $\pm$ SE). This difference in movements between the sexes was not significantly different due to high within-sex variance ($F_{1,8} = 0.65, P = 0.44$).
After one year, two females were within 730 m of their release site. Free-range males had moved from 740 m to 4.0 km from their release site (Table 2.2). At this time, both male and female bandicoots were dispersed between the two release sites and in habitat 1 km to the south of the familiar release site. There was no difference between dispersal distances between bandicoots at the familiar and unfamiliar release sites ($F_{1,8} = 0.61, P = 0.45$).

**Figure 2.2:** Release sites for western barred bandicoots on Heirisson Prong in May 1997, and the subsequent diurnal nest locations of males and females in the first ten days after release. Solid lines show details of male movement away from release site.
Table 2.2: Distance moved by bandicoots from point of release to free-range on Heirisson Prong in May 1997 and their last capture date.

<table>
<thead>
<tr>
<th>Bandicoot</th>
<th>Distance from point of release (m)</th>
<th>Last capture</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>One week</td>
<td>Two months</td>
</tr>
<tr>
<td><em>Familiar</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female 64</td>
<td>50</td>
<td>predator refuge</td>
</tr>
<tr>
<td>Female 1357</td>
<td>260</td>
<td>80</td>
</tr>
<tr>
<td>Male 6</td>
<td>40</td>
<td>not trapped</td>
</tr>
<tr>
<td>Male 128</td>
<td>840</td>
<td>200</td>
</tr>
<tr>
<td>Male 276</td>
<td>50</td>
<td>predator refuge</td>
</tr>
<tr>
<td><em>Unfamiliar</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female 1</td>
<td>80</td>
<td>230</td>
</tr>
<tr>
<td>Female 2</td>
<td>70</td>
<td>not trapped</td>
</tr>
<tr>
<td>Male 16</td>
<td>4120</td>
<td>predator refuge</td>
</tr>
<tr>
<td>Male 32</td>
<td>90</td>
<td>3910</td>
</tr>
<tr>
<td>Male 273</td>
<td>90</td>
<td>220</td>
</tr>
</tbody>
</table>

Of the ten bandicoots released in May 1997, all survived the first week after release. Three were returned to the predator refuge during the second week after release, and of the remaining seven animals, six were known to be alive one year after the release.

All animals from subsequent releases in 1999 (Table 2.1) were released adjacent to the predator refuge and were monitored by quarterly trapping. These animals were trapped for up to ten months after their release to free-range. Of those re-trapped after their release, females moved up to 3.1 km from their release site, with 54% remaining within 500 m of their release site (n = 13). Males moved up to 2.3 km from their release site, with 50% remaining within 500 m of their release site (n = 8).

Of the 41 animals released in 1999 (12 male, 29 female), 44% were not recaptured after their release (25% of released males, 52% of females), and 19% were captured only within the first two months after their release (33% of released males, 14% of released females).

2.3.4  **Trend of bandicoot numbers over time**

Sixty-eight bandicoots were known to be alive in October 1999 (Figure 2.1b). The KTBA population increased slowly until May 1998, then did not continue to
increase again until February 1999. A Jolly-Seber mark-recapture estimate of the population in October 1999 suggested that approximately 130 bandicoots were present on Heirisson Prong (lower and upper 95% confidence limits of 100 and 355). Recapture rates for bandicoots were extremely low (Figure 2.3), hence the high degree of error in the population estimate. Seventy-nine percent of free-range males and 78% of females were recaptured on less than four occasions (during a period of up to nine months) after their initial capture or after their release from the predator refuge to free-range. Both the KTBA and Jolly-Seber estimates are likely to underestimate bandicoot numbers as approximately 50% of habitat for females and 10% for males is unlikely to have been sampled by the trap lines. These areas were beyond the estimated radius of the home range of a bandicoot (140 m and 210 m assuming a circular home range of 6.2 hectares for females and 14.2 hectares for males (Friend and Burbidge 1995)) from the trap line around the road system.

On average, 3.95% of traps caught bandicoots. Trap success of the free-range population increased from 0.9% in October 1997 to 4.7% in May 1998, 6.4% in February 1999 and 8.2% in October 1999 (Table 2.3). Up to 54% (mean 29%) of available traps captured bettongs during monitoring sessions, therefore not all traps were available to capture bandicoots. Trap success declined during the period from May to October 1998, from 4.7% in May, to 3.1% in July and 1.0% in October, mirroring the decline in KTBA (Figure 2.1b). On average, 28% of individuals were recaptured during the same trapping session. The proportion of free-range bandicoots recaptured varied from 0 in March and October 1998 to 0.7 in July 1997. There was no difference in the recapture rate between males and females ($t_{(2)10} = 1.93, P = 0.08$).
Figure 2.3: The frequency with which free-range bandicoots were recaptured after their initial capture on Heirisson Prong.

Table 2.3: Trapping results for free-range western barred bandicoots at Heirisson Prong.

<table>
<thead>
<tr>
<th>Date of monitoring</th>
<th># Cage trap nights</th>
<th>Bandicoot captures (recaptures)</th>
<th>Trap success (%) for bandicoots</th>
</tr>
</thead>
<tbody>
<tr>
<td>July 1997</td>
<td>535</td>
<td>12(3)</td>
<td>2.24</td>
</tr>
<tr>
<td>October 1997</td>
<td>437</td>
<td>4(0)</td>
<td>0.92</td>
</tr>
<tr>
<td>January 1998</td>
<td>572</td>
<td>8(2)</td>
<td>1.75</td>
</tr>
<tr>
<td>May 1998</td>
<td>640</td>
<td>24(6)</td>
<td>4.69</td>
</tr>
<tr>
<td>July 1998</td>
<td>579</td>
<td>15(3)</td>
<td>3.11</td>
</tr>
<tr>
<td>October 1998</td>
<td>667</td>
<td>7(0)</td>
<td>1.05</td>
</tr>
<tr>
<td>February 1999</td>
<td>610</td>
<td>36(3)</td>
<td>6.39</td>
</tr>
<tr>
<td>June 1999</td>
<td>600</td>
<td>29(11)</td>
<td>6.67</td>
</tr>
<tr>
<td>August 1999</td>
<td>629</td>
<td>22(6)</td>
<td>4.45</td>
</tr>
<tr>
<td>October 1999</td>
<td>608</td>
<td>46(4)</td>
<td>8.22</td>
</tr>
</tbody>
</table>
2.3.5 *Population establishment*

In July 1998, one year after the initial release to free-range, bandicoots were found throughout the central section of Heirisson Prong between the two release sites (Figure 2.4a). By February 1999, male bandicoots had been caught both on the southern boundary fence and the northern tip of Heirisson Prong (Figure 2.4b). In October 1999 both male and female bandicoots were captured throughout the peninsula (Figure 2.4c).

A free-range bandicoot (other than the individuals released in May 1997) was first detected outside the predator refuge in May 1997, shortly after the first formal releases, indicating that bandicoots could escape from the predator refuge. At this point, the density of bandicoots within the predator refuge was 1.4/ha, almost three times the density shortly after the translocation from Dorre Island. This animal was a new adult male, captured 250 m from the predator refuge. In the ensuing years both adult and juvenile bandicoots are known to have moved back and forth between the predator refuge and free-range. Unassisted emigration ("escapes") from the predator refuge is likely to have contributed to growth in the free-range population. No evidence of dispersal to the buffer zone south of the barrier fence was found.

2.3.6 *Short-term criteria for successful establishment*

All criteria for success, other than the first, were met or exceeded. Forty-three percent of animals translocated from Dorre Island \((n = 14)\) are known to have survived the first month after release into the predator refuge. The first new recruit was captured in July 1996, approximately eight months after the first release. The animal was at least six months of age and was therefore a pouch young present shortly after the first translocation from Dorre Island. This first wild-bred bandicoot produced a litter in October 1996, eleven months after the initial translocation. The population persisted and increased over the subsequent two years after successful reproduction in the wild, and has been self-sustaining since the last transfer of animals from Dorre Island in August 1996.
Figure 2.4: Dispersal and establishment of reintroduced bandicoots on Heirisson Prong, (a) in July 1998 one year after release to free-range (n = 18, trap success = 3.11%), (b) February 1999 two years after release (n = 42, trap success = 6.4%), and (c) October 1999 two and a half years after release (n = 50, trap success = 8.22%).
2.4 Discussion

2.4.1 Translocations from Dorre Island

Western barred bandicoots were reintroduced to Heirisson Prong at Shark Bay, in 1995, to establish the first population on mainland Australia in over 60 years. The reintroduction site was intensively managed to exclude introduced predators. The reintroduced population was derived from a small sample of up to fourteen individuals from the remnant population on nearby Dorre Island. It is likely that as few as seven represented the founder population and have contributed to the current gene pool. The population persisted and appeared to be self-sustaining by October 1999, with an estimate of 130 individuals being present on the peninsula.

2.4.2 Predator refuge

The predator refuge provided a source of bandicoots for release to free-range on Heirisson Prong, and may have provided a portion of the population with a secure refuge from predation by feral cats and foxes. A similar predator refuge was a key factor in the success of the reintroduction of the burrowing bettong to Heirisson Prong. It acted as insurance against loss of all free-range animals to foxes in the earlier stages of that reintroduction, guaranteeing a supply of bettongs for release to free-range (Short and Turner 2000).

Bandicoots appeared less suited than bettongs to confinement in a refuge because of intraspecific aggression. The population in the refuge grew to 140/km$^2$. However, despite some problems with minor injuries, at least 68 new animals were recruited. Bandicoots are regarded as solitary animals (Gordon 1974; Heinsohn 1966; Stodart 1966). Mutual avoidance behaviour predominates between individual eastern barred bandicoots, although some antagonistic interactions occur when animals actively defend foraging patches (Dufty 1991). Maintaining a predator refuge for bandicoots at a suitable density therefore requires the construction of large enclosures. Unless a low level of predation can be guaranteed, the construction of a predator refuge is likely to remain an important insurance measure.

Reintroductions of wild-bred animals are thought to be more successful than those of captive-reared animals (Fischer and Lindenmayer 2000). For a solitary species such as a bandicoot, direct translocations from wild populations are to be encouraged, to both
increase the chance of success, and decrease the risk of problems due to intraspecific aggression and suppression of breeding due to high population densities (Section 3.4.2).

### 2.4.3 Population establishment

The reintroduction of the western barred bandicoot to Heirisson Prong appears successful, despite the initial loss of some translocated animals. Numbers have grown consistently and the population has expanded to fill all available habitat. There was no evidence of any problems associated with the small founder group, and the population size now appears to exceed that likely to be threatened by demographic stochasticity. Fischer and Lindenmayer (2000) found that reintroductions tended to be more successful when over 100 animals were released, however the majority of bird and mammal translocations conducted between 1973 and 1986 in Australia, Canada, Hawaii, New Zealand and the United States have consisted of 75 or fewer animals (Griffith et al. 1989). Maximising founder size is regarded as an important factor in the success of reintroductions (Fischer and Lindenmayer 2000; Griffith et al. 1989), however habitat quality, and the control of limiting factors may often be more important (Caughley and Gunn 1996).

For example, if threatening processes have not been controlled, even a large number of animals may not be enough to swamp the threat and guarantee a successful outcome. The founder sizes of seven reintroduced populations of the endangered eastern barred bandicoot in Victoria ranged from 50 to 130, spread over many releases (Watson and Halley 1999). Despite the comparatively large founder sizes, few, if any, of these reintroductions appear secure. The populations have decreased due to ineffective predator control and an extended drought (Watson and Halley 1999).

Large founder numbers increase the genetic diversity of the population, and may decrease the risk of future problems due to genetic erosion (Wolf, Garland and Griffith 1998). The potential for long-term consequences of the bottleneck at Heirisson Prong through the loss of genetic variation and subsequent decrease in the potential evolutionary adaptability of the population (Soulé 1983), should not be dismissed. However, island populations of mammals have been found to have very low levels of genetic variation when compared with mainland populations, due primarily to their small size and isolation (Eldridge 1998; Eldridge, King, Loupis, Spencer, Taylor, Pope and Hall 1999; Frankham 1997, 1998). While Eldridge (1998) and Eldridge et al.
(1999) recommended the hybridization of animals from multiple wild populations as an option to increase levels of genetic variation (e.g. Bernier and Dorre Islands), the legalities of such a suggestion have yet to be dealt with. In the meantime, reintroduction efforts for the western barred bandicoot rely on the hope that the probable low levels of genetic variation sustained for 8,000 – 10,000 years in the wild island populations, are not detrimental to the long-term persistence of reintroduced populations, such as at Heirisson Prong.

Problems were encountered with the first attempt to radio-collar western barred bandicoots at Heirisson Prong in 1995. The collars are likely to have contributed to significant mortality in the first two weeks after translocation of animals from Dorre Island. These problems appear common to attempts to re-establish bandicoots. The deaths of three of fourteen western barred bandicoots translocated to Roxby Downs in 2001 were associated with weight loss and the use of radio collars, either due to feet caught between the neck and collar, or capture myopathy during radio-collaring. Two bandicoots experienced neck ulceration due to the presence of collars (Moseby 2001). The use of radio-collars to monitor eastern barred bandicoots has resulted in numerous deaths (Booth and McCracken 1994; Murphy and Serena 1993; Seebeck and Booth 1996). Collars caused neck ulceration, paws became stuck between neck and collar, and the presence of the collar was thought to increase the risk of predation.

No deaths were encountered during subsequent collaring of western barred bandicoots at Heirisson Prong. Collars were modified to fit tightly, and to evenly distribute the battery and transmitter package around the lower half of the collar (instead of a larger package at the base of the neck). In addition, the duration animals were collared was decreased to < 14 days, animals were monitored for weight loss and chafing during the period they wore collars, and collars were removed if animals experienced excessive weight loss. Collars made from plastic electrical ties were used successfully for up to 14 days (Chambers and Dickman 2002), and collars lined with lamb skin with the fleece side in contact with the bandicoot to prevent chafing, were used for 6-8 week periods on the long-nosed bandicoot in New South Wales (Scott, Hume and Dickman 1999).

A number of alternative techniques for attaching radio-transmitters have been trialled on eastern barred bandicoots, with limited success (Booth and McCracken 1994; Murphy and Serena 1993; Seebeck and Booth 1996). Harnesses were removed by
bandicoots within 24 hours, and transmitters were lost. Some recent techniques have proven more successful. Transmitters attached by suturing and gluing to the skin of the rump have been retained for up to one month or longer (Jenkins 1998; Seebeck and Booth 1996). Transmitters implanted in the intraperitoneal cavity have been retained for over four months but problems with transmitter function have been experienced (A. Robley and J. Seebeck pers. comm.). However, the use of invasive techniques increases the risk of infection and requires veterinary experience (National Health and Medical Research Council 1997).

The movements of reintroduced western barred bandicoots post-release did not pose significant problems for their re-establishment at Heirisson Prong. Only one male left the release area. The use of a familiar release site appeared not to be important. Problems with dispersal have been encountered during reintroductions of golden bandicoots to the Gibson Desert Nature Reserve (85% dispersed to areas of dense spinifex up to 4 km from the release site within one week of release: Christensen and Burrows 1994), male brush-tailed phascogales to Gippsland and central and southern Victoria (all dispersed, up to 8 km within a few days; Soderquist 1994), male burrowing bettongs to Heirisson Prong in Shark Bay (several moved greater than 10 km from the release site: Short and Turner 2000), and chuditch to Cape Arid National Park in Western Australia (one male dispersed 180 km: K. Morris pers. comm.). Males, in particular, often dispersed away from the release site and contributed little or nothing to population establishment. Male brush-tailed phascogales released into established populations containing females were less inclined to disperse from release sites (Soderquist and Serena 1994) and when both male and female burrowing bettongs were released together, all tended to remain within two kilometres of their release site (Short and Turner 2000). Releasing both male and female bandicoots together, combined with the availability of good quality habitat with abundant dense cover at Heirisson Prong, may have decreased the impetus for bandicoots to disperse.

Mortality of bandicoots at Heirisson Prong appeared high, with 37% of all animals released from the predator refuge to free-range not being captured after the first month. Of those animals recruited to the free-range population, 39% were not recaptured after their first capture, and a further 26% were recaptured once only. No known causes of death of free-range bandicoots at Heirisson Prong have been established. Radio-collars were implicated in the death of animals translocated in 1995.
Wedge-tailed eagles have been sighted capturing a western barred bandicoot on Dorre Island during release after dawn (Richards and Short 1998). Other causes of mortality or loss may include predation by goannas, king brown snakes, owls, feral cats and foxes (that entered the core conservation zone despite control efforts), intraspecific aggression, and dispersal beyond the barrier fence to the buffer zone.

Dufty (1991) reported that 86% of eastern barred bandicoots trapped at Hamilton in Victoria were captured fewer than four times. Causes of mortality for eastern barred bandicoots have included: road deaths, predation (by introduced foxes, feral cats, domestic dogs and cats, and the native whistling kite), trapping, other trauma (radio-collaring, self-inflicted wounds and intraspecific aggression sustained in captivity, drowning in a swimming pool, and mishaps during transportation), toxoplasmosis or other infections, parasites, neoplasia, poisoning and old age (Booth and McCracken 1994; Brown 1989; Watson and Halley 1999). The primary causes of mortality of long-nosed bandicoots at Sydney Harbour National Park in New South Wales were road trauma, and predation by foxes and cats (Scott et al. 1999). With a minimum of predator control in the latter study, less than 10% of pouch young survived to subadultulthood, and of these animals, over 70% were not recaptured in the study area after two months, suggesting a high rate of mortality.

There was a brief period of decline in the bandicoot population after May 1998 that corresponded with an increase in the presence of cats on Heirisson Prong, lower recruitment, and a decrease in the proportion of females with pouch young or lactating (Section 3.3). Rainfall in 1998 was 18 mm above the average and rabbit numbers were low, therefore these factors are unlikely to have contributed to the reduced capture of bandicoots. The bandicoot population increased again from February 1999, however much of this increase was due to the transfer of bandicoots from the predator refuge to free-range.

Reproductive output of bandicoots on Heirisson Prong appeared greater than that on Bernier and Dorre Islands (Short et al. 1998; similar average litter size in each area, but an extended period of breeding on Heirisson Prong). Despite this however, the instantaneous rate of increase of bandicoots per year on Heirisson Prong was slightly lower than that assessed for Dorre Island (0.54 cf. 0.65; Short et al. 1998).

This is the first attempt to reintroduce the western barred bandicoot to mainland Australia. The free-range population has expanded in number and in range. As
described in Chapter 3, female bandicoots have bred throughout the year, produced up to three pouch young per litter, and the high fecundity is likely to contribute to successful population re-establishment. Mean trap-revealed longevity of western barred bandicoots at Heirisson Prong was similar to that for eastern barred bandicoots in Tasmania (7.9 months for males and 10.5 months for females; Mallick et al. 2000).

2.4.4 The impact of introduced species

Foxes were absent from the core conservation zone apart from two incursions, cats were present sporadically between 1995 and mid-1998, and in low numbers after this time, and rabbits ranged from very high to low on Heirisson Prong during the four-year period of the reintroduction and subsequent monitoring. All bandicoots were resident in the predator refuge during fox and cat incursions in 1996, so these incursions are unlikely to have had an impact. A second fox incursion occurred in July 1997, two months after the first formal release of bandicoots. At this time the density of free-range bandicoots on Heirisson Prong was 1/km$^2$, only eight bandicoots were known to be present in the free-range population, and all but one survived the incursion. By comparison, burrowing bettongs reintroduced to the site in 1993 and also at a population density of 1/km$^2$, suffered 77% mortality due to a single fox incursion at the time of release. During the 1996 and 1997 fox incursions, the bettong population suffered losses of 36% and 46% respectively, at population densities of 3.5/km$^2$ and 7/km$^2$ respectively (Short et al. 2002).

Sightings of cats during spotlighting and the regular mapping of cat tracks suggested that 2-3 cats had become permanently established on Heirisson Prong through 1998 and 1999, despite regular baiting with mice carcasses (Short, Turner, Rispby and Carnamah 1997b) and the known poisoning of at least one adult cat in November 1998. The bandicoot population was able to increase in number and colonise the peninsula despite the presence of low densities of feral cats. The density of free-range bandicoots reached a peak of at least 6-11/km$^2$. This density of bandicoots is less than a quarter of their estimated minimum density on Bernier and Dorre Islands (45.5/km$^2$; Short et al. 1997a).

Western barred bandicoots were able to persist on mainland Australia in the presence of feral cats prior to the twentieth century (e.g. both species occurred on the Nullarbor region of Western Australia in the early 1900s; bandicoots - Brooker 1977;
Friend 1990; cats - Mason 1897; Richards and Short 1996), but met their demise within 10 to 20 years of colonisation by the fox and within 30 to 40 years of colonisation by the rabbit. The eastern barred bandicoot is critically endangered on mainland Australia in the presence of foxes, cats, and rabbits. In Victoria, this species appears to be highly susceptible to fox predation (Short et al. 2002). This is not surprising, due to its use of open habitat with little cover to avoid predation (Heinsohn 1966). It remains locally common in Tasmania where cats and rabbits are present but foxes were absent until recently. There is some evidence of a decline in numbers in Tasmania, thought to be due to clearing for agriculture and stock-grazing (Mallick et al. 1997), and more recently, an extended period of drought between 1992 and early 1995 (Mallick et al. 2000). Alternatively, the loss of habitat and therefore cover due to changing land use, may have increased their susceptibility to predation by cats.

There has been no direct evidence of cat predation on western barred bandicoots. They may be susceptible to predation by cats due to their small size and their use of above ground nest sites that are easily accessible to predators. Feral and domestic cats are known predators of the eastern barred bandicoot (Booth and McCracken 1994; Brown 1989) and the long-nosed bandicoot Perameles nasuta (Dickman 1993), and can consume mammalian prey items ranging in size from planigales (5 g) to hare-wallabies (3 kg; Paltridge, Gibson and Edwards 1997). The cryptic behaviour and use of dense, prickly shrubs for cover by western barred bandicoots may render them less accessible to predators such as feral cats.

While it appears that western barred bandicoots can persist in the presence of one or two cats within the 12 km² area at Heirisson Prong, the potential impact of foxes and feral cats on the reintroduced population of western barred bandicoots in the long-term is unknown. Cats may have played some role in the high mortality rate of bandicoots on Heirisson Prong, but the low density of cats was not sufficient to prevent the establishment and increase of the reintroduced population.

The reintroduction of the western barred bandicoot to Heirisson Prong has provided an insight into the relative impact of foxes, cats and rabbits in the former decline of western barred bandicoots. It is unclear which facets of the reintroduction to Heirisson Prong were the most important in its success, and chance may even have played a role in this instance. However it is likely that predator control is the highest priority for any mainland bandicoot reintroduction. Unfortunately, the considerable
investment required to control feral cats in the presence of threatened mammals does not always yield significant returns. Cats were not eradicated successfully from Heirisson Prong for periods of more than ten months, despite a variety of intensive trapping and baiting methods. Good habitat with dense cover may be an important factor in the success of bandicoot reintroductions, particularly when complete eradication of predators cannot be guaranteed. There appeared to be no requirement for the control of rabbits, however the long-term effects of high densities remain unknown.

2.5 Conclusions

Heirisson Prong has assisted in providing a more secure future for the western barred bandicoot, however the conservation of the species would benefit greatly from the establishment of additional mainland populations, providing that adequate predator control is conducted and sustained in the long term. An additional reintroduced population was established at Roxby Downs in South Australia by the South Australian Department of Environment, Heritage and Aboriginal Affairs in conjunction with Western Mining Corporation and the University of Adelaide (Arid Recovery 2003; Richards 2003). Captive populations are currently managed by CALM at Kanyana Native Fauna Rehabilitation Centre, Peron Peninsula, and Dryandra Forest in Western Australia (Richards 2003). Further mainland reintroductions are planned at Peron Peninsula and in the wheatbelt zone of Western Australia by CALM, and to Faure Island in Shark Bay by the Australian Wildlife Conservancy. Further experimental work is required to examine more closely the role of introduced predators, rabbits, founder population size, and reserve size.

This chapter described the successful reintroduction and establishment of the western barred bandicoot to Heirisson Prong. The population increased over the four-year period outlined in this thesis. Chapter Three provides more detailed information about the dynamics of the reintroduced population, explaining how the population increased, similarities and differences to the source population on Dorre Island and other species of Australian bandicoot, and a discussion of the suitability of Heirisson Prong as a reintroduction site in terms of levels of reproduction and recruitment.
Chapter 3

Biology of the western barred bandicoot on Heirisson Prong

3.1 Introduction

This chapter examines aspects of the biology of reintroduced western barred bandicoots at Heirisson Prong. Until recently, little was known about the biology of the western barred bandicoot due to its demise from the mainland early last century, combined with the remote location of the remnant island populations. Earlier naturalists recorded some details of the general biology of the species, but often this information was derived from a small sample of individuals, and in some cases may have been from species other than the western barred bandicoot. A recent study by Short et al. (1998) provided basic biological and ecological data about the species on Dorre and Bernier Islands, including data on population structure, body size and condition, reproduction, group size, movements, rate of increase, and habitat use.

The objectives of this chapter are to compare the biology of the western barred bandicoot:

1. Between the population reintroduced on Heirisson Prong and the wild populations on Bernier and Dorre Islands;
2. Between the predator refuge and free-range populations reintroduced on Heirisson Prong; and
3. With other species of bandicoot.

A comparison of the reintroduced population at Heirisson Prong with the biology of the remnant populations on Dorre and Bernier Islands may provide information about the suitability of the habitat at the reintroduction site on Heirisson Prong, and hence, some indication of the stability of the reintroduced population and its likely persistence at a site where introduced predators have been controlled. The reintroduced population also provides an accessible mainland population, which in turn provided an opportunity for the collection of more comprehensive biological data throughout all seasons of the year. In particular, biological information for the island populations is lacking for the summer period between December and March. These data are available for the reintroduced population at Heirisson Prong. In addition, a comparison of the
reintroduced and island populations may provide some indication of any notable differences between a low and high-density population, a site with and without rabbits (implicated in the decline of the species on mainland Australia), and a site with low levels of introduced predators, and no introduced predators.

Due to the solitary nature of bandicoots (Gordon 1974; Heinsohn 1966; Stodart 1966), there was some concern over the use of a small predator refuge, and the effects of confining a relatively high-density bandicoot population. Comparisons between animals within the predator refuge and the free-range population may therefore provide an indication of the suitability of this particular technique for the reintroduction of western barred bandicoots at Heirisson Prong. Finally, comparisons with other bandicoot species may provide some insights into the biology of western barred bandicoots that may improve options for future management of this endangered species throughout Australia.

In this chapter, data on population structure, reproduction, body size and condition, movements, habitat use and longevity of western barred bandicoots on Heirisson Prong are presented. Data were collected by trapping, radiotracking and spotlighting, within both the predator refuge and in the free-range area on Heirisson Prong. Data were collected during a four-year period between November 1995 and December 1999.

### 3.2 Methods

Bandicoots were sampled on 26 trips to Heirisson Prong between November 1995 and December 1999 (Table 3.1).

<table>
<thead>
<tr>
<th>Year</th>
<th>Months of monitoring</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>November</td>
</tr>
<tr>
<td>1996</td>
<td>January, February, May, July, August, October</td>
</tr>
<tr>
<td>1997</td>
<td>February, April/May, July/August, October, November, December</td>
</tr>
<tr>
<td>1998</td>
<td>January, February, March, May, July, October</td>
</tr>
<tr>
<td>1999</td>
<td>February, June, August, September, October, November, December</td>
</tr>
</tbody>
</table>
3.2.1 **Monitoring of bandicoots**

Bandicoots within the predator refuge were sampled on a regular basis (at least three-monthly) from the original release into the refuge in November 1995. Free-range bandicoots were monitored at three-monthly intervals after their release in May 1997, as outlined in Section 2.2.4. Most data came from standard three-monthly trapping along the road network but additional data were acquired during trapping off the roads in October and November 1997, at nest sites in May 1997, May 1998 and February and June 1999. Trapping protocols are described in more detail in Section 2.2.4.

Bandicoots translocated from Dorre Island were identified individually by ear tagging. However, the use of ear tags was discontinued as tags were commonly ripped out, leaving a large tear in the ear. Animals born on Heirisson Prong were identified by ear punching, and in later years, by passive implant transponder (PIT) tagging under the skin at the base of the neck.

Upon capture, weight, sex, head length (tip of nose to occipital condyle), hind foot length (heel to tip of longest toe), and tail length were measured. Basal tail diameter was sometimes measured to look for any indication of fat storage in the tail. The pouch of females was checked for the presence of pouch young or enlarged nipples, and the number and developmental stage of pouch young was recorded. Sex of young was recorded if it could be done without distressing the mother. Scrotal length and width were measured for males. Signs of intraspecific aggression such as fur loss on the rump or a missing section of the tail were recorded.

Radio tracking of free-range bandicoots in May 1997, May 1998 and February and June 1999 provided additional details of movements and home range size. Daily nest locations were recorded using a GPS and then downloaded to the Geographical Information System (GIS) software program Arcview, where locations were mapped and distances measured.

3.2.2 **Data analysis**

One-factor ANOVAs were used for comparison of most variables between and within sexes, free-range and predator refuge populations, trapping sessions, years, breeding season, the reintroduced and island populations, and for comparisons between litter size and hind foot length, litter size and pouch life, and scrotal width of males at different times of the year. Data from wild bandicoot populations on Dorre and Bernier
Islands were taken from Short et al. (1998). Raw data were used for comparison with the reintroduced population at Heirisson Prong.

Functional regression was used to compare the ratio of male to female captures to the proportion of adult females without pouch young, the proportion of sub-adults in the population with rainfall over the previous three and six month periods for all trapping surveys, the arcsine of the square root of the proportion (arcsine $\sqrt{p}$) of sub-adults and number of bandicoots trapped per 100 trap nights, and tail diameter and body condition. The percentage of adult females (≥ 185 g) carrying pouch young or lactating was collated by month for the years 1995 to 1999. The relationship between the average litter size of bandicoots and rainfall in the previous four-month period, season, month, year, bandicoot and bettong trap success, and rabbit abundance (average number of rabbits per spotlight kilometre) was examined by multiple regression. The variables explaining the most variance in the data were chosen by maximizing $r^2$ (using an $F$ to enter and remove of 4.0), and maintaining a $t$-ratio of ≥ 3.0, to produce a regression equation predicting average litter size.

Chi-squared analyses were used to compare sub-adult sex ratios, and signs of intraspecific aggression between sexes, animals in the predator refuge and free-range populations, and small and large males.

Body condition was calculated following the method outlined in Krebs and Singleton (1993) by: (1) estimating the regression of weight on hind foot length for the Heirisson Prong population; (2) comparing this with similar data for Dorre Island using an analysis of covariance; (3) combining data from the two populations as the slopes of the regressions were not significantly different; (4) using this combined regression to predict weight of animals at Heirisson Prong from measured hind foot length for each individual; and (5) estimating the condition of each individual from the ratio of observed weight to predicted weight. Females with pouch young were not used in analyses comparing condition due to the additional unknown weight of pouch young.

An attempt was made to evaluate factors contributing to body condition of bandicoots by using a multiple regression. This incorporated a subset of the variables: mean bandicoot head length, estimated density of capture of bandicoots (number of bandicoots captured per 100 trap nights, excluding traps capturing burrowing bettongs; Caughley 1977), season, rabbit abundance, sex, sex ratio, rainfall over the previous three months lagged by one month, four months lagged by two months and burrowing...
bettong numbers (for free-range animals only). The variables explaining the most variance in the data were chosen by maximizing $r^2$, using an $F$ to enter and remove of 4.0, and maintaining a $t$-ratio of $\geq 3.0$, to produce a regression equation predicting body condition.

Only bandicoots born on Heirisson Prong were used in analyses of sex ratio, reproduction, recruitment, body size and body condition, sexual dimorphism, and comparative morphology between reintroduced and wild animals; those translocated from Dorre Island were excluded. Animals translocated from Dorre Island were used in analyses of movements and longevity.

Location data from radio tracking of bandicoots and trap locations were recorded as latitude/longitude and transferred to the home range software package CALHOME (Kie, Baldwin and Evans 1994). The distribution of all combined bandicoots within the predator refuge was tested for goodness of fit to a Poisson distribution, using chi-squared analyses. An indication of the area of habitat utilised was calculated using the minimum convex polygon method with a 90% confidence interval. Only data for those individuals with more than five locations were used to calculate home ranges.

Longevity was defined as the time period in which an individual bandicoot was known to be alive.

### 3.3 Results

#### 3.3.1 Sex ratio

The number of trap-captured males and females born on Heirisson Prong was close to parity (93:90), with a sex ratio of 1.03 males:1 female. The ratio of male:female bandicoots captured in traps (excluding recaptures of the same individuals) varied from 0.44 in October 1997 to 1.8 in July 1997. Overall, the number of captured males (excluding recaptures of the same individuals; combined free-range and predator refuge populations) was similar to that of females (174:183) during 14 standard three-monthly trapping sessions between October 1996 and October 1999. Data from the remaining 12 trapping sessions were not used due to the small sample sizes. The sex ratio of bandicoots, as determined by trapping within the peak breeding season (May to August), appeared to be a function of the proportion of adult females without pouch young (Figure 3.1; $F_{1,4} = 3.13, P = 0.02$).
The sex ratio recorded for pouch young was skewed towards females, at 1:3 \( (n = 8) \). Few young were sexed in the pouch due to the perceived risk of loss of pouch young.

![Graph showing the relationship between the proportion of females without pouch young and the male:female sex ratio.](image)

**Figure 3.1:** The sex ratio of western barred bandicoots, as determined by trapping within the peak breeding season, as a function of the proportion of females without pouch young, where each point represents the average for a single, independent trapping session. The relationship is described by the equation \( y = -2.51x + 1.75 \), where \( x \) is the proportion of females without pouch young \( (r^2 = 0.44) \).

### 3.3.2 Reproduction

#### 3.3.2.1 Breeding season

Pouch young were recorded in each month of the year except March, September, November and December (Figure 3.2). The only year in which bandicoots were monitored in the month of March was 1998, in September was 1999 and in November was 1997. While no pouch young were present in March \( (n = 7) \), September \( (n = 6) \) or November \( (n = 1) \) in these years, small to large pouch young were present in January and May 1998, and in August and October 1999. There was a peak in the presence of
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pouch young or females with lactating nipples over winter in June and July, similar to
the peak on Bernier and Dorre Islands (Figure 3.3; Short et al. 1998). The proportion of
adult females (≥ 185 g) within the predator refuge carrying pouch young or lactating
each month could be predicted by rainfall in the previous one-month period, while those
within the free-range population could not. The proportion of females carrying pouch
young or lactating each month could not be predicted by rainfall in the previous three-
month period, nor one-month lagged by two months or three-month lagged by two
months periods (Table 3.2).

Table 3.2: The proportion of females carrying pouch young or lactating each month
regressed against rainfall.

<table>
<thead>
<tr>
<th>Rainfall</th>
<th>$F$ value</th>
<th>d.f.</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predator refuge</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Previous 1 month</td>
<td>8.23</td>
<td>1,15</td>
<td>0.01</td>
</tr>
<tr>
<td>Previous 3 months</td>
<td>3.98</td>
<td>1,15</td>
<td>0.06</td>
</tr>
<tr>
<td>Previous 1 month lagged by 2 months</td>
<td>3.27</td>
<td>1,15</td>
<td>0.09</td>
</tr>
<tr>
<td>Previous 3 months lagged by 2 months</td>
<td>0.74</td>
<td>1,15</td>
<td>0.40</td>
</tr>
<tr>
<td>Free-range</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Previous 1 month</td>
<td>1.21</td>
<td>1,11</td>
<td>0.29</td>
</tr>
<tr>
<td>Previous 3 months</td>
<td>0.34</td>
<td>1,11</td>
<td>0.57</td>
</tr>
<tr>
<td>Previous 1 month lagged by 2 months</td>
<td>0.14</td>
<td>1,11</td>
<td>0.72</td>
</tr>
<tr>
<td>Previous 3 months lagged by 2 months</td>
<td>0.30</td>
<td>1,11</td>
<td>0.59</td>
</tr>
</tbody>
</table>

There was some variation in breeding season from year to year (Figure 3.2). The
number of adult females carrying pouch young or lactating in the peak breeding season
between May and October in 1997 was 81.8% ($n = 11$), for the same period in 1998 was
64.4% ($n = 45$) and in 1999 was 64.8% ($n = 81$).
Figure 3.2: Time of breeding of adult females ($\geq 185$ g) in the predator refuge (black) and free-range (grey) on Heirisson Prong. Numbers above bars show sample sizes.

There was a difference in breeding season between animals residing in the predator refuge and those free-ranging on Heirisson Prong in 1998 (Figure 3.2). The onset of breeding in the predator refuge did not occur in 1998 until after the first substantial rain in autumn, following summer drought. However, breeding in the free-range population continued through the summer months, despite high rabbit density and the lack of significant rainfall between October 1997 and April 1998. There was no difference in the condition of bandicoots between the predator refuge and those in the free-range population in January or May 1998 ($F_{1,11} = 0.10, P = 0.76$ and $F_{1,19} = 0.64, P = 0.43$ respectively), despite differences in the commencement of breeding (Figure 3.2) and large differences in trap-revealed population density (Table 3.3) at these times. In 1998 only 2 new recruits were captured within the predator refuge with a peak in density of 0.71 bandicoots/ha, whereas 13 were captured in 1997 and 45 in 1999 at peak densities of 1.38/ha and 2.12/ha respectively. However, between February 1997 and
March 1998, 38 rabbits were removed from the predator refuge prior to the rabbit population crash in May 1998 (Figure 2.1c).

Over the summer of 1998/99 breeding continued in both populations, despite a similar summer drought with no substantial rainfall between September 1998 and February 1999 (Figure 3.2). The proportion of females breeding in the predator refuge and in the free-range population appeared to be similar in 1999, after good rainfall in March that year. Breeding continued in the free-range population past October, despite only 14 mm of rainfall being recorded between August and December 1999. However, breeding had ceased within the predator refuge by September 1999.

**Table 3.3**: Estimated density (number of bandicoots known to be alive/ha) and condition of bandicoots within the predator refuge (17 ha) and the free-range population (1200 ha) at Heirisson Prong in January and May 1998.

<table>
<thead>
<tr>
<th>Date</th>
<th>January 1998</th>
<th>May 1998</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Condition</td>
<td>Density</td>
</tr>
<tr>
<td>Predator refuge</td>
<td>1.11</td>
<td>0.71</td>
</tr>
<tr>
<td>Free-range</td>
<td>1.09</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Figure 3.3: The percentage of adult females (≥ 185 g) with pouch young or lactating nipples at each season of the year. Closed circles are data from the combined predator refuge and free-range populations on Heirisson Prong, and open circles are from Bernier and Dorre Islands (Short et al. 1998). Circles represent means ± SE.

3.3.2.2 Litter size and development

Litter size for adults weighing ≥ 185 g ranged from one to three pouch young, with an average of 1.94 (n = 151). Eighteen percent of females that were reproductively active (n = 112) carried one young or had one enlarged lactating nipple; 64% had either two young or two enlarged lactating nipples, and 18% had three young or three enlarged lactating nipples. Average litter size during each month ranged from 1.0 to 3.0 (Table 3.4). The litter size within the predator refuge (n = 49) was very similar to that of free-range bandicoots (n = 62, F1,109 = 0.10, P = 0.75). In 1999 when bandicoot densities within the predator refuge were high, litter size tended to be lower there (mean = 1.9, n = 28) than within the free-range population (mean = 2.1, n = 38), but the difference was not significant (F1,64 = 1.85, P = 0.18).
Table 3.4: Litter size of adult females ≥ 185 g in the predator refuge and free-range on Heirisson Prong.

<table>
<thead>
<tr>
<th>Date</th>
<th>Adult females</th>
<th>Average litter size</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Predator refuge</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>October 1996</td>
<td>3</td>
<td>1.7</td>
</tr>
<tr>
<td>April/May 1997</td>
<td>4</td>
<td>1.7</td>
</tr>
<tr>
<td>July/August 1997</td>
<td>2</td>
<td>2.0</td>
</tr>
<tr>
<td>October 1997</td>
<td>4</td>
<td>2.0</td>
</tr>
<tr>
<td>July 1998</td>
<td>7</td>
<td>1.5</td>
</tr>
<tr>
<td>October 1998</td>
<td>8</td>
<td>2.3</td>
</tr>
<tr>
<td>February 1999</td>
<td>14</td>
<td>2.0</td>
</tr>
<tr>
<td>June 1999</td>
<td>16</td>
<td>1.9</td>
</tr>
<tr>
<td>August 1999</td>
<td>22</td>
<td>2.0</td>
</tr>
<tr>
<td><strong>Free-range</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>October 1997</td>
<td>1</td>
<td>1.0</td>
</tr>
<tr>
<td>January 1998</td>
<td>3</td>
<td>1.5</td>
</tr>
<tr>
<td>May 1998</td>
<td>16</td>
<td>1.6</td>
</tr>
<tr>
<td>July 1998</td>
<td>6</td>
<td>2.4</td>
</tr>
<tr>
<td>October 1998</td>
<td>2</td>
<td>3.0</td>
</tr>
<tr>
<td>February 1999</td>
<td>12</td>
<td>1.7</td>
</tr>
<tr>
<td>June 1999</td>
<td>9</td>
<td>2.7</td>
</tr>
<tr>
<td>August 1999</td>
<td>11</td>
<td>2.2</td>
</tr>
<tr>
<td>October 1999</td>
<td>17</td>
<td>1.8</td>
</tr>
</tbody>
</table>

The average litter size on Heirisson Prong (n = 151) was not significantly different ($F_{1,184} = 2.46$, $P = 0.12$) to the average litter size of 1.77 (n = 35) recorded on Dorre and Bernier Islands by Short et al. (1998). At least some females were able to produce up to four litters per year (n = 2).

Litter size could be explained by a multiple regression incorporating two variables: average number of rabbits per spotlight kilometre, and rainfall over the previous four-month period in millimetres. The equation $y = 1.952 - 0.092[rabbit\ index] + 0.00368[\text{rain4}]$ explained 79% of the variance of the data, using an $F$ to enter of 4.0. Litter size increased with a decrease in rabbit abundance and an increase in rainfall. A doubling of the rabbit index from 2 to 4 resulted in a shift in litter size from 1.86 to 1.58. There did not appear to be any relationship to season, month, year, or trap success for bandicoots or bettongs.

Few small females with hind foot lengths of ≤ 47.5 mm were captured (n = 5), and there was little indication of any increase in litter size with hind foot length of females. Litter sizes of three were recorded only for females with a hind foot length ≥
48.2 mm at Heirisson Prong, and a single female on Bernier and Dorre Islands with a hind foot length of 50.0 mm (Short and Richards *unpublished data*). There appeared to be no significant difference in litter size over pouch life for those bandicoots where pouch young size was noted \((F_{1, 91} = 0.02, P = 0.88)\), with an average litter size of 2.0, both when pouch young were small and large.

Furred pouch young were found during trapping in February, July, August and October \((n = 12\), which included pouch young of two females translocated from Dorre Island that had produced pouch young sired on Heirisson Prong). One furred litter was still present in the pouch after nine days, suggesting that young may remain in the pouch for well over a week after the development of fur.

The recorded period between successive litters was 61 – 71 days. For example, one female was captured with large furred pouch young, and recaptured 61 days later with large recently furred pouch young at a developmental stage within 5 – 10 days of the first litter. Another female was captured with newborn pouch young and recaptured 70 days later with newborn pouch young, and one other was captured with newborn pouch young and recaptured 73 days later with small pouch young that were up to 5 days old. The young of one litter increased in body length from 20 to 70 mm over a period of 18 days, displaying rapid development in body size in the pouch. One large unfurred pouch young marked in the pouch at approximately 45-50 days of age was recaptured 97 days later weighing 137 g, at an estimated age of 145 days (5 months). One large just-furred pouch young marked in the pouch at approximately 50-55 days of age, was recaptured 196 days later weighing 160 g, at an estimated age of 250 days (8 months). The first recruit into the Heirisson Prong population was captured at 191 g, at an estimated age of 250 - 290 days (8 - 9 months).

### 3.3.2.3 Sexual maturity

The smallest female recorded with pouch young on Heirisson Prong was 185 grams. Three females weighing 176 g, 181 g and 184 g were recorded with two enlarged nipples but were not lactating.

Scrotal width of males ranged from 10.0-29.7 mm \((n = 75)\) and tended to plateau when animals reached a weight of c. 215 g. At body weights \(\geq 215\) g, 93 % of scrotal widths were \(\geq 20\) mm \((n = 70)\). Scrotal width of males was greater during the peak breeding season between May and September \((\text{mean} = 23.7\) mm, \(n = 39)\) than in
October to March (mean = 21.8 mm, \( n = 35; F_{1,72} = 4.73, P = 0.03 \)). There was no significant difference in weight (\( F_{1,72} = 0.59, P = 0.44 \)) or condition (\( F_{1,72} = 0.31, P = 0.58 \)) between these groups. The mean scrotal width in western barred bandicoots was 24.1 mm for adult males \( \geq 215 \text{ g} \) (mean body weight of 237 g). This was not significantly larger than the average of 23.7 mm for adult males \( \geq 215 \text{ g} \) on Dorre Island (\( F_{1,91} = 0.69, P = 0.41 \)).

### 3.3.3 Recruitment

One hundred and seventy-seven bandicoots (91 males, 86 females) were known to have been recruited into the population between November 1995 and October 1999. Sixty-eight of these were born within the predator refuge. The annual number recruited rose from seven in 1996 to 116 in 1999 (Figure 3.4).

![Figure 3.4: Reintroduction and natural recruitment of bandicoots into the combined captive and free-range populations on Heirisson Prong.](image)
The percentage of sub-adults (< 185 g) in the captured population varied between 0% in May 1997, May, July and October 1998, and June 1999, to 67% in August 1997 and February 1998 (Table 3.5), with an average over 21 trapping sessions of 21%. In all, 33% of bandicoots < 185 g that were captured were male (n = 19). The lower number of males compared to females (19:39) was a significant departure from parity ($\chi^2 = 6.90, P < 0.01$). There was no link between the proportion of sub-adults and rainfall over the previous 3- or 6-month periods between the months ($F_{1,19} = 3.52, P = 0.08$) and years sampled ($F_{1,19} = 0.30, P = 0.59$). There did not appear to be a relationship between the transformed proportion of sub-adults and number of bandicoots trapped per 100 trap nights ($y = -1.73x + 0.34; r^2 = 0.04; F_{1,8} = 0.36, P = 0.56$).

Table 3.5: Percentage of sub-adult bandicoots (< 185 g) in the captured population by month and year.

<table>
<thead>
<tr>
<th>Date</th>
<th>Total captured</th>
<th>Sub-adults</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>October 1996</td>
<td>7</td>
<td>3</td>
<td>43</td>
</tr>
<tr>
<td>February 1997</td>
<td>14</td>
<td>4</td>
<td>29</td>
</tr>
<tr>
<td>April 1997</td>
<td>13</td>
<td>4</td>
<td>31</td>
</tr>
<tr>
<td>May 1997</td>
<td>7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>July 1997</td>
<td>15</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>August 1997</td>
<td>3</td>
<td>2</td>
<td>67</td>
</tr>
<tr>
<td>October 1997</td>
<td>13</td>
<td>5</td>
<td>38</td>
</tr>
<tr>
<td>November 1997</td>
<td>6</td>
<td>1</td>
<td>17</td>
</tr>
<tr>
<td>December 1997</td>
<td>10</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>January 1998</td>
<td>23</td>
<td>7</td>
<td>30</td>
</tr>
<tr>
<td>February 1998</td>
<td>3</td>
<td>2</td>
<td>67</td>
</tr>
<tr>
<td>March 1998</td>
<td>14</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>May 1998</td>
<td>24</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>July 1998</td>
<td>23</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>October 1998</td>
<td>15</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>February 1999</td>
<td>53</td>
<td>7</td>
<td>13</td>
</tr>
<tr>
<td>June 1999</td>
<td>50</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>August 1999</td>
<td>60</td>
<td>9</td>
<td>15</td>
</tr>
<tr>
<td>September 1999</td>
<td>14</td>
<td>6</td>
<td>43</td>
</tr>
<tr>
<td>October 1999</td>
<td>47</td>
<td>4</td>
<td>8</td>
</tr>
<tr>
<td>December 1999</td>
<td>10</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>Total</td>
<td>424</td>
<td>58</td>
<td>-</td>
</tr>
</tbody>
</table>
3.3.4 Body size and body condition

Bandicoots caught in traps ranged in size from 94-280 g for males (mean of 219 g, \( n = 190 \)), and 79-394 g (including weight of pouch young) for females (mean of 238 g, \( n = 239 \)). All female bandicoots over 346 g carried pouch young (\( n = 7 \)). Pouch young were not weighed individually due to the difficulty of successfully replacing them in the pouch after their removal. Average bandicoot weight for all captures was 230 g (\( n = 429 \)). All the smaller bandicoots (\( \leq 150 \) g, \( n = 25 \)) were caught independently of their mothers, suggesting that young typically become independent at about 80-100 g. Of these smaller animals, six were male and 19 were female.

Body weight (in grams) was predicted for animals at Heirisson Prong (both sexes combined) from measured hind foot length for each individual using the regression equation:

\[
\text{predicted weight} = \exp [-0.37 + 3.63(\log_{e}\text{hind foot length})]
\]

in which \( r^2 = 0.51 \) (\( F = 604.19, P < 0.001 \)). The condition of each individual was estimated from the ratio of observed weight to predicted weight.

Adult females \( \geq 185 \) g without pouch young were in significantly better condition than adult males (female mean condition index of 1.12, \( n = 96 \); male mean 0.97, \( n = 164 \); \( F_{1,258} = 84.56, P < 0.001 \)) during combined sampling periods.

There was no significant difference in condition of adult bandicoots (both sexes combined) between years of sampling (\( F_{2,256} = 2.27, P = 0.11 \)). There was a significant difference in condition of adult bandicoots between seasons (\( F_{3,255} = 5.22, P = 0.001 \)), with those in summer and spring (mean = 1.06, \( n = 68 \); mean = 1.06, \( n = 57 \) respectively) being in better condition than those in autumn and winter (mean = 1.02, \( n = 42 \); mean = 0.99, \( n = 92 \) respectively). However, there was no relationship between condition and head length, estimated density of capture of bandicoots, season, year, sex ratio, rainfall, bettong or rabbit abundance for bandicoots \( \geq 185 \) g on Heirisson Prong that could be detected by multiple regression.

The regressions of weight on hind foot length for the Heirisson Prong and Dorre Island populations did not differ significantly from each other in slope (\( P = 0.42 \)). There was a significant relationship of \( \log_{e}\text{weight} \) on hind foot length for the combined populations (\( P < 0.001 \)). Females without pouch young were in similar condition on Heirisson Prong (mean = 1.04) and Dorre Island (mean = 1.08; \( F_{1,222} = 2.12, P = 0.15 \)). Males were in significantly poorer condition on Heirisson Prong (mean = 0.96) than on
Dorre Island (mean = 1.01; $F_{1, 356} = 15.78, P < 0.001$). However, this lower condition of males on Heirisson Prong was not obvious from their physical appearance.

The hind foot lengths of males on Heirisson Prong (mean = 49.5 mm) were significantly longer than on Dorre Island (mean = 48.2 mm; $F_{1, 356} = 43.22, P < 0.001$). This difference in male hind foot length may have contributed to the apparent difference in condition between the two populations. In contrast, there was no significant difference in hind foot length between females without pouch young on Heirisson Prong (mean = 48.4 mm) and Dorre Island (mean = 47.8 mm; $F_{1, 222} = 3.57, P = 0.06$).

Tail diameter (a measure of body fat build up in the tail) was a significant predictor of body condition (Figure 3.5; $F_{1, 39} = 15.71, P < 0.001$).

![Figure 3.5](image)

**Figure 3.5:** The relationship between tail diameter and body condition of bandicoots at Heirisson Prong is described by the equation $y = 0.087x + 0.386$ ($r^2 = 0.287$).

Thirty-one males and 22 females of 188 bandicoots born on Heirisson Prong were captured with potential signs of intraspecific aggression, such as tail loss or scarring on the rump, both in the predator refuge and the free-range population. There was no
significant difference in the proportion of males and females that suffered such injuries \( (\chi^2 = 1.63, P = 0.20) \), nor between those animals in the predator refuge and free-range populations \( (\chi^2 = 0.16, P = 0.69) \). There was no apparent difference in the incidence of potential signs of intraspecific aggression between sub-adult \(< 215 \text{ g}\) and larger males \( (\geq 215 \text{ g}; \chi^2 = 0.22, P = 0.64) \).

### 3.3.5 Sexual dimorphism

Adult female bandicoots had significantly shorter hind foot lengths \( (F_{1,355} = 11.78, P < 0.001) \) and adult female bandicoots without pouch young were heavier than their male counterparts (Table 3.6; \( F_{1,272} = 16.63, P < 0.001 \)). The average difference was 1.2% for mean hind foot length and 8.8% for mean weight. Head length and tail length did not differ significantly between males and females respectively (Table 3.6; \( F_{1,287} = 0.02, P = 0.88; F_{1,90} = 0.24, P = 0.63 \)).

### Table 3.6: Differences between sexes of morphometric characteristics of adult \( (\geq 185 \text{ g}) \) bandicoots.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Head length (mm)</th>
<th>Hind Foot length (mm)</th>
<th>Weight (g)</th>
<th>Tail length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>mean ± SE</td>
<td>range</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>69.0 ± 0.3</td>
<td>58.2-79.0</td>
<td>226 ± 2</td>
<td>95.2 ± 1.1</td>
</tr>
<tr>
<td></td>
<td>range</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>mean ± SE</td>
<td>range</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>68.9 ± 0.3</td>
<td>56.2-76.0</td>
<td>239 ± 3</td>
<td>96.0 ± 1.3</td>
</tr>
</tbody>
</table>

### 3.3.6 Comparative morphology between reintroduced and wild animals

Average head length, hind foot length and body weight were compared for adult same-sex bandicoots between Heirisson Prong and the source population on Dorre Island. The head length, hind foot length and body weight of males and the hind foot length of females on Heirisson Prong were significantly greater than on Dorre Island (Table 3.7; males: \( F_{1,212} = 24.81, P < 0.001 \); \( F_{1,277} = 61.94, P < 0.001 \); \( F_{1,278} = 11.03, P = 0.001 \) and females: \( F_{1,246} = 10.75, P = 0.001 \) respectively). However, there was no
significant difference in the head length and body weight of females between the reintroduced and island populations (Table 3.6; $F_{1,179} = 2.70, P = 0.10; F_{1,259} = 2.67, P = 0.10$ respectively).

### Table 3.7: Differences in morphometric characteristics of adult ($\geq 185$ g) western barred bandicoots between the reintroduced Heirisson Prong and wild Dorre Island populations.

<table>
<thead>
<tr>
<th>Location</th>
<th>Sex</th>
<th>Head length (mm)</th>
<th>Hind Foot length (mm)</th>
<th>Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>mean ± SE</td>
<td>range</td>
<td></td>
</tr>
<tr>
<td>Heirisson Prong</td>
<td>Male</td>
<td>69.0 ± 0.3</td>
<td>58.2-79.0</td>
<td>226 ± 2</td>
</tr>
<tr>
<td></td>
<td>range</td>
<td>69.0 ± 0.3</td>
<td>58.2-79.0</td>
<td>226 ± 2</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>69.0 ± 0.3</td>
<td>58.2-79.0</td>
<td>226 ± 2</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>68.9 ± 0.3</td>
<td>56.2-76.0</td>
<td>239 ± 3</td>
</tr>
<tr>
<td></td>
<td>range</td>
<td>68.9 ± 0.3</td>
<td>56.2-76.0</td>
<td>239 ± 3</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>68.9 ± 0.3</td>
<td>56.2-76.0</td>
<td>239 ± 3</td>
</tr>
<tr>
<td>Dorre Island</td>
<td>Male</td>
<td>66.5 ± 0.3</td>
<td>59.6-73.1</td>
<td>218 ± 2</td>
</tr>
<tr>
<td></td>
<td>range</td>
<td>66.5 ± 0.3</td>
<td>59.6-73.1</td>
<td>218 ± 2</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>66.5 ± 0.3</td>
<td>59.6-73.1</td>
<td>218 ± 2</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>67.8 ± 0.5</td>
<td>61.6-78.8</td>
<td>247 ± 4</td>
</tr>
<tr>
<td></td>
<td>range</td>
<td>67.8 ± 0.5</td>
<td>61.6-78.8</td>
<td>247 ± 4</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>67.8 ± 0.5</td>
<td>61.6-78.8</td>
<td>247 ± 4</td>
</tr>
</tbody>
</table>

#### 3.3.7 Group size

Bandicoots recorded during spotlighting by vehicle in the free-range population ($n = 21$) and on foot in the predator refuge ($n = 6$) were sighted alone. Radio collared bandicoots were found alone when radio tracked to diurnal nest sites (Section 4.3.3).

#### 3.3.8 Movements and habitat use

Recaptures of bandicoots within and between monitoring trips were examined to establish the scale of movement by bandicoots. Initial movements of bandicoots in the first two weeks after release to free-range are covered in Section 2.3.3. These movements were excluded in this section as these animals were assumed to be in the process of establishing home ranges and may have had artificially long movements.

Recaptures ($n = 40$) varied between 0 m (i.e. recaught at the same trap) and 6050 m over the duration of the study. Median distance of maximum movement (greatest
distance between any two locations recorded for an individual) between capture or radio tracking locations (diurnal nest sites) was 1020 m for males \((n = 24, \text{ mean } = 1370 \text{ m})\) and 485 m for females \((n = 16, \text{ mean } = 470 \text{ m})\). The difference in mean movements between sexes was significant \((F_{1,38} = 5.98, P = 0.02)\). Fifty-eight percent of bandicoots moved distances greater than 500 m and 32 % moved distances greater than 1000 m. Median distances moved by bandicoots over a period up to 28 months equated to areas of 82 ha for males and 18 ha for females if these distances are taken to be the diameter of a home range, and a circular home range is assumed. The maximum distances moved between capture or radio tracking locations were 6050 m over eight months for a male and 1060 m over 13 months for a female.

Within the predator refuge prior to the release of bandicoots to free-range in May 1997, individual captures at each of the 49 trap locations varied from 0 to 4 bandicoots. Two or more bandicoots were captured at 53.1% percent of trap locations, compared to 28.6 % with a single bandicoot and 18.4 % that caught no bandicoots. Bandicoots were distributed randomly throughout the predator refuge \(\chi^2_5 = 1.24, P = 0.94\), with no difference in dispersion to a Poisson distribution. Up to four different males were captured at one trap location, three males and one female at six other trap locations, and two males and two females at another. There were eight instances of different females being captured at the same trap location, 13 trap sites where different males were captured, and both a male and female were caught at the same trap at 18 sites. Both males and females were distributed randomly throughout the predator refuge \(\chi^2_4 = 3.29, P = 0.51; \chi^2_3 = 0.73, P = 0.87\) respectively), showing no difference in dispersion to a Poisson distribution.

Habitat usage determined by trapping or radio tracking within the predator refuge varied from 0.7 ha to 5.6 ha for males \((n = 7; \text{ Figure 3.6})\) and 0.2 ha to 0.9 ha for females \((n = 6; \text{ Figure 3.7})\) prior to the release of bandicoots to free-range on Heirisson Prong. Areas are calculated as minimum convex polygons with a 90% confidence interval. The average ± SE area of habitat used by these males was 2.4 ± 0.7 ha, and by females was 0.6 ± 0.1 ha.

For those free-range animals radio-collared and located for periods of up to eight days, to diurnal nest sites or trap locations, habitat usage ranged from 2.8 - 99.3 ha for
males and 3.1 - 10.1 ha for females. Males utilised a significantly greater area with an average of 36.6 ha ($n = 6$) and females averaged 6.6 ha ($n = 8$; $F_{1,12} = 5.46$, $P = 0.04$).

**Figure 3.6:** Male home ranges within the nine hectare predator refuge (A1 to F9 form a grid of trapping locations 50 metres apart) between July 1996 and May 1997 prior to the release of bandicoots to free-range on Heirisson Prong. Note the high degree of overlap in home range area.

**Figure 3.7:** Female home ranges within the 9 ha predator refuge between July 1996 and May 1997 prior to the release to free-range. Note the low degree of overlap.
Bandicoots were trapped throughout Heirisson Prong (Figure 3.8) and therefore in a range of habitat types. They tended to be more common in areas immediately surrounding and to the south of the predator refuge (Valleys 4 and 7; Figure 3.9), in areas dominated by *Acacia tetragonophylla*, *A. ligulata*, *Melaleuca cardiophylla*, *Thryptomene baeckeacea*, and *Atriplex bunburyana*, and interspersed with considerable areas of open ground.

![Graph showing number of bandicoot captures in each valley on Heirisson Prong](image)

**Figure 3.8:** Number of bandicoot captures in each valley on Heirisson Prong, from ‘1’ in the south to ‘13’ in the north (Figure 3.9) between 1997 and 1999.

### 3.3.9 Longevity

The oldest surviving female bandicoot born on Heirisson Prong was at least four years and three months of age. She was still carrying pouch young at her last capture. The oldest male was at least 2 years and 10 months of age. Mean ± SE minimum longevity for females (10.9 ± 1.8 months) was not significantly different to that of males (7.2 ± 1.2 months; $F_{1,82} = 2.93$, $P = 0.09$). These are likely to be underestimates of their longevity due to the absence of detailed information on the age at which bandicoots entered the population, and their fate when they disappeared.
Figure 3.9: Valley numbering system on Heirisson Prong, showing system of roads and sand dune ridges.
3.4 Discussion

3.4.1 Sex ratio

The sex ratio of western barred bandicoots captured at Heirisson Prong was close to parity. However, as for the island populations (Short et al. 1998), the proportion of females without pouch young appeared to be associated with the capture rate of males. Trapping results from the Bernier and Dorre Island surveys suggested a predominance of males over females, however this deviation from parity was thought to have been an artifact of the greater mobility (and therefore trappability) of males at times when the number of females likely to be sexually receptive (at or approaching oestrous) was highest (Short et al. 1998). More males were trapped at Heirisson Prong during the peak breeding season, suggesting a similar relationship.

The sex ratio of captured eastern barred bandicoots in Tasmania and Victoria varied from being close to parity (Brown 1989: 53.3%; Heinsohn 1966: 50.6% male) to predominantly male (Dufty 1991: 68%; Dufty 1994c: 62.1%; Minta, Clark and Goldstraw 1990: 61.9%). A similar variety of results has been recorded for the long-nosed bandicoot *P. nasuta* in the Sydney Harbour National Park (Scott et al. 1999: 54.2%), the southern brown bandicoot in Tasmania (Heinsohn 1966: 58.3%; Mallick, Driessen and Hocking 1998: 44.7%), and the northern brown bandicoot in the Northern Territory (G. Friend 1990: 60%) and northern Western Australia (Kemper, Kitchener, Humphreys, How, Schmitt and Bradley 1990: 66%). Dufty (1994b; 1994c) and Gordon (1974) thought that a male bias in capture results may have been due to high mortality of juvenile and sub-adult females, mediated by older males usurping high quality nest sites and forcing sub-adult males and females into sub-optimal habitat. At Heirisson Prong, due to the low density of bandicoots and plentiful availability of habitat, it is unlikely that such intraspecific interactions had any impact on the sex ratio of trapped animals. Alternatively, males may simply be more trappable than females, perhaps due to their larger home range size (Dufty 1991; Dufty 1994b, Friend & Burbidge 1995).

The sex ratio of pouch young on Heirisson Prong appeared to be female biased (though \( n = 8 \)) but at Bernier and Dorre Islands was slightly male biased (54.5%). Studies of eastern barred bandicoots have found pouch sex ratios close to parity (Brown 1989: 50.0%; Dufty 1991: 45%; Heinsohn 1966: 46.0% male) or with a significant predominance of females (Dufty 1994c: 42.9%). Female-biased sex ratios of pouch young have also been recorded for the southern brown bandicoot on the Nuyts
Archipelago (Copley, Read, Robinson and Watts 1990: 41.7% male) and a male biased sex ratio was recorded for the northern brown bandicoot (Kemper et al. 1990: 55.6%). The sample size from Heirisson Prong is too small to provide strong confidence in the results. Unfortunately, the perceived risk of loss of pouch young during sexing may have been exaggerated at the time in the field, as no problems were encountered during the sexing of the few litters at Heirisson Prong. With careful inspection, there should be little risk to pouch young.

3.4.2 Reproduction

3.4.2.1 Breeding season

Pouch young were present in all months of the year, except March, September, November and December. Sample sizes of captured females were small. It is likely that a few pouch young were present in the population in March and September, as they were present in the months before and after. There was a peak in breeding in the winter months, similar to that on Bernier and Dorre Islands (Short et al. 1998).

Breeding in bandicoots often occurs throughout the year with seasonal peaks during the wetter months (Brown 1989; Copley et al. 1990; Dufty 1994c; G. Friend 1990; Gemmell 1990; Gordon 1974; Heinsohn 1966; Kingston 1994; Seebeck 1979; Stodart 1977; Thomas 1990). For example, the number of female eastern barred bandicoots recorded lactating was greatest in spring in Victoria, with 91% lactating in August/September and only 47% in June/July (Dufty 1991). More definite breeding seasons have been recorded for the western barred bandicoot in South Australia (Jones 1924: May and June), and on Bernier and Dorre Islands (Friend and Burbidge 1995: April to November; Short et al. 1998: March to November) but this is likely to be due to limited sampling periods. The breeding season at Heirisson Prong may have been extended due to three years of good rainfall, a plentiful food supply, and lack of intraspecific competition due to the low densities of free-range bandicoots.

There was little indication of an impact of rainfall on the breeding season at Heirisson Prong. Breeding within the free-range population occurred throughout the year in two of three years. Breeding in the predator refuge tended to be more seasonal, with a period of seasonal anoestrus over the summer months in three of four years. The years in which the onset of breeding occurred later followed years of both below and above average rainfall. The year in which breeding continued throughout the summer
was not notably different, suggesting little influence of rainfall on breeding within the predator refuge. It is possible that the higher density of bandicoots, combined with high rabbit density within the predator refuge and low rainfall depressed the incidence of continued breeding throughout the year in 1998. Reasons for this difference in breeding between the free-range population and those animals residing in the predator refuge were investigated by Visser (2000). There was no relationship between invertebrate prey availability, bandicoot density and breeding during 1999, even with densities of up to 2.12 bandicoots per hectare that year. However, it is still possible that the greater densities of up to 1.4 bandicoots per hectare within the predator refuge in 1997 may have suppressed breeding that year, resulting in lower recruitment over the following months. In addition, an increase in the sighting of tawny frogmouths *Podargus strigoides* on Heirisson Prong in 1998 may have resulted in predation of juveniles (Section 6.5.1, Mortality). Combined with a cessation in breeding over the summer due to low rainfall and high rabbit density, these may have been reasons for the low number of new recruits captured in 1998. Western barred bandicoots are thought to occur in the wild at densities of about 0.45 per hectare (Short *et al.* 1997a). Eastern barred bandicoots are typically found in the wild at densities of 1-1.5 bandicoots per hectare in Hamilton, Victoria (Minta *et al.* 1990) and 0.35-2.35 per hectare in south-eastern Tasmania (Mallick *et al.* 2000). However, food supply in more mesic habitats is likely to be more abundant and reliable than that typically available to western barred bandicoots in the semi-arid and arid zone.

### 3.4.2.2 Litter size and development

The mean litter size for the western barred bandicoot at Heirisson Prong was 1.9 with a range of one to three; usually two. This was similar to that recorded by Short *et al.* (1998) on Bernier and Dorre Islands. Up to four pouch young per litter have been recorded for mainland forms (Gould 1863; Krefft 1866), however no litters of four were found at Heirisson Prong or on Bernier and Dorre Islands (Short *et al.* 1998). Such large litters are probably a very rare occurrence, if they occur at all. It is possible that Gould (1863) and Krefft (1866) may not have been referring to the same species of bandicoot. At least some females were able to produce up to four litters per year, however 2-3 litters per year were more common.
Western barred bandicoots have eight teats arranged in a circle, contrary to comments that the island form has only four (Ride and Tyndale-Biscoe 1962). The presence of eight teats implies the use of the “alternate nipple strategy” (Heinsohn 1966) to maximise the output of young by allowing for the rapid succession of litters during the breeding season (Stodart 1977).

The number of pouch young recorded for bandicoots varies between species. Eastern barred bandicoots produce litters of 1-5 but usually two or three (Brown 1989; Dufty 1991; Dufty 1994c; Kingston 1994; Seebeck 1979; Stodart 1977). For the long-nosed bandicoot litter size ranges also between 1-5 and is usually 2-3 (Lyne 1982), the southern brown bandicoot between 1-7 with 3-4 common (Copley et al. 1990; Lobert and Lee 1990; Stoddart and Braithwaite 1979; Thomas 1990), the northern brown bandicoot between 1-7 and usually 3-4 (G. Friend 1990; Gemmell 1982; Gordon 1974; Lyne 1982), and the golden bandicoot may have 1-4 pouch young (Short and Turner 1994). Western barred bandicoots therefore produce fewer young per litter than other species of bandicoots.

Average litter size did not vary with population density (between the predator refuge and free-range populations), during the breeding season, or with the size of the mother at Heirisson Prong, whereas on Bernier and Dorre Island there was a peak in litter size in July/August and litter size increased with the size of the mother (Short et al. 1998). There was no indication of a significant difference in litter size over pouch life in the reintroduced population, or in the island populations (Short et al. 1998), suggesting no shortage in the abundance of food during the breeding season. Litter size did appear to increase with a decrease in rabbit abundance and an increase in rainfall on Heirisson Prong, suggesting both the possibility of some detrimental impact of high densities of rabbits, and a beneficial impact of rainfall with food abundance, on bandicoot reproduction.

Litter size in eastern barred bandicoots was greatest in spring (Dufty 1991) and the first and last litters of the season for the southern brown bandicoot in Tasmania were the smallest (Heinsohn 1966). In the Nuyts Archipelago southern brown bandicoots bred all year but produced litter sizes of 2.4 during their peak of breeding in spring, decreasing to 1.6 in summer (Copley et al. 1990), and in Victoria litter size increased as the breeding season progressed (Stoddart and Braithwaite 1979).
A positive relationship between female body weight and litter size was noted in the eastern barred bandicoot (Seebeck 1979), suggesting that larger females produce more young. However, Dufty (1991) found no significant correlation between litter size and head length, or litter size and body weight for the same species. Litter size was correlated with female body weight in the southern brown bandicoot (Stoddart and Braithwaite 1979) and the northern brown bandicoot (Hall 1983), however Lobert and Lee (1990) found no such relationship in southern brown bandicoots in Tasmania and Victoria.

Attrition of pouch young during pouch life occurs in the northern brown bandicoot with litter size declining from 3.6 early in lactation to 2.1 after day 40 of lactation (Gemmell 1982), and in the golden bandicoot litter sizes may decline from four young at birth with only one or two surviving to independence (Short and Turner 1994). There was no indication that litter size changed throughout the breeding season of southern brown bandicoots (Lobert and Lee 1990). Western barred bandicoots may be quite successful at maintaining young through lactation. This may be related to their smaller litter size generally, and the low density of the reintroduced population.

Western barred bandicoots were able to produce up to four litters per year, with a period between subsequent litters of 61 – 71 days. Pouch young are carried for up to 60 days, emerge from the nest a few days later and reach independence at 62 - 73 days in other species of *Perameles* (Brown 1989; Dufty 1995; Heinsohn 1966; Kingston 1994; Stodart 1966, 1977). This relatively rapid growth and development of pouch young is a common feature of bandicoots when compared with other similarly-sized marsupials (Cockburn 1990). Furred young were found in the pouch at Heirisson Prong. This means that females carry their young to an advanced stage, rather than leaving them in the nest once furred, as suggested by Short *et al.* (1998).

### 3.4.2.3 Sexual maturity

The smallest female carrying pouch young weighed 185 g (78% of the average adult female weight); an age of c. 7-9 months. It is possible that females as small as 176 g had bred, due to the presence of enlarged nipples in females of this size. Western barred bandicoots on Bernier and Dorre Islands reached sexual maturity at a similar stage, at 175 g (Short *et al.* 1998). Female eastern barred bandicoots reach sexual maturity at around 3-3.5 months (Dufty 1994c; 1995), southern brown bandicoot
females are estimated to breed at 4-5 months (Heinsohn 1966) and seven months in the season following their birth (Lobert and Lee 1990), northern brown bandicoots breed as young as 4 months (Lyne 1982; Mackerras and Smith 1960), and breeding in the long-nosed bandicoot has been recorded at 500 g (Lyne 1982) and four months of age (Ride 1970). Female bandicoots may therefore breed in their first year. Female western barred bandicoots appear to take longer to reach sexual maturity than other species of bandicoot.

Sexual maturity in male western barred bandicoots on Heirisson Prong may occur slightly later than in females and for island males (195 g; Short et al. 1998) at c. 215 g (98% of the average adult male weight) and a testes width of 20 mm. Scrotal width of males was greater during the peak breeding season between May and September. Both reintroduced and island males were not likely to breed in the same year of their birth. Island males appeared to mature at a lower body weight, however they are smaller on average than males at Heirisson Prong (Section 3.3.4), so may in fact reach sexual maturity at a similar age.

Male bandicoots generally mature later than females. Male eastern barred bandicoots are sexually mature at 3-6 months when they reach adult size (Dufty 1994c; Dufty 1995; Heinsohn 1966), male southern brown bandicoots mature at a minimum of six months (Heinsohn 1966), northern brown bandicoots have been recorded to sire their first litters at 11.5 months (Gemmell 1987) and long-nosed bandicoots become sexually mature at five months (Ride 1970). No seasonal variation in scrotal size was noted in eastern barred bandicoots in Tasmania (Heinsohn 1966), however scrotal length in southern brown bandicoots peaked in the middle of the breeding season (Lobert and Lee 1990), and in northern brown bandicoots scrotal size peaked just after the beginning of the female breeding season in September (Kemper et al. 1990).

Testes size in the western barred bandicoot appears to be quite large relative to body size when compared with other species of bandicoot. For example, the mean scrotal width in the western barred bandicoot is about the same as for the northern brown bandicoot (24.1 mm cf. 25.4 mm), despite adult male western barred bandicoots being one seventh the body weight of adult male northern brown bandicoots (219 g cf. 1585 g; Gemmell 1987). Large testes size is typically associated with multi-male breeding systems (promiscuous or polygynous) where several different males mate with each female at the same oestrous (Harcourt, Harvey, Larson and Short 1981; Kenagy
and Trombulak 1986). Large testes allow for frequent copulation and high sperm production, which is necessary when there is competition amongst sperm from different males to fertilise the same female. Frequent copulation (> 13 times) by a single male over a two-hour period has been observed in captive long-nosed bandicoots (Stodart 1966).

### 3.4.3 Recruitment

Recruitment increased over time at Heirisson Prong, contributing strongly to the establishment of the reintroduced population. The percentage of sub-adult western barred bandicoots on Heirisson Prong varied between 0 and 67% (average 21%) of captures for any given trapping session and was 67% female biased. No seasonal or annual patterns associated with rainfall were evident, and there was no relationship between the proportion of sub-adults captured and trap success. On Bernier and Dorre Islands there appears to be a high juvenile mortality rate, either during pouch life or after independence, and this is reflected in a lower proportion of sub-adults in the captured population (Short et al. 1998).

In general, high survival rates have been noted for bandicoot pouch young (Dufty 1994c: 92% and Heinsohn 1966: 61% eastern barred bandicoot; Hall 1990: 77% northern brown bandicoot; Copley et al. 1990: 78% southern brown bandicoot). Heinsohn (1966) suggested that pouch mortality is due to overcrowding, particularly in the later stages of pouch life.

Low survival rates of young after emerging from the pouch have been noted in the eastern barred bandicoot. Dufty (1994c) recorded 73% survival for young-at-foot but suggested a 10% survival rate of pouch young to sub-adulthood (Dufty 1991). Similar patterns for survival to adulthood are recorded in southern brown bandicoots (Stoddart and Braithwaite 1979: predicted 11.9-17.5% recruitment of all pouch young produced) and northern brown bandicoots (Gordon 1974: 11.5% of young surviving pouch life known to reach maturity within the study area). Causes of mortality include road kills, predation, lack of food and shelter, disease or infection. Mortality of western barred bandicoots prior to reaching adulthood on Heirisson Prong and Dorre Island may have been due to predation by snakes, goannas, birds of prey, owls, and feral cats that entered the core conservation zone despite control methods), and possibly disease or infection, though there was no evidence of either.
### 3.4.4 Body size and body condition

The western barred bandicoot is the smallest of the *Perameles* species (Seebeck *et al.* 1990), with an average weight of 230 g on Heirisson Prong and a range as adults of 185-394 g, inclusive of pouch young. The species is slightly smaller on Dorre and Bernier Islands with an average weight of 219 g and a range as adults of 175-374 g, inclusive of pouch young (Short *et al.* 1998). Young appear to become independent of their mothers at 80 - 100 g. Fewer newly independent male young were captured than females. Males may therefore have a higher mortality rate at this stage of development than females, or alternatively may reach independence slightly later than females.

Females without pouch young were larger and appeared to be in better condition than males at Heirisson Prong, which is similar to Dorre and Bernier Island animals (Short *et al.* 1998). Males were in significantly poorer condition on Heirisson Prong than Dorre Island, however the condition of females was similar between locations. The difference in male condition may have been an artifact of the longer hind foot length of males on Heirisson Prong, as any difference in condition was not obvious from their physical appearance.

The condition of bandicoots on Heirisson Prong varied between seasons, but not between years or with rainfall. Bandicoots appeared to be in better condition in spring and summer, compared with those in autumn and winter, perhaps due to the greater abundance of their invertebrate food supply in the warmer months. Despite higher densities of rabbits in 1997, particularly at the end of the year (Figure 2.1c), condition did not appear to vary with rabbit abundance.

Body condition of eastern barred bandicoots did not alter with season or sex, and body condition and weight of lactating females did not change with age of the pouch young (Reimer and Hindell 1996). Female northern brown bandicoots with pouch young were significantly heavier than those without and their body condition changed with season, being heaviest in September, while male condition did not change with season (Hall 1983).

Tail diameter was a significant predictor of body condition of western barred bandicoots at Heirisson Prong. Gordon and Hall (1994) found that tail fat storage occurred in species of *Perameles* from arid and semi-arid areas, but did not appear to occur in mesic areas. Morton (1980) found that tail fat storage occurred in small
insectivores with an undependable short-term food supply. The western barred bandicoot appears to be sensitive to drought on Bernier and Dorre Islands (Short et al. 1997a), however it may be buffered from food shortages due to its omnivorous diet, and ability to consume a variety of seeds, plant matter and soil invertebrates, even when surface-dwelling insects are scarce. Gordon and Hall (1994) suggested that tail fat storage is due to the small body size of bandicoots in arid areas, and Morton (1980) proposed that smaller animals may store fat in the “only organ that can be increased in size without changing the bulk of the body, i.e. the tail”.

Both male and female western barred bandicoots suffered signs of intraspecific aggression, within the predator refuge and free-range, including scars and fur loss on the rump, and tail loss. The injuries are unlikely to be associated with the use of cage traps in the free-range population, and while there were a few instances of injuries due to the use of Elliott traps, these were generally restricted to the predator refuge and were recorded as trapping injuries. Two males captured on Bernier and Dorre Islands had no tail (Short and Richards unpublished data), suggesting that similar interactions may occur in the wild. No other signs of intraspecific aggression were noted, however many injuries heal quickly and may have been overlooked.

Male eastern barred bandicoots occasionally chase and attack other males, however scarring or injury is rare, unless within confined, reintroduced populations with a strong male bias (Dufty 1994a; Heinsohn 1966; Seebeck 2001). Fighting amongst unconfined southern brown bandicoots at the Harry Waring Marsupial Reserve south of Perth in Western Australia resulted in temporary fur loss, and the area of fur lost tended to be larger among males than females (Thomas 1990).

3.4.5 Sexual dimorphism

Adult female western barred bandicoots on Heirisson Prong had shorter hind foot lengths and were heavier than their male counterparts. There was no significant difference in head length and tail length between the sexes. On Dorre and Bernier Islands females had slightly longer heads and were also heavier than males, but there was no difference in hind foot length between the sexes. Gould (1863) speculated that adult male western barred bandicoots on the mainland were larger than females, however the scant results of Jones (1924) suggested that females were larger.
Heinsohn (1966) found that male and female eastern barred bandicoots in Tasmania were almost identical in length measurements; however, males on average weighed 9% more than females. However, Mallick et al. (2000) found that males had a greater body weight and hind foot length than females. Dufty (1991) found that males in Victoria had significantly larger hind foot lengths than females but no other size or colour dimorphism was observed. He later observed significantly larger hind foot and head lengths for adult males but body weight, ear and tail length were similar between the sexes (Dufty 1994c). George, Dixon, Challis and Lacy (1990) found significantly larger hind foot lengths for adult males from Tasmania and Victoria, but no other body measurements were significantly different. Reimer and Hindell (1996) found that male eastern barred bandicoots were significantly heavier than females.

Southern brown bandicoot males also tend to be larger than females (Copley et al. 1990: 50-100 g larger; Heinsohn 1966: males 19% heavier; Stoddart and Braithwaite 1979: 30%) and similar relationships occur in long-nosed bandicoots (Lyne 1982) and northern brown bandicoots (Hall 1983; Lyne 1982). Hall (1983) and Reimer and Hindell (1996) excluded pouch young from female body weights but it is unknown whether pouch young weight was excluded from the remainder of the references quoted. Whether they are removed or not, in these other species of bandicoots, males all tend to be larger than females. It is unusual that the reverse is true for western barred bandicoots, both in the reintroduced population and on the islands.

The Nuyts Island subspecies of southern brown bandicoot is smaller than the mainland form (Jones 1924) and while the island males are still larger than females, the difference between the body size of the sexes is less marked than in the mainland form (Copley et al. 1990; Lobert and Lee 1990). Dwarfism of island stock (Williamson 1981) may be playing a role in these differences in body size of the Nuyts Island southern brown bandicoot Isoodon obesulus nauticus and the western barred bandicoot on Dorre and Bernier Islands.

A tendency towards dwarfism of island stock in the western barred bandicoot may be constrained in females by the physiological demands of lactation and by the need to physically carry a large litter of pouch young. Additionally, equal or larger body size in females relative to males may assist females in defending nest sites from males (Jarman 1983). Male western barred bandicoots are known to inhabit the nests of females (Section 4.3.2).
3.4.6 **Comparative morphology between reintroduced and wild populations**

Male bandicoots were larger on Heirisson Prong than those on Dorre Island, whereas females had longer hind foot lengths on Heirisson Prong, but were similar in head length and body weight. A decrease in competition for food, shelter and females on Heirisson Prong, may have played some role in this increase in size of males.

3.4.7 **Group size**

Spotlighting results on both Heirisson Prong and Bernier and Dorre Islands (Short *et al*. 1998) indicate that western barred bandicoots are solitary animals, generally foraging as individuals. This is in agreement with observations for other species of *Perameles* and *Isoodon* in Australia (Gordon 1974; Heinsohn 1966; Stodart 1966). Gould (1863) reported nest sharing in the western barred bandicoot, however Friend and Burbidge (1995) reported that the only nest sharing observed in western barred bandicoots on Dorre Island was between females and their young. Diurnal nest sharing between females or a female and a male has been noted in the long-nosed bandicoot in captivity (Stodart 1966).

Eastern barred bandicoots are generally solitary and non-gregarious. Mutual avoidance behaviour predominates within and between both sexes, although some antagonistic interactions have been observed. These occur mostly between males but scars occur on both sexes (Dufty 1994a) as they actively defend foraging patches (Dufty 1991) or fight during mating (J. Seebeck *pers. comm.*).

3.4.8 **Movements and habitat use**

The area of habitat utilized by free-range bandicoots on Heirisson Prong averaged 37 hectares for males, and seven hectares for females. Friend and Burbidge (1995) reported home range sizes for male western barred bandicoots on Dorre Island varying between 2.5 and 14.2 ha at high and low densities and for females between 1.4 and 6.2 ha, respectively. Short *et al*. (1998) estimated a minimum home range size on the islands of 2.0 hectares for males and 1.6 hectares for females, however their limited trapping period is likely to have underestimated home range size to a substantial degree.

The median greatest movements between trapping locations of bandicoots on Heirisson Prong were 1020 metres for males and 485 metres for females. Most
recorded movements by western barred bandicoots on Dorre and Bernier Islands were less than 400 m, however males did move up to 1020 m and females up to 490 m over a two day period. The smaller size and distribution of the island trapping grids are likely to have restricted the identification of longer range movements of bandicoots.

Home range of bandicoots has been widely studied for species of both *Perameles* and *Isoodon*. Males tend to have larger home ranges than females (Dufty 1991: mean male eastern barred bandicoot 12.9 ha, females 2.4 ha; and Dufty 1994b: male eastern barred bandicoot 0.8 - 9.0 ha, females 0.02 - 5.9 ha; Broughton and Dickman 1991: mean male southern brown bandicoot 2.3 ha, females 1.8 ha; Copley *et al.* 1990: male southern brown bandicoot 2.1 - 2.2 ha, females 1.5 - 1.6 ha; Gordon 1974: male northern brown bandicoot 1.7 - 5.2 ha, females 0.9 - 5.2 ha; Heinsohn 1966: male eastern barred bandicoot up to 40 ha, females 1.0 - 11.3 ha, male southern brown bandicoot 4.1 - 6.5 ha, female 2.3 ha; Southgate *et al.* 1996: male golden bandicoots on Marchinbar Island 4.4 – 35.6 ha, females 1.7 – 12.7 ha).

Dufty (1991) recorded young male eastern barred bandicoots moving up to 2.3 km while no female moved more than 150 m between trapping locations. Maximum observed range lengths were 430 m for males (mean 249 m) and 364 m for females (mean 173 m), but males did move up to 1.15 km (Dufty 1994b). G. Friend (1990) found maximum distances between captures for male northern brown bandicoots of 565 m (mean 64 m) and 402 m (mean 61 m) for females.

Male western barred bandicoots within the predator refuge shared much of the available habitat, whereas females tended to show a far lower degree of overlap. The mean overlap for combined sexes of eastern barred bandicoots in Victoria was 6.9% (Dufty 1991), and greater overlap occurred between male home ranges than between female home ranges (Dufty 1994b). In Tasmania, the overlap between male home ranges was 4.4% and between females 15.8% (Mallick *et al.* 2000). Northern brown bandicoots in Brisbane overlap home ranges from 30 - 100% but also have discrete core areas (Gordon 1974). Heinsohn (1966) recorded overlapping home ranges for eastern barred bandicoots but thought that overlap in southern brown bandicoots was limited, whereas Lobert (1990) noted high degrees of overlap within and between sexes for the same species. Golden bandicoots on Marchinbar Island in the Northern Territory maintained home ranges of 10 - 35 ha which overlapped within and between sexes (Southgate *et al.* 1996).
Results from Heirisson Prong suggest that bandicoots are capable of long distance movements, and are likely to have much larger home ranges than previously suggested, at least at low densities. They display greater movement compared to other species of bandicoot that occur in the more mesic areas of Australia. The need for larger home ranges may therefore be a function of life in drier environments, where food resources are less, requiring animals to forage over a wider area. The large home ranges and degree of overlap of males relative to females is likely to reflect intense sperm competition amongst males and hence a polygynous or promiscuous reproductive strategy (Lee and Cockburn 1985).

Bandicoots were trapped throughout Heirisson Prong, but occurred at greater densities in areas where dense Acacia, Atriplex, Melaleuca and Thryptomene shrubs were present, interspersed with considerable areas of open ground. These areas were adjacent to the southern release site and the predator refuge, so it is possible that there was some tendency to remain in areas already occupied by bandicoots. On Dorre and Bernier Islands bandicoots were trapped and spotlighted in all habitats; however, they were least likely to be found in tall scrub (Short et al. 1998). Ride and Tyndale-Biscoe (1962) reported that they were commonly found in the sandhills on the islands while Friend and Burbidge (1995) reported that they are common in the scrub associated with stabilised dunes behind the beaches, but also occur in open steppe associations. Gould (1863) noted that the western barred bandicoot in south-west Western Australia favoured dense scrub, while in South Australia and New South Wales it was found amongst stony ranges and reported by Governor Grey as occurring on “vast open plains”.

Eastern barred bandicoots in Tasmania favour high-quality agricultural land with deep soils and areas with high rainfall (Driessen et al. 1996). Foraging areas in Hamilton, Victoria have few native grasses, high ground cover, tall plants and acid soils of low to medium compaction (Dufty 1991). In both Tasmania and Victoria, they use open areas for foraging (Minta et al. 1990) and more sheltered sites nearby for nesting (Dufty 1991; Heinsohn 1966; Seebeck 1979). Dufty (1994b) and Dufty, Seebeck, McKay and Watson (1994) found that bandicoots favoured structurally complex habitat and have survived in human-modified habitats such as the Hamilton rubbish tip and pastoral land, that provide added habitat complexity. They have been reported as
inhabiting rabbit burrows in Tasmania, which is thought to have aided in their survival in regions highly modified by agriculture (Brown 1989).

The long-nosed bandicoot also lives in areas of more open grassland and scrub (Stodart 1977) and prefers open forests, woodlands and heathlands associated with moist soils (Opie, Gullan and Mansergh 1990). Southern brown bandicoots use more sheltered, less open areas in heath and scrub, tending to avoid paddocks (Heinsohn 1966), and preferring the denser vegetation of coastal lowland areas, sclerophyllous woodland, forest and heath (Opie et al. 1990).

It is likely that western barred bandicoots were found originally in a wide range of habitats throughout the drier, semi-arid areas (Friend and Burbidge 1995). Their decline and extinction across the mainland suggests that they may have been distributed in more open habitats like other *Perameles* where they were susceptible to predation from introduced carnivore species.

### 3.4.9 Longevity

Whilst reintroduced bandicoots are able occasionally to live to four years of age on Heirisson Prong, the average longevity is far lower. It is more likely that a considerable proportion of the population tends to survive for less than a single year, with diminishing proportions surviving for up to three years, but rarely four. Females tended to survive longer than males. Although this difference was not significant, it may once again suggest that males suffer a higher mortality rate or disperse further than females.

Mean longevity for eastern barred bandicoots in Tasmania was 7.9 months for males and 10.5 months for females (Mallick et al. 2000), and in Victoria was probably less than two years for both sexes (Dufty 1991). Mean longevity for southern brown bandicoots in Tasmania was 10.0 months for males and 13.5 months for females (Mallick et al. 1998).
3.5 Conclusions

Lee and Cockburn (1985) regarded the life history strategies of all Australian bandicoots as broadly similar, in terms of litter size, food habits, body size, rate of growth and duration of parental investment. Many population parameters of the reintroduced western barred bandicoot at Heirisson Prong are similar to those of the wild populations on Dorre and Bernier Islands, and to other species of bandicoots. They are similar in that females mature earlier than males and juvenile mortality appears to be high. Their breeding on Heirisson Prong continued throughout the year, while breeding in the island populations was linked to regular winter rainfall, but may also be opportunistic during years of summer rainfall. Western barred bandicoots are solitary animals with a similar difference in home range size between sexes to other bandicoots. Their habitat requirements are broad, but like congeneric species, they may prefer a combination of dense cover interspersed with areas of open ground. Their general similarity to the island populations, particularly in reproductive parameters, suggests that the habitat at Heirisson Prong, including food and shelter resources, is suitable for their persistence at the site, provided introduced predators are controlled.

There are also a number of notable differences between the western barred bandicoot and other bandicoot species. Adult sex ratios are close to parity at Heirisson Prong, whereas the island populations and those of other species are often male biased. They are the smallest of the bandicoots, have fewer young per litter, may be sexually mature later, males have larger testes size relative to body size, and are the only species in which females are larger than males. This is particularly unusual where polygynous mating strategies are displayed, and males tend to be larger than females (Jarman 1974; 1983).

The reasons for these differences are unclear but some may arise from the competing pressures of dwarfism on the one hand and the lactational requirements of females to maintain a reasonable body size to support the carrying of young on the other. The tendency towards dwarfism of island species (Williamson 1981) is common among many island taxa. Dwarfism arises due to competition for food and the maintenance of a large population size in a small area. However, females must be large enough to support lactation and large litters of pouch young, so dwarfism may act more strongly on males. The smaller litter size of western barred bandicoots suggests development of a mechanism to cope with the smaller body size. Females may also
need to be as large or larger than males if they are to defend their nest sites from males (Jarman 1983). Thus there may be a trade-off between island dwarfism, lactational pressures, and nest defence for this species, which may in part explain its differences to other species of bandicoot.

The home range size of the western barred bandicoot appears to be larger than that of other bandicoot species, at least at low densities. This may be an adaptation to life in a more arid environment, where food resources are patchier and less abundant. The high degree of overlap in male home ranges compared to females and the male bias in sex ratio when females are approaching oestrous, combined with their large testes size relative to body size, is likely to reflect a polygynous or promiscuous reproductive strategy, similar to that of the eastern barred bandicoot (Dufty 1994a). Lee and Cockburn (1985) suggested that all Australian bandicoots probably display a polygynous or promiscuous mating strategy.

This chapter summarised the biology of the reintroduced western barred bandicoot population at Heirisson Prong, allowing some comparisons to be drawn with other species of bandicoot, and with the wild island populations. There was some suggestion that the presence of rabbits may have affected the reproductive output of western barred bandicoots at Heirisson Prong. The following chapter outlines the nesting biology of the western barred bandicoot at Heirisson Prong; another aspect of their biology that may be affected by rabbits.
Nesting biology of the western barred bandicoot

4.1 Introduction

Nest construction and function in marsupials have been examined for some species of hare-wallabies, wallabies, potoroos, bettongs and bandicoots (e.g. Dawson and Bennett 1978; Dufty 1991; Ingleby 1990; Murphy and Serena 1993; Rübsamen, Hume and Rübsamen 1983; Sampson 1971; Wallis, Jarman, Johnson, and Liddle 1989). Dickman (1991) described the construction of nests by the red-tailed phascogale Phascogale calura, the dibbler Parantechinus apicalis, and a number of Antechinus species as a means of predator avoidance. Most potoroids probably construct nests for diurnal shelter, but their precise function is unclear (Seebeck, Bennett and Scotts 1989). Due to the use of nests by day, Wallis et al. (1989) suggested that the primary function of the nests of the rufous bettong Aepyprymnus rufescens may be protection from both aerial and terrestrial predators that hunt by sight. However, Rübsamen et al. (1983) suggested that nests of the rufous bettong act as a means of thermoregulatory control as well as reducing predation risk. Nests of these marsupials have been found to offer an important insulative function during the day when animals are resting, maintaining similar or warmer temperatures in more mesic environments, and slightly cooler temperatures in arid environments, than the ambient temperature.

Little is known of the nesting biology of the western barred bandicoot, other than that animals occupy a concealed nest during the day made from grasses and other vegetation in a small hollow dug under shrubs (Burbidge 1981). The species may construct nests as shelter from diurnal predators, for thermoregulatory reasons, or for both. Native predators such as goannas Varanus spp., snakes and birds of prey are abundant throughout the former range of the western barred bandicoot, particularly in the warmer summer months. In the arid climate of much of its former range it is likely that nests would also offer some protection from high diurnal temperatures (> 40°C) during the summer period, and low temperatures (< 0°C) in winter.

This chapter describes the nest structure, the plant species most commonly chosen for nest sites, and the use of nests by western barred bandicoots at Heirisson Prong,
where introduced predators are typically absent, but native diurnal predators such as monitors, snakes and birds of prey are present. The use of nests as a potential refuge site from predators is examined, and the thermoregulatory benefits of nests in the warmer summer months are described.

4.2 Methods

4.2.1 Nest and shrub structure

Eleven bandicoots were radio collared during the May 1997 release from the predator refuge to two free-range sites as per the methods outlined in Section 2.2.3. Each animal was radio tracked to its diurnal nest site in the morning and nest data were gathered over six to 11 days after their release to free-range. Thirty-five nests and their associated shrubs were described at the two release sites. It is possible that bandicoots nested in atypical locations, due to their recent release, short period during which animals were radio tracked, and their lack of an established home range.

Once bandicoots were located, nest structure was recorded unless bandicoots did not construct nests (four occasions), or because neither the animal nor the nest was sighted (two occasions). Nests and shrubs were not described in detail until radio collars were removed from bandicoots so as not to disturb the nest site and prevent bandicoots returning to the same nest on subsequent days. Where two animals utilised the same nest site, the nest and shrub structure were measured only once.

A variety of nest and shrub descriptors was used in an attempt to determine the precise nesting requirements of western barred bandicoots. Measurements of nest and shrub structure included:

1. Shrub species;
2. Percentage canopy cover of shrub – estimation by eye of percentage canopy covering the ground, estimated for total continuous shrub cover and from above where possible;
3. Shrub height – vertical height of shrub from ground to tip of canopy;
4. Shrub length – horizontal length of shrub measured at widest part of shrub;
5. Shrub width – horizontal width of shrub measured across shrub perpendicular to shrub length;
6. *Height of underside of canopy above nest* – height of first section of shrub touching a pole placed at the centre of nest;

7. *Average height of canopy above ground* – average height of nearest section of shrub touching a pole placed at four corners of a 500 x 500 mm quadrat with the center of the quadrat at the centre of the nest;

8. *Distance of nest to shrub perimeter* – shortest horizontal distance from center of nest to edge of shrub;

9. *Percentage litter cover in the vicinity of nest* - percentage of ground covered by litter in a 500 x 500 mm quadrat with nest at centre of quadrat;

10. *Average litter depth in the vicinity of nest* – average litter depth taken from litter depth at four corners of a 500 x 500 mm quadrat with nest at centre of quadrat;

11. *Total litter depth at centre of nest* – depth of litter from base of hollow lined with litter to surface of nest (usually elevated above ground surface);

12. *Nest depth from ground surface to base of nest* – depth from base of hollow to ground surface adjacent to the nest;

13. *Litter depth above ground surface at the nest* – depth of litter from ground surface adjacent to nest to surface of nest;

14. *Litter depth lining base of nest* – depth of litter from base of hollow to immediately beneath where a resident bandicoot would sit;

15. *Distance to nearest neighbour* – distance from edge of shrub measured to closest neighbouring shrub of any species;

16. *Percentage visibility of bandicoot* – percentage of bandicoot visible in nest at a distance of one metre directly above the nest at the time of radio tracking the bandicoot to its nest;

17. *Percentage occasions bandicoots flushed* – percentage of all nests measured at which a bandicoot was flushed from the nest upon approach to within one metre of nest by observer; and

18. *Ease of penetration of shrub* – ranking from 1-5 of ease at which a terrestrial predator might approach the nest, from 1 (no barriers; Plate 4.1), 2 (small sticks), 3 (many sticks and branches; Plate 4.2), 4 (prickly, quite dense and difficult to penetrate) to 5 (very prickly and dense and likely to be impenetrable to a predator; Plate 4.3).
The average of each measurement, the range and standard error were recorded for all nests and shrubs, and for nests under the three most commonly used shrub species. Shrub area was calculated as shrub width x shrub length.

Plate 4.1: *Acacia tetragonophylla* shrub with a penetrability score of 1. There are no barriers to a predator reaching any nest located under the canopy of the shrub.

Percentage litter cover surrounding the nests and percentage canopy cover were arcsine transformed prior to analyses. A linear regression was used to examine the relationship between ground litter present under a shrub (average litter depth in the vicinity of the nest) and the amount of litter used by bandicoots in nest construction (represented as the total litter depth at the centre of the nest). Pearson’s correlations were used to examine the relationships between each of the nest and shrub variables measured.

The average size of nests was not measured in May 1997, but the lengths and widths of five nests were measured in February 1999 during radio tracking studies outlined in Section 5.2.1.
Plate 4.2: *Acacia tetragonophylla* shrub with a penetrability score of 3. There are some barriers to a predator reaching any nest located under the canopy of the shrub, in the form of sticks and branches.

Plate 4.3: *Acacia tetragonophylla* shrub with a penetrability score of 5. The dense prickly canopy growing close to the ground would prevent any introduced predator, such as a fox or cat, reaching a bandicoot nest site underneath the canopy.
4.2.1.1 Characteristics of nest shrubs

A range of randomly selected shrubs not known to be used as nest sites in May 1997 was measured in October 1997. Eleven shrub species selected by bandicoots as nest sites in May 1997, May 1998 and February 1999 (Section 5.3.1) were chosen (Acacia ligulata, A. tetragonophylla, Alectryon oleifolius, Atriplex bunburyana, Eucalyptus obtusifolia, Exocarpus aphyllus, Melaleuca cardiophylla, Pimelea microcephala, Rhagodia eremiana, Scaevola spinescens, and Thryptomene baeckeacea), and for each of these species, ten shrubs were chosen randomly and measured (five at each of the release sites). Measurements included: percentage canopy cover of shrub, shrub height, shrub length, shrub width, average height of canopy above ground at five random points within the shrub, percentage litter cover at five random points under the shrub, average litter depth at five random points under the shrub, distance to nearest neighbour, and ease of penetration of the shrub.

The characteristics of the randomly selected shrubs that were not known to contain bandicoot nest sites were then compared to the characteristics of those shrubs that had contained a nest site. Each variable for each species was compared separately using a one factor ANOVA, to determine if there were any aspects of shrub structure that may have been preferred or avoided by bandicoots when choosing a nest site.

Non-metric multidimensional scaling (nMDS) was used to explore differences between shrub attributes chosen by bandicoots and shrub attributes for the randomly selected shrub species. This form of analysis was chosen because it uses a minimum of assumptions and is simple to interpret, with samples represented two-dimensionally such that points that are close together are samples with similar composition, and points that are far apart correspond to samples with very different composition (Clarke and Gorley 2001). The attribute matrix was square-root transformed and converted to a similarity matrix using the Bray-Curtis similarity coefficient, and ordinated by nMDS, using a stress value of ≤ 0.15. The null hypothesis that there was no significant difference between the two groups of shrub attributes was tested using a one-way analysis of similarities (ANOSIM) using 999 random permutations from the PRIMER v.5 program (Clarke and Gorley 2001).

The combination of all measured shrub attributes chosen by bandicoots was then compared to all measured shrub attributes for the randomly selected shrub species using a multi-dimensional scaling analysis of similarity-percentages, or SIMPER, procedure.
from the PRIMER v.5 program (Clarke and Gorley 2001). Data were fourth root transformed and a Bray-Curtis similarity matrix was created prior to use of the SIMPER routine. This routine determined which individual variables contributed the most to any observed separation between the actual shrub (used by bandicoots as nest sites) and random shrub attributes.

### 4.2.2 Patterns of nest use

The number and location of nests (recorded with a GPS and mapped using Arcview GIS software as per the methods of Section 2.2.2) used by each bandicoot over the six to 11 day period of radio tracking was recorded. Evidence of nest sharing was noted, as was the use of a single nest by more than one bandicoot on subsequent days.

### 4.2.3 Shrub preference

The species of shrubs chosen as nest sites by bandicoots were recorded, as outlined in Section 4.2.1. Line-intercept transects of vegetation (Canfield 1941) were conducted at the two release sites where nest sites were typically located (Section 2.2.3). Shrub species were recorded along five randomly placed 50 m transects and the total percentage of each species intercepting along the five transects at each release site was calculated.

The proportion of each shrub species chosen for nest sites by bandicoots was then compared to the proportional availability of that species at each release site, as measured by the line transects. A Chi-squared test was computed to determine whether the number of shrubs used as actual nest sites (observed) was different to the overall number of shrub species available (expected) based on the vegetation transects. Shrubs were grouped as *Acacia tetragonophylla*, *Melaleuca cardiophylla*, *Thryptomene baeckeacea* and ‘Other’. An electivity index $E^*$ (Vanderploeg and Scavia 1979) was then used to determine if any individual shrub species were preferred or avoided by bandicoots. The equations to calculate the electivity index were:

$$W_i = \frac{(R_i/P_i)}{\sum (R_i/P_i)};$$

and

$$E^* = \frac{[W_i - (1/n)]}{[W_i + (1/n)]};$$

where $R_i$ is the proportion of shrub species $i$ used as nest sites, $P_i$ is the proportion of shrub species available in the field (represented by vegetation transects), $W_i$ is the normalized ratio (so that the sum of all such proportions in a sample equals one), and $n$
is the number of shrub species. $E^*$ ranges from $-1$ (highly selected against) to $+1$ (highly selected for) with $0$ for randomly selected shrub species. A comparison using small sample sizes (such as those of rare shrub species chosen for nest sites) often results in extreme electivity values, thus those shrub species representing less than 1% of either the nest use or shrub availability were considered to be insufficient to demonstrate selectivity and were assigned equal values in the analysis as per the methods of Evans (1992). A shrub species used as a nest site but not detected in the vegetation transects indicated that this species was likely to be rare on Heirisson Prong in the areas surveyed and so it was assigned a small (0.1%) field proportion.

### 4.2.4 Nest temperature

Seven bandicoots (two males and five females) were radio collared and tracked daily to their diurnal nest sites in February 1999, at the height of summer. Methods were as outlined in Section 2.2.3. Temperature probes connected to a data logger were placed in 14 of their nests for a period of at least 24 hours. Temperature probes were placed in vacated nests in an attempt to minimise disturbance of the position of the probes by bandicoots in the nest and to avoid any effect on the ambient temperature due to body heat generated by bandicoots. Four temperature probes were placed at each nest site at:

1. Approximately 100 mm depth in the centre of the nest below the surface litter where the bandicoot would rest;
2. Approximately 20 mm below the surface of the nest amongst the litter just above where the bandicoot would rest;
3. On the surface of the nest underneath the shrub canopy where a bandicoot might sit if not within its nest but sheltering under the shrub; and
4. On the ground in the sun adjacent to the shrub where the nest was located.

The data loggers recorded the temperature of each of the probes every half hour. These results were then downloaded to a computer. The temperatures in and surrounding the 14 nests were examined. These included nine different shrub species, with canopy covers ranging from 10 to 75%, and constructed by seven different bandicoots.
A multiple linear regression was computed to describe the relationship between the temperature range in nests (dependent variable) and the percentage canopy cover, shrub height and total litter depth in nests (independent variables).

4.3 Results

4.3.1 Nest and shrub structure

Nests of western barred bandicoots have a single entrance that tends to be obscured by litter (Plate 4.4). Nests are ovoid in shape, with a bandicoot-sized depression at the base, which is lined with litter (Plate 4.5). Litter is typically comprised of leaves of the shrub species above the nest site; however, where grasses were present within close proximity of the nest (only in February 1999; Section 5.3.1), they were also found as part of the nest structure. While leaves are the main litter type, small sticks are present also, particularly when nests are located under species with small leaves such as *Melaleuca cardiophylla* or *Thryptomene baeckeacea*.

Plate 4.4: Western barred bandicoot nest under an *Acacia tetragonophylla* shrub. Note that the bandicoot is not visible and the nest entrance is not conspicuous. Scale is 1:1.
Plate 4.5: The beginning of nest construction by a western barred bandicoot includes scraping a shallow depression on the ground under a shrub and lining the base of the depression with litter; in this case, sticks and foliage from a *Melaleuca cardiophylla*. Photo by Jiri Lochman, Lochman Transparencies.

The average shrub attributes and nest characteristics are recorded in Table 4.1. Nest sites tended to be extremely variable. Nests were constructed under shrubs with a variable degree of canopy cover and height, though no nests were found in shrubs less than 500 mm tall. They were situated at the edge of shrubs or towards the centre, and the height of the canopy directly above the nest varied also, from immediately above the nest to 650 mm above the nest. The percentage of ground covered by litter surrounding the nests was always greater than 50%, and litter depth varied from 12 - 68 mm.
Table 4.1: Shrub attributes and characteristics of sites used by western barred bandicoots as nests after release to free-range on Heirisson Prong in May 1997 (n = 35).

<table>
<thead>
<tr>
<th>Shrub attributes and nest characteristics</th>
<th>Mean ± SE</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage canopy cover of shrub</td>
<td>45 ± 3</td>
<td>15 – 90</td>
</tr>
<tr>
<td>Shrub height (mm)</td>
<td>1068 ± 70</td>
<td>500 – 2300</td>
</tr>
<tr>
<td>Shrub length (mm)</td>
<td>2989 ± 214</td>
<td>1500 – 8000</td>
</tr>
<tr>
<td>Shrub width (mm)</td>
<td>2114 ± 133</td>
<td>1000 – 4000</td>
</tr>
<tr>
<td>Shrub area (m²)</td>
<td>7.0 ± 0.9</td>
<td>1.5 – 28.0</td>
</tr>
<tr>
<td>Height of canopy above nest (mm)</td>
<td>177 ± 27</td>
<td>10 – 650</td>
</tr>
<tr>
<td>Average height of canopy above ground (mm)</td>
<td>161 ± 15</td>
<td>38 – 398</td>
</tr>
<tr>
<td>Distance of nest to shrub perimeter (mm)</td>
<td>641 ± 108</td>
<td>0 – 2600</td>
</tr>
<tr>
<td>Percentage litter cover in the vicinity of nest (mm)</td>
<td>82 ± 3</td>
<td>50 – 100</td>
</tr>
<tr>
<td>Average litter depth in the vicinity of nest (mm)</td>
<td>27 ± 3</td>
<td>1.2 – 68</td>
</tr>
<tr>
<td>Total litter depth at centre of nest (mm)</td>
<td>151 ± 15</td>
<td>100 – 240</td>
</tr>
<tr>
<td>Nest depth from ground surface to base of nest (mm)</td>
<td>95 ± 6</td>
<td>25 – 160</td>
</tr>
<tr>
<td>Litter depth above ground surface at the nest (mm)</td>
<td>43 ± 2</td>
<td>20 – 80</td>
</tr>
<tr>
<td>Litter depth lining base of nest (mm)</td>
<td>41 ± 3</td>
<td>10 – 70</td>
</tr>
<tr>
<td>Distance to nearest neighbour shrub (mm)</td>
<td>467 ± 64</td>
<td>50 – 1600</td>
</tr>
<tr>
<td>Percentage visibility of bandicoot</td>
<td>5 ± 2</td>
<td>0 – 40</td>
</tr>
<tr>
<td>Percentage of occasions bandicoots flushed</td>
<td>6</td>
<td>–</td>
</tr>
<tr>
<td>Ease of penetration of shrub</td>
<td>2.3 ± 0.1</td>
<td>1 – 4</td>
</tr>
</tbody>
</table>

Nests were on average 151 mm deep, and the amount of litter used to line the base and cover the top of the nest varied from 10 – 80 mm. There did not appear to be any relationship between the availability of litter in the vicinity of the nest and the amount used in nest construction (Figure 4.1; $F_{1, 33} = 0.22$, $P = 0.64$). Bandicoots were able to scrape litter from a wide area to construct their nest if necessary. The ground adjacent to nests under shrubs that generate little litter, such as *Melaleuca cardiophylla*, was often noticeably scraped clear of litter in a radius of up to two metres. By comparison, where surface litter was abundant, bandicoot scrapings typically occurred only within a radius of 500 mm.

The distance to neighbouring shrubs varied from being directly adjacent to the nesting shrub to up to 1600 mm away, requiring bandicoots to cross an expanse of bare ground before regaining cover after departing from their nest. Few bandicoots were visible in their nests and few were flushed when the nest was approached to within one metre, and often closer. Nest sites tended to be easily accessible to predators, with the average nest site surrounded only by a few sticks and small branches.
Figure 4.1: The relationship between the depth of surface litter in the vicinity of bandicoot nests and litter depth at the centre of those nests in May 1997.

Nest sites within rabbit burrows were not measured, as no nests were constructed. One female bandicoot escaped into a rabbit burrow during an attempt to capture the animal from its nest to remove the radio collar, and remained in the burrow for two nights until it was recaptured and the collar removed. One male rested over a four-day period in the entrance to three different rabbit burrows, with no nests constructed. Some litter appeared to be scraped into a small area where the bandicoot rested, however no depression was dug, and litter depth in the region where the bandicoot was resting was less than 20 mm. One other male also rested down a rabbit burrow for one day, but no nest was constructed.

A variety of shrub attributes and nest characteristics were significantly correlated with each other (Table 4.2). For example, the total nest litter depth, nest depth from the surface to the base of nest, depth of litter lining the base of nests, and the average litter depth surrounding the nest were all significantly and positively correlated with each other. As the average canopy height of shrubs increased, the average litter depth and height of the shrubs tended to increase, but the amount of litter used by bandicoots to
construct their nests tended to decrease. The distance from nests to the perimeter of shrubs tended to increase with an increase in shrub height and the average canopy height above the ground. Bandicoot nests under shrubs that were easier to penetrate tended to be constructed with more litter and were deeper, and bandicoots were less visible while in their nest. As the litter cover surrounding the nests increased, the average litter depth, shrub height, average height of the canopy above the ground and the flush distance tended to increase, while the nest depth from the surface to the base of the nest decreased. The transformed percentage canopy cover and shrub area were not significantly correlated with any of the other variables measured.

The average size of nests measured in February 1999 was 278 mm wide and 386 mm long ($n = 5$).

Nine different shrub species were used as nest sites in May 1997. The most common were *Acacia tetragonophylla*, *Melaleuca cardiophylla* and *A. ligulata* (Section 4.3.4). The average shrub attributes and nest characteristics for each of the predominant three shrub species are recorded in Table 4.3. These three shrub species tended to display a similar range of variation in attributes to the entire complement of nest and shrub attributes outlined in Table 4.1.

When the shrub attributes and nest characteristics of these three species were combined ($n = 26$) and compared to those of the other plant species used as nest sites ($n = 9$), the only attributes that were significantly different were the total litter depth at the centre of the nest, which was lower for the common shrubs (144 mm) than for the other species (171 mm; $F_{1,33} = 6.01, P = 0.02$), and the penetration score, which was higher for the common shrubs (2.5) than for the other species (1.5; $F_{1,33} = 11.41, P = 0.002$).
Table 4.2: Matrix of Pearson’s correlation coefficients between shrub attributes and characteristics of nest sites used by western barred bandicoots on Heirisson Prong in May 1997 ($n = 35$). Significantly correlated variables at $P < 0.05$ are shaded in grey.

<table>
<thead>
<tr>
<th>Attributes</th>
<th>Nest litter</th>
<th>Nest depth</th>
<th>Surface litter</th>
<th>Base litter</th>
<th>Average litter</th>
<th>Height</th>
<th>Canopy height at nest</th>
<th>Average canopy height</th>
<th>Perimeter</th>
<th>Nearest neighbour</th>
<th>Visibility</th>
<th>Flush distance</th>
<th>Penetration</th>
<th>Canopy cover</th>
<th>Litter cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest depth</td>
<td>0.75</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface litter</td>
<td>0.54</td>
<td>0.58</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Base litter</td>
<td>0.72</td>
<td>0.67</td>
<td>0.67</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average litter</td>
<td>-0.08</td>
<td>-0.29</td>
<td>-0.02</td>
<td>-0.10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td>-0.06</td>
<td>-0.14</td>
<td>-0.15</td>
<td>-0.19</td>
<td>0.60</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy height at nest</td>
<td>-0.25</td>
<td>-0.30</td>
<td>-0.44</td>
<td>-0.40</td>
<td>0.14</td>
<td>0.28</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average canopy height</td>
<td>-0.23</td>
<td>-0.40</td>
<td>-0.40</td>
<td>-0.46</td>
<td>0.39</td>
<td>0.63</td>
<td>0.60</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perimeter</td>
<td>0.21</td>
<td>0.06</td>
<td>0.15</td>
<td>-0.02</td>
<td>0.29</td>
<td>0.36</td>
<td>0.10</td>
<td>0.33</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nearest neighbour</td>
<td>0.19</td>
<td>0.10</td>
<td>-0.09</td>
<td>-0.07</td>
<td>0.04</td>
<td>0.33</td>
<td>0.31</td>
<td>0.09</td>
<td>0.26</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visibility</td>
<td>-0.25</td>
<td>-0.04</td>
<td>0.09</td>
<td>-0.08</td>
<td>-0.14</td>
<td>-0.24</td>
<td>-0.04</td>
<td>-0.13</td>
<td>-0.10</td>
<td>-0.23</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flush distance</td>
<td>-0.06</td>
<td>-0.19</td>
<td>-0.15</td>
<td>-0.13</td>
<td>0.26</td>
<td>0.47</td>
<td>0.18</td>
<td>0.29</td>
<td>0.50</td>
<td>0.39</td>
<td>0.04</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Penetration</td>
<td>-0.49</td>
<td>-0.38</td>
<td>-0.24</td>
<td>-0.39</td>
<td>-0.10</td>
<td>-0.30</td>
<td>0.17</td>
<td>-0.11</td>
<td>-0.01</td>
<td>-0.05</td>
<td>0.58</td>
<td>0.03</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy cover</td>
<td>0.21</td>
<td>-0.06</td>
<td>-0.03</td>
<td>0.09</td>
<td>0.11</td>
<td>0.04</td>
<td>-0.23</td>
<td>-0.10</td>
<td>0.02</td>
<td>-0.21</td>
<td>-0.28</td>
<td>-0.10</td>
<td>-0.12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter cover</td>
<td>-0.16</td>
<td>-0.40</td>
<td>-0.18</td>
<td>-0.25</td>
<td>0.72</td>
<td>0.52</td>
<td>0.12</td>
<td>0.55</td>
<td>0.32</td>
<td>-0.04</td>
<td>-0.15</td>
<td>0.40</td>
<td>-0.13</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>Shrub area</td>
<td>-0.16</td>
<td>-0.20</td>
<td>-0.16</td>
<td>-0.22</td>
<td>-0.05</td>
<td>0.20</td>
<td>0.24</td>
<td>0.14</td>
<td>0.12</td>
<td>0.14</td>
<td>0.10</td>
<td>0.18</td>
<td>0.28</td>
<td>0.22</td>
<td>0.12</td>
</tr>
</tbody>
</table>
Table 4.3: Mean ± SE shrub attributes and characteristics of nest sites used by western barred bandicoots for each of the three most commonly used shrub species after release to free-range on Heirisson Prong in May 1997 ($n = 26$).

<table>
<thead>
<tr>
<th>Shrub attributes and nest characteristics</th>
<th>Acacia tetragonophylla</th>
<th>Melaleuca cardiophylla</th>
<th>Acacia ligulata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage canopy cover of shrub</td>
<td>34 ± 4</td>
<td>53 ± 15</td>
<td>48 ± 5</td>
</tr>
<tr>
<td>Shrub height (mm)</td>
<td>889 ± 67</td>
<td>658 ± 3</td>
<td>1760 ± 136</td>
</tr>
<tr>
<td>Shrub length (mm)</td>
<td>2978 ± 316</td>
<td>3550 ± 903</td>
<td>3260 ± 248</td>
</tr>
<tr>
<td>Shrub width (mm)</td>
<td>2186 ± 182</td>
<td>2283 ± 277</td>
<td>2620 ± 364</td>
</tr>
<tr>
<td>Shrub area ($m^2$)</td>
<td>7.0 ± 1.3</td>
<td>9.2 ± 3.8</td>
<td>8.8 ± 1.9</td>
</tr>
<tr>
<td>Height of canopy above nest (mm)</td>
<td>230 ± 45</td>
<td>53 ± 15</td>
<td>194 ± 44</td>
</tr>
<tr>
<td>Average height of canopy above ground (mm)</td>
<td>154 ± 15</td>
<td>78 ± 15</td>
<td>224 ± 19</td>
</tr>
<tr>
<td>Distance of nest to shrub perimeter (mm)</td>
<td>450 ± 107</td>
<td>533 ± 154</td>
<td>1020 ± 267</td>
</tr>
<tr>
<td>Percentage litter cover in the vicinity of nest</td>
<td>76 ± 4</td>
<td>67 ± 7</td>
<td>96 ± 4</td>
</tr>
<tr>
<td>Average litter depth in the vicinity of nest (mm)</td>
<td>20 ± 3</td>
<td>12 ± 2</td>
<td>51 ± 9</td>
</tr>
<tr>
<td>Total litter depth at centre of nest (mm)</td>
<td>149 ± 6</td>
<td>157 ± 8</td>
<td>124 ± 11</td>
</tr>
<tr>
<td>Nest depth from ground surface to base of nest (mm)</td>
<td>101 ± 8</td>
<td>97 ± 12</td>
<td>68 ± 18</td>
</tr>
<tr>
<td>Litter depth above ground surface at the nest (mm)</td>
<td>43 ± 3</td>
<td>485 ± 7</td>
<td>384 ± 7</td>
</tr>
<tr>
<td>Litter depth lining base of nest (mm)</td>
<td>41 ± 4</td>
<td>45 ± 3</td>
<td>32 ± 8</td>
</tr>
<tr>
<td>Distance to nearest neighbour (mm)</td>
<td>404 ± 82</td>
<td>327 ± 102</td>
<td>680 ± 250</td>
</tr>
<tr>
<td>Percentage visibility of bandicoot</td>
<td>11 ± 4</td>
<td>0 ± 0</td>
<td>0 ± 0</td>
</tr>
<tr>
<td>Percentage of bandicoots flushed</td>
<td>7</td>
<td>17</td>
<td>0</td>
</tr>
<tr>
<td>Ease of penetration of shrub</td>
<td>3 ± 0.2</td>
<td>2 ± 0.4</td>
<td>2 ± 0.2</td>
</tr>
</tbody>
</table>

4.3.1.1 Characteristics of nest shrubs

A number of attributes of the shrubs that had contained a nest site were significantly different to the attributes of the randomly selected shrubs that were not known to contain bandicoot nest sites (Table 4.4). Bandicoots appeared to choose shrubs that had a lower canopy height above ground, a greater litter depth, greater litter cover and a shorter distance to the nearest neighbouring shrub. Shrub height, shrub area, transformed percentage canopy cover and the penetration score were not significantly different between the two groups of shrubs.
Table 4.4: Mean ± SE attributes of shrubs chosen as nest sites by western barred bandicoots after release to free-range on Heirisson Prong in May 1997 (n = 35) compared with randomly chosen shrubs (n = 110). One-factor ANOVAs were used for comparison between the two groups of shrub attributes. * denotes those attributes that are significantly different between the groups.

<table>
<thead>
<tr>
<th>Shrub attributes</th>
<th>Random shrubs</th>
<th>Nest shrubs</th>
<th>$F_{1,143}$ value</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrub height (mm)</td>
<td>1149 ± 52</td>
<td>1069 ± 70</td>
<td>0.63</td>
<td>0.43</td>
</tr>
<tr>
<td>Shrub length (mm)</td>
<td>289 ± 14</td>
<td>299 ± 21</td>
<td>1.91</td>
<td>0.17</td>
</tr>
<tr>
<td>Shrub width (mm)</td>
<td>242 ± 12</td>
<td>211 ± 13</td>
<td>0.12</td>
<td>0.73</td>
</tr>
<tr>
<td>Shrub area (m$^2$)</td>
<td>8.7 ± 0.8</td>
<td>7.0 ± 0.9</td>
<td>1.16</td>
<td>0.28</td>
</tr>
<tr>
<td>Arcsine transformed percentage</td>
<td>48 ± 2</td>
<td>45 ± 3</td>
<td>0.80</td>
<td>0.37</td>
</tr>
<tr>
<td>canopy cover of shrub</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy height above ground (mm)</td>
<td>241 ± 12</td>
<td>161 ± 15</td>
<td>11.45</td>
<td>*0.001</td>
</tr>
<tr>
<td>Litter depth (mm)</td>
<td>16 ± 1</td>
<td>27 ± 3</td>
<td>13.23</td>
<td>&lt;*0.001</td>
</tr>
<tr>
<td>Arcsine transformed percentage</td>
<td>58 ± 3</td>
<td>82 ± 3</td>
<td>8.11</td>
<td>&lt;*0.001</td>
</tr>
<tr>
<td>litter cover</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nearest neighbour (mm)</td>
<td>891 ± 86</td>
<td>467 ± 64</td>
<td>7.35</td>
<td>*0.007</td>
</tr>
<tr>
<td>Penetration</td>
<td>2.1 ± 0.1</td>
<td>2.3 ± 0.1</td>
<td>1.71</td>
<td>0.19</td>
</tr>
</tbody>
</table>

Ordination by nMDS indicated overall similarity in the shrub attributes between those chosen as nest sites by bandicoots and those selected randomly (Figure 4.2). ANOSIM confirmed that there was no difference between these groups of shrubs ($R = 0.54$, $P = 0.06$), although the result bordered on significance.

Seven shrub attributes (all those listed in Table 4.4, except ‘penetration’) together contributed 8.9% only to the overall dissimilarity between characteristics of shrubs chosen as nest sites by western barred bandicoots and randomly chosen shrubs; individual contributions were all $\leq 2.1\%$. This reaffirmed the lack of difference between the groups of shrubs.
Figure 4.2: Ordination produced by non-metric multi-dimensional scaling of the attributes of those shrubs chosen as nest sites by bandicoots (blue ▼) and those selected randomly (green ▲).

4.3.2 Patterns of nest use

The number of nests used by individual bandicoots over the six to 11 day period after release in May 1997 varied from 3 - 6, with an average of 3.2 nests used per bandicoot per week. Males used significantly more nests than females, with an average of 3.7 and 2.6 nests per week respectively ($F_{1,9} = 7.77$, $P = 0.02$). All animals used at least one of their nests more than once during the period of radio tracking, and two females used the same nest six times over periods of seven and eight days. Three females used the same nest on five consecutive days and one male used the same nest on four consecutive days.

Four bandicoots used the same nest that had been used by another individual on a previous day. This joint use of nest sites was always between one male and one female; never individuals of the same sex, and not by more than two individuals. Three males used nests previously inhabited by females, and one female used a nest previously inhabited by a male.
Of the three bandicoots flushed from their nests, two did not use the same nest again, but one used the same nest site (the entrance of a rabbit burrow) on the following day.

The closest distance between nest sites of the same individual was 25 m for a male and 26 m for a female, and between different individuals was 44 m between females, 14 m between males, and 5 m between males and females (excluding those that used the nest of another individual). Four of the six males at Release Sites 1 and 2 had overlapping nesting ranges in the first eight to 11 days after their release. None of the five females had overlapping nesting ranges during the same time period.

### 4.3.3 Nest sharing

Only one incidence of nest sharing between adults was noted. Two radio-collared bandicoots (male and female) were found in the same nest two mornings after both were released to free-range in May 1997. The male was flushed from the nest during radio tracking, leaving the female in the nest. At the time, she was carrying two small pouch young, approximately one week old. These two bandicoots had previously occupied overlapping home ranges in the predator refuge prior to their release to free-range. The male was likely to have been a dominant male, for the following reasons: he had occupied the largest home range area within the yards prior to release (5.6 ha; Figure 3.6); was one of the males originally transferred from Dorre Island in 1995; and was one of the largest and oldest males.

One female was flushed from her nest in the process of nest measurement, and shortly after, her two nearly independent offspring (approximately 80 mm head body length) were flushed also from the nest.

### 4.3.4 Shrub Preference

Of the nine shrub species used as nest sites by western barred bandicoots after release to free-range on Heirisson Prong in May 1997 (Table 4.5), the most commonly used shrub species was *Acacia tetragonophylla* (43%), followed by *Melaleuca cardiophylla* (17%) and *Acacia ligulata* (14%; Table 4.5). Male and female bandicoots used a similar array of shrub species for nest sites.
Table 4.5: Shrub species utilised for nest sites by male and female western barred bandicoots after release to free-range at Release Sites 1 and 2 on Heirisson Prong in May 1997 ($n = 35$).

<table>
<thead>
<tr>
<th>Shrub species</th>
<th>Release Site 1 nests</th>
<th>Release Site 2 nests</th>
<th>Percentage total nests</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acacia tetragonophylla</em></td>
<td>4</td>
<td>11</td>
<td>42.8</td>
</tr>
<tr>
<td><em>Melaleuca cardiophylla</em></td>
<td>3</td>
<td>3</td>
<td>17.1</td>
</tr>
<tr>
<td><em>Acacia ligulata</em></td>
<td>2</td>
<td>3</td>
<td>14.3</td>
</tr>
<tr>
<td><em>Alectryon oleifolius</em></td>
<td>2</td>
<td>1</td>
<td>8.5</td>
</tr>
<tr>
<td><em>Eucalyptus obtusifolia</em></td>
<td>2</td>
<td>0</td>
<td>5.7</td>
</tr>
<tr>
<td><em>Eremophila glabra</em></td>
<td>1</td>
<td>0</td>
<td>2.9</td>
</tr>
<tr>
<td><em>Exocarpus aphyllus</em></td>
<td>1</td>
<td>0</td>
<td>2.9</td>
</tr>
<tr>
<td><em>Pimelea microphylla</em></td>
<td>0</td>
<td>1</td>
<td>2.9</td>
</tr>
<tr>
<td><em>Marsdenia sp.</em></td>
<td>1</td>
<td>0</td>
<td>2.9</td>
</tr>
<tr>
<td>TOTALS</td>
<td>16</td>
<td>19</td>
<td></td>
</tr>
</tbody>
</table>

Bandicoots appeared to choose particular shrub species for nest sites. The overall number of shrubs chosen for nest sites was significantly different to the availability of all shrub species available at the release sites ($\chi^2 = 67.15$, $P < 0.001$). The most common shrub species at both Release Sites 1 and 2 was *Thryptomene baecckeacea* (Figure 4.3), however this species was not used by radio collared bandicoots for nest sites in 1997. The next most common shrub species were *Melaleuca cardiophylla* and *Acacia tetragonophylla*. Both these species were used as nest sites, however *M. cardiophylla* was used to a lesser degree than their availability in the habitat at the release sites, and *A. tetragonophylla* to a greater degree (Figure 4.3).
Figure 4.3: Shrub species chosen for nest sites ($n = 35$) compared with shrub availability determined by line transects at Release Sites 1 and Site 2.
As the number of nests expected under each shrub species was predominantly less than five, proportions were used to test for differences between the shrubs chosen for nest sites and those typically available within the habitat. The Vanderploeg and Scavia index of shrub utilization $E^*$ (Table 4.6) suggested that western barred bandicoots showed positive selection for one of the common shrub species *Acacia tetrogonophylla*, and three of the less common species *Acacia ligulata*, *Alectryon oleifolius* and *Eucalyptus obtusifolia*. Despite being common, both *Thryptomene baeckeacea* and *Melaleuca cardiophylla* were strongly selected against, as were five of the other less common shrub species. The remaining four less common species can be regarded as randomly selected.

**Table 4.6**: Vanderploeg and Scavia $E^*$ index of shrub utilization for nest sites by bandicoots in relation to shrub availability within the habitat. Values towards +1 indicate high selection for a shrub species; values towards −1 indicate high selection against a shrub species, and values near 0 represent random selection.

<table>
<thead>
<tr>
<th>Shrub species</th>
<th>$E^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Thryptomene baeckeacea</em></td>
<td>-1</td>
</tr>
<tr>
<td><em>Melaleuca cardiophylla</em></td>
<td>-0.66</td>
</tr>
<tr>
<td><em>Acacia tetrogonophylla</em></td>
<td>+0.20</td>
</tr>
<tr>
<td><em>Scaevola sp.</em></td>
<td>-1</td>
</tr>
<tr>
<td><em>Rhagodia eremiana</em></td>
<td>-1</td>
</tr>
<tr>
<td><em>Cryptandra sp.</em></td>
<td>-1</td>
</tr>
<tr>
<td><em>Baeckea pentagonantha</em></td>
<td>-1</td>
</tr>
<tr>
<td><em>Pimelea microcephala</em></td>
<td>-0.02</td>
</tr>
<tr>
<td><em>Alectryon oleifolius</em></td>
<td>+0.48</td>
</tr>
<tr>
<td><em>Exocarpus aphyllus</em></td>
<td>-0.02</td>
</tr>
<tr>
<td><em>Atriplex bunburyana</em></td>
<td>-1</td>
</tr>
<tr>
<td><em>Acacia ligulata</em></td>
<td>+0.65</td>
</tr>
<tr>
<td><em>Eucalyptus obtusifolia</em></td>
<td>+0.31</td>
</tr>
<tr>
<td><em>Eremophila glabra</em></td>
<td>-0.02</td>
</tr>
<tr>
<td><em>Marsdenia sp.</em></td>
<td>-0.02</td>
</tr>
</tbody>
</table>

### 4.3.5 Nest temperature

Data were collected on the nest temperature of 14 nests. On three occasions (nests of one male and two females) a bandicoot returned to its nest and disturbed the position of the temperature probes within the nest. This was evident as an unexpected or sudden change in temperature, followed by temperature measurements not consistent with the
original position of the probe. Movement of temperature probes was not discovered until the end of the 24-hour monitoring period when their position was checked prior to their removal. These results were therefore not used.

For the remaining 11 nests, the temperature at 100 mm depth within the nests varied from a minimum of 23°C to a maximum of 44°C (Table 4.7). For example, under an *Alectryon oleifolius* with 40% canopy cover, and a nest litter depth of 180 mm, nest temperatures varied 6°C, from 26°C to 32°C (Figure 4.4). During the same time period under an *Acacia tetragonophylla* with a 25% canopy cover, and a nest litter depth of 160 mm, nest temperatures varied 9°C, from 25°C to 34°C (Figure 4.5). The temperature curves over the same time period were similar between the two nests, suggesting that any differences in shrub species, the degree of canopy cover above the nest and the litter depth of the nests had minor effects on temperature.

**Table 4.7**: Variation in nest and surface temperature at nests under different shrub species with varying canopy cover in February 1999.

<table>
<thead>
<tr>
<th>Dates of monitoring period</th>
<th>Shrub species</th>
<th>% Canopy cover</th>
<th>Temperature (°C) range 100 mm in nest</th>
<th>Temperature (°C) range at nest surface</th>
</tr>
</thead>
<tbody>
<tr>
<td>8 – 10th</td>
<td><em>Atriplex bunburyana</em></td>
<td>15</td>
<td>25 – 33</td>
<td>21 - 48</td>
</tr>
<tr>
<td>10 – 12th</td>
<td><em>Alyogyne cuneiformis</em></td>
<td>20</td>
<td>24 – 33</td>
<td>22 - 40</td>
</tr>
<tr>
<td>10 – 12th</td>
<td><em>Pimelea microcephala</em></td>
<td>20</td>
<td>25 – 32</td>
<td>22 - 44</td>
</tr>
<tr>
<td>10 – 12th</td>
<td><em>Scaevola spinescens</em></td>
<td>20</td>
<td>25 – 37</td>
<td>21 - 47</td>
</tr>
<tr>
<td>8 – 10th</td>
<td><em>Acacia tetragonophylla</em></td>
<td>25</td>
<td>25 – 34</td>
<td>22 - 43</td>
</tr>
<tr>
<td>8 – 10th</td>
<td><em>Acacia tetragonophylla</em></td>
<td>30</td>
<td>30 – 35</td>
<td>22 - 45</td>
</tr>
<tr>
<td>8 – 10th</td>
<td><em>Alectryon oleifolius</em></td>
<td>40</td>
<td>26 – 32</td>
<td>22 - 44</td>
</tr>
<tr>
<td>10 – 12th</td>
<td><em>Atriplex bunburyana</em></td>
<td>40</td>
<td>23 – 36</td>
<td>22 - 47</td>
</tr>
<tr>
<td>5 – 8th</td>
<td><em>Atriplex bunburyana</em></td>
<td>60</td>
<td>26 – 40</td>
<td>23 - 54</td>
</tr>
<tr>
<td>3 – 5th</td>
<td><em>Rhagodia eremiana</em></td>
<td>60</td>
<td>24 – 31</td>
<td>20 - 41</td>
</tr>
<tr>
<td>12 – 13th</td>
<td><em>Thryptomene baecceacea</em></td>
<td>75</td>
<td>29 – 44</td>
<td>25 - 53</td>
</tr>
</tbody>
</table>
Figure 4.4: Temperatures adjacent to and within a bandicoot nest under an *Alectryon oleifolius* with a canopy cover of 40%.

Figure 4.5: Temperatures adjacent to and within a bandicoot nest under an *Acacia tetragonophylla* with a canopy cover of 25%.
The temperature just below the surface of the nests amongst the litter fluctuated a little more widely, from a minimum of 21°C to a maximum of 48°C (Figures 4.4 and 4.5). During the day the temperature just below the nest surface rose to 10°C higher than the temperature 100 mm beneath the nest surface, and during the night, the temperature just below the surface of the nest was typically two degrees lower than towards the base of the nest.

The relationships between percentage canopy cover and the range of temperatures experienced within bandicoot nests over the 24 hour periods of monitoring ($F_{1,9} = 2.77$, $P = 0.13$; Figure 4.6), between shrub height and temperature range ($F_{1,9} = 1.45$, $P = 0.26$), and between total litter depth of the nest and temperature range ($F_{1,9} = 0.14$, $P = 0.72$) were not significant.

**Figure 4.6:** Temperature range in bandicoot nests measured in February 1999 under shrubs of varying percentage canopy cover. The relationship is described by the equation $y = 6.518 + 0.082x$ ($r^2 = 0.24$), with $P = 0.13$. 
The surface temperature adjacent to the nests and under the shrub canopy varied from a minimum of 20°C at 00:00 to 06:00 hours under a *Rhagodia eremiana* with a 60% canopy cover (Figure 4.7) to a maximum of 54°C at approximately 13:30 hours under an *Atriplex bunburyana* with a 60% canopy cover (Figure 4.8, Table 4.7). The surface temperature on the ground in an exposed location adjacent to the shrub varied from a minimum of 18°C at 04:00 to 06:00 hours to a maximum of 60°C in full sun at approximately 13:00 hours. The minimum temperatures in an exposed location were typically similar to or slightly lower than those recorded on the surface underneath the shrub, and the maximum temperatures tended to be more than 5°C higher.

**Figure 4.7:** Temperatures adjacent to and within a bandicoot nest under a *Rhagodia eremiana* with a canopy cover of 60%.
Figure 4.8: Temperatures adjacent to and within a bandicoot nest under an *Atriplex bunburyana* with a canopy cover of 60%.

In two unoccupied nests over a 72-hour period the nest temperature was always between 28° and 35°C, while surface temperatures ranged from 22 - 54°C (Figure 4.9). There appears to be a trend for the nest temperature to approximate the surface temperature at 29 - 34°C.

Although data for 14 bandicoot nest sites was collected, data on four representative nests only were displayed in the preceding figures (Figures 4.4, 4.5, 4.7 and 4.8).
Figure 4.9: Temperature in two unoccupied nests (data combined for both) at different ambient temperatures measured over a period of 72 hours. Line denotes nest temperature equivalent to surface temperature. ● = hourly measurement. Dotted lines show temperature range at which nest and surface temperature are similar.
4.4 Discussion

4.4.1 Nest and shrub structure

Reintroduced western barred bandicoots at Heirisson Prong constructed ovoid-shaped nests under a variety of shrub species, with a bandicoot-sized depression at the base, lined with litter. Nests had a single entrance that tended to be obscured by litter, which were predominantly comprised of the leaves of the shrub under which the nest was constructed. Nests consisted also of grasses when present, and small sticks and twigs when leaf litter in the vicinity was limited. On average, nests on Heirisson Prong were 280 mm wide and 390 mm long.

The depth of litter within the nest varied, but averaged 150 mm, and nests were always constructed in areas where at least 50% of the surrounding area was covered by surface litter, though the surrounding litter depth varied from as little as 10 mm to up to 80 mm. A lack of deep leaf litter did not affect the ability of a bandicoot to construct a nest; animals scraped litter from up to a two-metre radius around a nest site when litter was scarce. The only other common characteristic appeared to be that shrubs chosen for nest sites were over 500 mm in height. The shrub species used as nest sites varied considerably, in shape, size, degree of canopy cover, and amount of cover immediately above the nests.

The vegetative cover offered by the shrubs tended to be limited, with the majority of nests being within 500 mm of the perimeter of the shrub, having a penetration value of three or less, and a canopy cover of 60% or less, typically providing reasonably easy access to the nest site for terrestrial predators such as goannas, snakes, foxes or feral cats. However, nests were usually well concealed, and bandicoots were rarely flushed from their nests during the day, even upon approach to less than one metre. Without radio telemetry, it is unlikely that humans would be able to locate bandicoot nests.

Rabbit burrows also were used as diurnal resting sites. This was not common, and occurred only after the bandicoots’ release to free-range in May 1997, and not during successive periods of monitoring in May 1998 or February 1999, suggesting that the use of rabbit burrows may have been a consequence of the disturbance of bandicoots from their established home range. Similarly, the nests examined in May 1997 may have been temporary resting places, and not necessarily representative of more permanent nesting sites constructed after settling in to their new home range. However, nests constructed by free-range bandicoots during monitoring in May 1998 and
February 1999 (Section 5.3.1) appeared to be similar in structure to those constructed by bandicoots in May 1997. The majority of bandicoots monitored in May 1997 remained within the release area in the first two months after their release (Section 2.3.3), suggesting that they quickly established a home range.

Nine species of shrubs were used as nest sites by bandicoots released to free-range on Heirisson Prong in May 1997, though the most commonly used were *Acacia tetragonophylla*, *Melaleuca cardiophylla* and *A. ligulata*. While these three species showed a similar range of shrub attributes to the other six species of shrubs used by bandicoots, the three common species possessed significantly less litter cover, a higher penetration score, and nests were less deep. An increase in the penetration score of a shrub (that is, a decrease in the penetrability of the shrub) was significantly correlated with a decrease in the amount of litter used to construct a nest. It is therefore possible that bandicoots may have showed some preference for shrub species that offer greater protection from predators conferred by prickly branches covering access to the nest, rather than greater levels of litter for nest construction.

The combined attributes of those shrubs chosen as nest sites by western barred bandicoots at Heirisson Prong were not significantly different from the shrub attributes of a random selection of shrubs chosen from the vicinity of the nest sites. However, the shrub attributes at nest sites did appear to represent a distinct subset of those attributes displayed by the randomly selected shrubs. Western barred bandicoots appeared to choose shrubs that had a lower canopy height above ground, a shorter distance to the nearest neighbouring shrub, deeper litter, and higher litter cover. Despite these differences, their contribution to the dissimilarity between the two groups of shrubs was minor.

Nests of western barred bandicoots on Dorre and Bernier Islands are made from “local plant material in a hemispherical hollow scrape beneath a low or prostrate shrub”, and near the coast, are filled with seagrass litter. Nests are well concealed, except for a “slight disruption of the litter surface where the animal entered” and a runway forms the entrance and exit at one end of the nest (Friend and Burbidge 1995). Gould (1863) reported that *Perameles myosurus* (= *bougainville*) made a compact nest in a hollow on the ground that was very difficult to detect and had no obvious entrance. Krefft (1866) noted that *P. fasciata* (= *bougainville*) sought shelter during the day in hollow logs, under stones, or constructed a nest.
All Australian bandicoots appear to construct nests of a similar form. Eastern barred bandicoots construct nests at or just below ground level and occasionally use rabbit burrows, hollow logs, piles of rubbish (at the Hamilton rubbish tip in Victoria), or nest underneath rocks (Seebeck 2001). Nests are commonly made from grass, leaves and twigs, with an oval mound of plant material about 200 – 300 mm long with a hollow centre, resting over a scraped depression in the ground 50 – 140 mm deep. The base is sometimes bare earth, but more commonly is lined with grass, and some of the larger nests contain soil mixed in with the roof structure (Dufty 1991). Nests may be made at the base of a grass tussock (Murphy and Serena 1993), and abandoned rabbit burrows have been used in Tasmania (Heinsohn 1966). Long-nosed bandicoots at the Sydney Harbour National Park use cryptic nests constructed of dry grass, twigs and leaf litter, often amongst dense undergrowth (Scott et al. 1999).

Southern brown bandicoot nests in Victoria are oval-shaped mounds of leaf litter and soil, from 0.5 to 0.75 metres long, with an opening at either end of the nest and a small, dry chamber lined with twigs and leaves. Upon entering or exiting a nest, these entrances collapse, sealing the nest and leaving the opening inconspicuous (Lobert 1990). Northern brown bandicoots in south-eastern Queensland construct concealed nests of plant litter amongst tall ground cover. Nests are oval-shaped, 400 mm in length with a hollow chamber in the centre over a depression 50 to 80 mm deep, and a single entrance of loose vegetation. Two nests found during wet weather had a layer of soil scraped over the top, thought to assist in waterproofing (Gordon 1974). Golden bandicoots on Marchinbar Island construct rudimentary nests, typically shallow scrapes or depressions under *Triodia* clumps, grasses and shrub thickets, and rocky shelves (Southgate et al. 1996).

Chambers and Dickman (2002) found that the long-nosed bandicoot at Sydney Harbour National Park used areas of dense undergrowth and leaf litter in scrub for nest sites, emphasizing the “importance of the structural component of the habitat in nest site selection”. The choice of shrub species by western barred bandicoots for nest sites at Heirisson Prong appears to reflect considerable flexibility in the ability of the species to construct nests in a variety of microhabitats, providing that enough litter is present.
4.4.2 Nest use

On Heirisson Prong, male western barred bandicoots used an average of 3.7 nests per week during the first 11 days after their release while females used significantly less (2.6). Between three and six nest sites were constructed and used by an individual during the same period, though some bandicoots spent up to five consecutive days in the same nest. All bandicoots used at least one of their nests on more than one occasion, and two females used the same nest on six days over periods of seven and eight days in which they were radio tracked. Four individuals used the same nest as another individual of the opposite gender, but on different days. However, this use of the nest of another bandicoot was not recorded within bandicoots of the same gender. Flushing a bandicoot from its nest may result in preventing the bandicoot from reusing the same nest on subsequent days, and should therefore be avoided during monitoring studies.

Nests of released bandicoots were often constructed in close proximity to one another. However, while the diurnal nesting ranges of two thirds of released males overlapped, the diurnal nesting ranges of released females did not overlap at either release site.

On Dorre and Bernier Islands most western barred bandicoots used the same nest repeatedly over a period of a week, though some animals were found to use a different nest each night (Friend and Burbidge 1995). Eastern barred bandicoots may use the same nests for several days, but many nest sites are also “temporary” (Seebeck 2001). Adult males were found to occupy more nests than females, and one female occupied the same nest for six consecutive days (Dufty 1991). Long-nosed bandicoots radio tracked at least once a week at the Sydney Harbour National Park used an average of two nests during a tracking period of 6 – 8 weeks (Scott et al. 1999). It is therefore likely that reintroduced western barred bandicoots at Heirisson Prong utilise nests in a similar fashion to Dorre and Bernier Island western bandicoots and other species of bandicoots in Australia.

4.4.3 Nest sharing

Nest sharing was observed once between a male and female western barred bandicoot on Heirisson Prong, and once between a female and her two nearly independent offspring. The only incidence of nest sharing observed on Dorre Island
was between females and their young (Friend and Burbidge 1995). However, Gould (1863) reported that “the nest [of *P. myosurus*] is generally inhabited by pairs”, and Burbidge (1981) suggested that two animals may occasionally share one nest. Nest sharing between adults is probably rare, but may occur between sexes during oestrous.

Dufty (1991) found no incidence of nest sharing between adult eastern barred bandicoots during radio tracking studies in Victoria.

### 4.4.4 Shrub preference

Western barred bandicoots released at Heirisson Prong in May 1997 appeared to show some preference for the use of particular shrub species as nest sites. In particular, bandicoots showed a strong preference for two of the common shrub species *Acacia ligulata* and *Acacia tetragonophylla*, and two of the less common species *Alectryon oleifolius* and *Eucalyptus obtusifolia*. These species were selected as nest sites in a far greater proportion than that reflected by their availability within the environment. These four species of shrubs preferred by bandicoots were associated typically with greater litter depth than the shrub species avoided. These shrub species may in turn therefore offer greater ease of construction of nests, greater protection from predators and thermoregulatory benefits, due primarily to the presence of a deeper layer of ground litter.

Despite being common, *Thryptomene baeckeacea* and *Melaleuca cardiophylla* appeared to be avoided by western barred bandicoots, as were a number of other less common shrub species. *Thryptomene baeckeacea* in particular, was the most common shrub species at the release sites, however none were used as nest sites by bandicoots in May 1997. This species was not used for nest sites in May 1998, but was used in February 1999 (Section 5.3.1). It is possible that this variation in shrub species chosen was a seasonal anomaly, or that once settled within their new environment, bandicoots chose a wider variety of shrub species.

### 4.4.5 Nest temperature

The nests of western barred bandicoots appeared to be important as refuges from the heat of summer on Heirisson Prong, offering considerable thermoregulatory benefits. The temperatures within nests during monitoring in February 1999 were typically maintained between 24°C and 40°C, varying by up to only nine degrees within
any single nest. By comparison, during the same period of monitoring, ambient temperatures in the sun varied from 18°C to 60°C. Temperatures within nests rose and climbed slowly, not showing the rapid rise and fall of surface temperatures commonly experienced both in the sun, and in the shade underneath shrubs. Bandicoots resting in their nests during the day would therefore not be as exposed to extremes of ambient temperature that might cause heat stress.

During the nights most nests were vacated as bandicoots foraged for food or searched for mates. However, for large furred young left in the nest, temperatures within the nest would remain warmer than the ambient temperature, offering the young a more constant environment, typically of 24 – 30°C. Similarly, the insulative properties of the nests may be just as important to young left in the nest in the winter months, as during summer. Young long-nosed bandicoots are left in the nest for approximately ten days before weaning is complete (Gordon and Hulbert 1989).

There appears to be a trend for the temperature of western barred bandicoot nests to approximate the surface temperature at 29 - 34°C. There was a similar trend for the temperature of occupied rufous bettong nests to approximate ambient temperature at 30°C (Rübsamen et al. 1983). Researchers in the latter study found that nest wall temperatures were well above the ambient temperature on cold days and approximated the ambient temperature on warm days.

Sampson (1971) thought that nests may be important as heat refuges during summer for brush-tailed bettongs. With a daily maximum temperature of 35°C, the temperature in their nests was only 29.5°C, slightly less than 30°C, the temperature at which heat stress may occur. Dawson and Bennett (1978) found that porcupine grass Triodia angusta hummocks used by the spectacled hare-wallaby Lagorchestes conspicillatus on Barrow Island provided an effective barrier against thermal radiation.

There were no significant effects of canopy cover, shrub height or litter depth of nests on the temperature range experienced within nests. This suggests that the nests themselves confer considerable thermoregulatory benefits to resident bandicoots, and that the shrub contributes little, if any, additional thermoregulatory benefits.
4.4.6 Possible reasons for nest construction

One of the primary reasons for the construction of nests by western barred bandicoots is likely to be the thermoregulatory benefits, accruing both to adults during the day time, and to nearly independent young left in the nest during the day and night. However, this is probably not the sole reason for nest construction.

Chambers and Dickman (2002) have suggested that nests of long-nosed bandicoots may provide protection from wind and rain. Wallis et al. (1989) suggested that the nests of rufous bettongs in northeastern New South Wales do more than shade animals from solar radiation, as overhead cover alone would achieve this without the need to build an elaborate nest. They suggested that nests offered protection from both aerial and terrestrial predators; particularly those nests that incorporated part of the local vegetation into their outer layer.

The majority of nests constructed by western barred bandicoots at Heirisson Prong offered protection from diurnal predators that hunt by sight. Rarely was any portion of a bandicoot exposed in a nest, and nests were typically well concealed underneath a layer of surface litter at least 40 mm deep. For example, diurnally hunting snakes such as the king brown (Shine 1991), or raptors such as the wedge-tailed eagle (Reymond and Wolfe 1981) that occur at Heirisson Prong, would not be expected to be predators of the western barred bandicoot, despite sharing the same habitat. However, as many of the nests were easily accessible by predators due to a lack of dense shrub cover at ground level, diurnal predators that hunt by smell would often have easy access to a bandicoot in its nest. For example, resident Gould’s monitors use a combination of visual, olfactory and auditory cues to detect their prey (Thompson 1996), and thus might be expected to detect a western barred bandicoot in its nest. The inconspicuous nature of western barred bandicoot nests, combined with the lack of flushing of bandicoots upon approach to their nest, would suggest that even a monitor might not easily locate a bandicoot in its nest by appearance alone. If disturbed, the bandicoot would also have a chance to exit its nest and escape to neighbouring shrubs or rabbit burrows, as occurred on two occasions at Heirisson Prong following human disturbance.

Despite the energy cost associated with nest construction, the western barred bandicoots at Heirisson Prong used a number of nests, and usually changed nest sites every one or two days. The benefits of constructing multiple nests may lie in predator
evasion, by reducing the likelihood of a “sit-and-wait predator”, choosing to wait at an occupied nest, and by reducing odour build-up and other signs of nest occupation, so that even an olfactory predator could be avoided.

Nests would not be expected to confer any protection from nocturnal predators such as owls, feral cats, and foxes, as adult bandicoots typically depart from their nests after dusk. In this case, the density of vegetative cover in the vicinity of nests would be more important in avoiding aerial predators. However, bandicoots would be exposed to a risk of predation by feral cats on vacating their nest of an evening, as feral cats hunt by sight, are accomplished “sit-and-wait predators” (Newsome 1995), and may be able to chase bandicoots through less dense, prickly areas of shrub cover. The most common items found in their diet in Australia are rabbits, small mammals and reptiles (e.g. Dickman 1996; Paltridge 2002; Risbey, Calver and Short 1999). Cats eat a wide variety of native and introduced mammals, and have been found to consume bandicoots when available (Christensen and Burrows 1994; Dufty 1991).

Foxes are regarded as opportunistic hunters and scavengers, with no specialized food requirements (Henry 1986; Saunders, Coman, Kinnear and Braysher 1995). Henry (1986) suggested that they have a predisposition to stalk and ambush prey, rather than chasing for long distances. The most common items in the diet of foxes in Australia are rabbits, sheep, house mice and insects, but they also consume many other native vertebrates, including macropods, possums and bandicoots (Booth and McCracken 1994; Coman 1973; Croft and Hone 1978; Scott et al. 1999; Short et al. 2002; Watson and Halley 1999). Their surplus killing behaviour (Short et al. 2002) renders them a serious threat to species in a confined area, such as the reintroduced western barred bandicoot at Heirisson Prong. The areas of dense shrub on Heirisson Prong may offer some protection from foxes and cats, however in times of drought and/or high rabbit density when vegetation is severely defoliated, the ability of vegetative cover to offer a refuge from predators may be limited.

Eastern barred bandicoots that once occurred in open grasslands in Victoria are likely to have had little defense against predation by foxes due to the lack of dense cover and refuge sites. Short et al. (2002) detailed examples of surplus killing of eastern barred bandicoots by foxes near Hamilton in Victoria in 1906 – 1914, and at a nearby reintroduction site in 1998 – 1999, despite the implementation of a fox control program. Eastern barred bandicoots do construct nests in a similar fashion to western
barred bandicoots; however, little cover was available in these open grassland areas once bandicoots had vacated their nests.

4.5 Conclusions

Western barred bandicoots construct and utilise nests in a similar fashion to other species of bandicoots in Australia. While they appear to favour certain shrub species for nest sites, they display flexibility in being able to use a variety of shrub species, as long as surface litter is present for nest construction.

It is likely that the inconspicuous nests of western barred bandicoots offer protection from both solar radiation and from predators that hunt by sight in daylight. However, while nests offer protection during the day, the density of vegetation is likely to be more important in protecting bandicoots from nocturnal predators. With the introduction of novel predators to Australia, both nest sites and vegetation that offered suitable protection from predators would have been critical for the persistence of the western barred bandicoot on the mainland.

Periods of high rabbit abundance or drought may lead to reduced shrub cover. Such negative impacts on vegetation may in turn limit the ability of bandicoots to construct nests that adequately convey protection from extremes of temperature and predators. This chapter described the nesting biology of the western barred bandicoot at Heirisson Prong. The importance of a high rabbit density as a factor that may cause disturbance to nests at Heirisson Prong is discussed in Chapter Five.
Chapter 5

The impact of rabbits on the shelter sites of the western barred bandicoot

5.1 Introduction

One hypothesis for the decline of medium-sized mammals is that grazing by exotic species (sheep, goats and rabbits) has led to changes in the structure and species composition of native vegetation, and thus greatly reduced the quality of habitat for native fauna (Calaby and Grigg 1989; Lunney 2001; Marlow 1958; Morton 1990; Newsome 1975). These changes may affect the quality of habitat by reducing the amount or continuity of the food supply, and available cover for shelter from predators and temperature extremes.

More specifically, it has been suggested that the rabbit was one of the causal factors in the decline of native fauna, exerting its effects by: competition for food, burrows and warrens; destruction of habitat structure or cover; and by supporting populations of feral predators, thereby facilitating the reduction of less fecund and more vulnerable native species through predation (Robley et al. 2002; Sandell and Start 1999). The impact of rabbits is of particular concern in dry inland areas where some tree and shrub species do not germinate regularly because of irregular rainfall patterns, so that the opportunity for regeneration is limited by both rabbits and rainfall (Williams et al. 1995). Crisp and Lange (1976) and Lange and Graham (1983) suggested that some species of woodland trees and tall shrubs of the arid zone may be destined for extinction due to the selective elimination of their seedlings.

Although the impacts of grazing by introduced herbivores on native vegetation have been widely studied in Australia, most studies have dealt with sheep and cattle (e.g. Graetz 1978; King and Hutchinson 1983; Matus and Tothmeresz 1990) or a combination of impacts by livestock, kangaroos and rabbits (e.g. Andrew 1988; Foran 1980; Friedel 1985; Landsberg, James, Morton, Hobbs, Stol, Drew and Tongway 1997; Lange and Graham 1983; Leigh, Wood and Holgate 1989; Neave and Tanton 1989; Newsome 1971). Little research has been conducted on the specific impacts of rabbits on vegetation structure, despite suggestions that their impacts have contributed to the
demise of many medium-sized mammals in Australia (e.g. Calaby 1969; Finlayson 1961; Frith 1973; Harper 1945; Le Souef 1923; Woinarski, Milne and Wanganeen 2001).

Rabbits were introduced to the Australian mainland with the arrival of the First Fleet in 1788 (Stodart and Parer 1988). However, the species did not successfully establish until after 1859 with the introduction of the wild type rabbit. It subsequently spread to occupy most of its present range by 1910 (Sandell and Start 1999; Stodart and Parer 1988). The impact of rabbits on specific plant species has been inferred from studies of diet (e.g. Chesterfield and Parsons 1985), and they have been implicated in preventing the regeneration of many plant species (e.g. Auld 1990, 1993, 1995; Cooke 1991; Foran, Low and Strong 1985; Lange and Graham 1983). Rabbits have their worst effects on native vegetation during periods of drought after a period of plenty. When populations are high and food resources begin to dwindle, rabbits ringbark and defoliate small trees and shrubs, strip bark and snip off smaller twigs in their search for succulent vegetation. While the end result is usually a crash in the rabbit population, in the meantime it may also result in substantial damage to the vegetation, through elimination of seedlings, ringbarking or defoliation of small trees and shrubs, and shrub death (Williams et al. 1995).

While it is often obvious that rabbits have an impact on the structure of vegetation, little effort has been made in Australia to quantify the extent of this impact in isolation from other grazing species (Auld 1995; Williams et al. 1995). Previous efforts have concentrated on impacts across broad landscapes, rather than at the level of individual shrubs. The impacts of rabbits on grasses and herbs, Acacia spp., chenopods such as bluebush Maireana sedifolia, M. pyramidata and canegrass Zygochloa paradoxa, cypress pine Callitris columellaris, woody weeds and a number of other palatable species in the semi-arid and arid regions of Australia are summarised by Williams et al. (1995). Most examples relate to the lack of regeneration of these species due to grazing by rabbits. For example, Auld (1990, 1993, 1995) conducted studies on the impact of rabbits on the regeneration of Acacia carnei and A. oswaldii at Kinchega National Park in western New South Wales and found that rabbits greatly limited seedling regeneration.

Western barred bandicoots utilise shrubs as cover from predators, shelter from temperature extremes, and as a foraging site for invertebrate food. Grazing by
herbivores such as rabbits may therefore reduce the availability of cover, suitable nest sites (for predator avoidance and thermoregulatory benefits; Chapter 4), and foraging areas. In addition, there is some evidence of a decline in litter size in bandicoots, and therefore fecundity, as a result of high densities of rabbits at Heirisson Prong (Section 3.4.2). As a consequence, rabbits and other introduced herbivores may have contributed to the demise of the western barred bandicoot from mainland Australia in the early 1900s, in addition to any impacts arising from predation.

In this chapter, I examine the impact of rabbits on the three shrub species most commonly used by bandicoots as nest sites after their release to free-range on Heirisson Prong in 1997 over a three year period between 1997 and 1999. High rabbit numbers of up to 13.3 per spotlight kilometre on Heirisson Prong over the summer of 1997/1998 (Figure 5.1) due to the absence of predators, compared with a long-term average of 2.6 per spotlight kilometre (Robley et al. 2002; Short 1999) prior to, and after this period, provided an ideal opportunity to quantify the impact of a high density rabbit population on the native vegetation over a 2-3 year frame.

The changes in vegetation, combined with changes in the use of shrubs for nest sites by western barred bandicoots during these periods of high and low rabbit densities, were expected to provide some indication of whether grazing by introduced herbivores such as rabbits, can limit the availability of cover for nest sites, and shelter from predators and high temperature extremes, for the western barred bandicoot at Heirisson Prong. The aims of this chapter are therefore to:

- Quantify the impact of rabbits on native vegetation used by bandicoots as nest sites at Heirisson Prong; and
- Assess the responses of bandicoots to this impact.
Figure 5.1: Monthly rainfall for Denham from 1995 - 1999 (grey bars), long-term median rainfall for Denham 1893 - 2000 (thick black line), and rabbit sightings per kilometre ± SE on Heirisson Prong between April 1995 and October 1999 (thin black line; Robley et al. 2002; Short 1999). Red arrows denote time of nest choice measurements (Table 5.7).

5.2 Methods

5.2.1 Variation in nest use between years

Rabbit density varied from low to high over the period of study (Figure 5.1). This variation provided an opportunity to study the response of bandicoots to changes in rabbit abundance and associated changes to vegetation structure on Heirisson Prong by examining nest construction. In May 1997 when rabbit density was 5.5 per spotlight kilometre, ten bandicoots were radio collared and tracked daily to their nest sites over periods of 6 - 11 days, as outlined in Section 4.2.1. In May 1998 (rabbit density had declined to 3.0 per spotlight kilometre) and February 1999 (rabbit density was 0.7 per spotlight kilometre) groups of nine and eight bandicoots, respectively, were radio-collared and tracked daily to their nest sites over periods of 2 - 8 days, following similar methods as in May 1997. The shrub species chosen by bandicoots for diurnal shelter
were identified and their attributes and those of the nest were measured as per the methods outlined in Section 4.2.1. The variation in nest use between years was examined by chi-squared contingency tests, comparing shrub species used for > 5 nest sites in any one monitoring period with all other shrub species and nest locations during that same monitoring period. Due to the use of the same data sets for successive chi-squared contingency tests (increasing the risk of type-I error), the sequential Bonferroni correction was used, with chi-squared contingency tests carried out in order of highest to lowest percentage nest use (Rice 1989; Cabin and Mitchell 2000).

5.2.2 Impact of rabbits on vegetation at Heirisson Prong

Three species of shrubs commonly used by western barred bandicoots for nest sites in May 1997 were chosen: Acacia tetragonophylla, A. ligulata and Melaleuca cardiophylla (Tables 4.5 and 5.1). Ten shrubs of each species were fenced with wire mesh to a height of 80 cm to exclude rabbits, with a 20 cm mesh skirt at ground level to prevent burrowing (Plate 5.1). Each of these shrubs was paired with an unfenced shrub of the same species. Unfenced shrubs were chosen to be in close proximity, and as similar in size, structure and canopy cover as possible to the fenced shrub. All shrubs were marked with flagging tape and metal stakes for identification. The paired shrubs allowed a comparison of shrubs free of the impact of rabbits (fenced) with those subject to the impact of rabbits (unfenced). Sixty shrubs were therefore chosen at 11 locations on Heirisson Prong and monitored on 6 – 7 occasions between July or October 1997 and September 1999 (Figure 5.2).
Plate 5.1: *Acacia ligulata* shrub on Heirisson Prong fenced to exclude rabbits.

Measurements of percentage canopy cover, shrub height, canopy height above ground, litter depth, percentage ground litter cover, and ease of penetration of the shrub by a potential predator were taken for each of the 60 shrubs during each monitoring period. Canopy cover was expressed as the percentage of ground covered by the shrub canopy, when the edges of the canopy were projected down to the ground surface (Barbour, Burk and Pitts 1987). Both the foliage and branches were regarded as part of the canopy, as it was expected that bandicoots would not distinguish between these two forms of cover over their nest sites. Shrub height was measured from the central base to the tip of the highest branch or leaf of each shrub, whether dead or alive. Canopy height above ground was assessed as the average height of the canopy above the ground in five random locations within each shrub. Litter depth was taken as the average depth in five random locations under each shrub, and percentage ground litter cover was the average percentage of ground covered by litter in three randomly placed 50 x 50 cm quadrats under each shrub. Ease of penetration was a subjective measurement based on a scale of 1 – 5 (Plates 4.1 – 4.3), where ‘1’ represented a shrub that was easily penetrable at ground level with no obstacles to a fox accessing a bandicoot in a nest, and ‘5’ was regarded as inaccessible by a fox due to dense, prickly branches and foliage obscuring a potential bandicoot nest site, as outlined in Section 4.2.1.
Figure 5.2: The location of vegetation exclosures and adjacent paired (unfenced) shrubs on Heirisson Prong.
Shrub monitoring began in July 1997 (for some *Acacia tetragonophylla*) and October 1997 (for the majority of *A. tetragonophylla* and all *A. ligulata* and *Melaleuca cardiophylla*) during a peak in rabbit density on Heirisson Prong of over 13 rabbits per spotlight kilometre, and continued through a crash in rabbit numbers (down to 0.4 rabbits per spotlight kilometre). The final monitoring period was in September 1999 when rabbit numbers were on the increase again at 1.7 rabbits per spotlight kilometre (Figure 5.1). All shrubs were monitored at two to four monthly intervals in October 1997, January, May, July and October 1998, and approximately one year later in September 1999. Measurements of dead shrubs (those that died during the study) were included in analyses.

Only two fenced and one unfenced *A. tetragonophylla* shrubs were measured in July 1997 when first fenced to exclude rabbits, and not all measurements were taken. Those samples available were used graphically only to denote the beginning of the experiment. Due to the limited samples it would be unwise to draw any definitive conclusions about the beginning state of this species, and as such, these measurements were not used in the analyses.

Data were checked for normality using the univariate Anderson-Darling test described by Aitchison (1986) and performed by GenStat Edition 6.2 (Lawes Agricultural Trust 2002). Percentage canopy cover and percentage litter cover were arcsine-transformed prior to analyses.

Single-factor repeated measures ANOVAs were conducted for each plant species. Univariate repeated measures ANOVAs were chosen in preference to a multivariate approach due to the greater degrees of freedom and power associated with the analysis (Green 1993). For each fenced shrub (no rabbit damage) there was a matched unfenced shrub (subject to rabbit damage) and the response variables were the shrub measurements. The difference between the paired fenced and unfenced shrub measurements within species, within time periods was analysed (as per the method of Driscoll and Roberts 1997). There were ten subjects or blocks (location of paired shrubs), two treatments (fenced and unfenced), and five repeated measures (two during and three after the period of high rabbit abundance). The null hypothesis ($H_0$) was that there was no difference between monitoring periods in the mean difference of the response variables between the fenced and unfenced shrubs, or that rabbit damage to unfenced shrubs did not cause these shrubs to respond differently to the fenced shrubs.
A statistically significant effect was defined as a significant change in a response variable between monitoring periods. Tests of blocks were not made in any of these analyses, because they would require the unwarranted assumption of no time x block interaction.

5.2.3 Impact of rabbits on regeneration of Acacia ligulata

Observations on the regeneration of Acacia ligulata on Heirisson Prong were noted during the period of study for this thesis, between 1995 and 1999, providing a further opportunistic insight into the impact of rabbits on vegetation structure. These observations were descriptive, and not intended for formal analysis.

5.3 Results

5.3.1 Variation in nest use between years

5.3.1.1 May 1997

In May 1997 the shrub species most frequently used by bandicoots for nest sites was Acacia tetragonophylla at 33%, followed by Melaleuca cardiophylla at 13% (Table 5.1). The ground litter cover under the A. tetragonophylla shrubs ranged from 50 – 100%, the average litter depth from 1 – 42 mm, shrub height from 500 – 1500 mm, percentage canopy cover from 15 – 60%, and ease of penetration from 1 – 4. The ground litter cover of the Melaleuca cardiophylla shrubs ranged from 50 – 90%, the average litter depth from 5 – 18 mm, shrub height from 600 – 800 mm, percentage canopy cover from 50 – 90%, and ease of penetration from 1 – 3.
Table 5.1: Use of nest sites by bandicoots radio tracked in May 1997 immediately after release to free-range, and in May 1998 and February 1999. Shrubs used ≥ 5 times within a monitoring period are underlined.

<table>
<thead>
<tr>
<th>Nest location</th>
<th>May 1997</th>
<th>% Nests used (#)</th>
<th>May 1998</th>
<th>% Nests used (#)</th>
<th>February 1999</th>
<th>% Nests used (#)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acacia ligulata</td>
<td>11.1 (5)</td>
<td>60.5 (23)</td>
<td></td>
<td></td>
<td>14.7 (5)</td>
<td></td>
</tr>
<tr>
<td>Acacia tetragonophylla</td>
<td>33.3 (15)</td>
<td>2.6 (1)</td>
<td></td>
<td></td>
<td>14.7 (5)</td>
<td></td>
</tr>
<tr>
<td>Alectryon oleifolius</td>
<td>6.7 (3)</td>
<td>2.6 (1)</td>
<td></td>
<td></td>
<td>2.9 (1)</td>
<td></td>
</tr>
<tr>
<td>Alyogyne cuneiformis</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td>2.9 (1)</td>
<td></td>
</tr>
<tr>
<td>Atriplex bunburyana</td>
<td>0</td>
<td>2.6 (1)</td>
<td></td>
<td></td>
<td>11.8 (4)</td>
<td></td>
</tr>
<tr>
<td>Eucalyptus obtusifolia</td>
<td>4.4 (2)</td>
<td>2.6 (1)</td>
<td></td>
<td></td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Eremophila glabra</td>
<td>4.4 (2)</td>
<td>0</td>
<td></td>
<td></td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Exocarpus aphyllus</td>
<td>2.2 (1)</td>
<td>0</td>
<td></td>
<td></td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Marsdenia sp.</td>
<td>2.2 (1)</td>
<td>2.6 (1)</td>
<td></td>
<td></td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Melaleuca cardiophylla</td>
<td>13.3 (6)</td>
<td>5.3 (2)</td>
<td></td>
<td></td>
<td>5.9 (2)</td>
<td></td>
</tr>
<tr>
<td>Pimelea microcephala</td>
<td>2.2 (1)</td>
<td>0</td>
<td></td>
<td></td>
<td>5.9 (2)</td>
<td></td>
</tr>
<tr>
<td>Rhagodia eremiana</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td>2.9 (1)</td>
<td></td>
</tr>
<tr>
<td>Scaevola spinescens</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td>2.9 (1)</td>
<td></td>
</tr>
<tr>
<td>Stylobasium spathulatum</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td>2.9 (1)</td>
<td></td>
</tr>
<tr>
<td>Thryptomene baeckeacea</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td>17.6 (6)</td>
<td></td>
</tr>
<tr>
<td>Rabbit burrow</td>
<td>11.1 (5)</td>
<td>10.5 (4)</td>
<td></td>
<td></td>
<td>2.9 (1)</td>
<td></td>
</tr>
<tr>
<td>No nest</td>
<td>8.9 (4)</td>
<td>10.5 (4)</td>
<td></td>
<td></td>
<td>11.8 (4)</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>45</td>
<td>38</td>
<td></td>
<td></td>
<td>34</td>
<td></td>
</tr>
</tbody>
</table>

5.3.1.2 May 1998

In May 1998, immediately after a period of high rabbit abundance on Heirisson Prong (Figure 5.1), the predominant shrub species used by bandicoots for nest sites was Acacia ligulata at 60% (Table 5.1). Of the 23 A. ligulata shrubs measured, 74% were dead. The ground litter cover under these shrubs ranged from 77 – 100%, the average litter depth from 26 – 80 mm, shrub height from 850 – 2750 mm, percentage canopy cover from 20 – 85%, and ease of penetration from 1 – 5.

5.3.1.3 February 1999

In February 1999, during a period of low rabbit abundance on Heirisson Prong (Figure 5.1), bandicoots selected a wide variety of shrub species for nest sites, choosing Thryptomene baeckeacea at 18 %, followed by A. ligulata and A. tetragonophylla at
14.7 %. (Table 5.1). They showed no marked preferences for particular shrub species, as they had done in previous monitoring periods. The three main species chosen were markedly different in structure. *A. ligulata* forms tall shrubs about two metres in height with substantial quantities of ground leaf litter (Plate 5.2), *A. tetragonophylla* forms medium shrubs up to 1500 mm in height, with good ground litter (Plate 5.3), whereas *T. baeckeacea* is a low heath about 400 mm in height and is characterised by very little litter, most of which is composed of small twigs (Plate 5.4).

### 5.3.1.4 Comparison between years

Four shrub species used for > 5 nest sites in any one monitoring period (*Acacia ligulata, A. tetragonophylla, Thryptomene baeckeacea* and *Melaleuca cardiophylla*) were compared with all other shrub species and nest locations during the same monitoring period. There was a significant difference in the frequency of *A. ligulata* ($\chi^2 = 28.67, p < 0.001, \alpha = 0.012$), *A. tetragonophylla* ($\chi^2 = 13.99, p = 0.001, \alpha = 0.025$) and *Thryptomene baeckeacea* ($\chi^2 = 15.26, p = 0.001, \alpha = 0.017$) used for nest sites compared to all other shrub species and locations (rabbit burrows or no nest) used for nest sites by bandicoots between years of monitoring. There was no significant difference for the frequency of use of *M. cardiophylla* ($\chi^2 = 2.27, p = 0.321, \alpha = 0.05$).

Six of the 34 nests used in February 1999 were comprised of native grasses and/or introduced *Brassica* sp., in addition to the leaf litter and twigs used in the previous two years. Three of those six were constructed under *Thryptomene baeckeacea* shrubs. This was the first occasion on which grasses were sighted in any obvious abundance on Heirisson Prong (Plate 5.5), and the first period of radio tracking when bandicoots had used grass as nest material. One nest constructed under a *T. baeckeacea* was covered with a layer of sand, in addition to the presence of grass. This was the only nest recorded where sand was used in its construction.
Plate 5.2: Bandicoot nest under an *Acacia ligulata* (during monitoring of nest temperature) with a substantial amount of ground litter, and dense canopy cover, consisting mainly of branches.

Plate 5.3: Nest of a western barred bandicoot under an *Acacia tetragonophylla* in May 1997 showing the nest entrance, with substantial litter for nest construction.
Chapter 5: Impact of rabbits

Plate 5.4: An example of a *Thryptomene baeckeacea* in February 1999 with a bandicoot nest under the canopy.

Plate 5.5: Grass regeneration on Heirisson Prong in February 1999 when rabbits were at low density, which was then used as nesting material by bandicoots.
5.3.2  **Impact of rabbits on vegetation at Heirisson Prong**

Of the 30 fenced exclosures, 29 appeared successful in excluding rabbits. One *Acacia ligulata* was damaged by rabbits, but all other fenced shrubs showed no signs of rabbit damage during the experiment.

In May 1997 the first signs of shrub defoliation on Heirisson Prong were evident, and rabbits were recorded at a density of 5.5 per spotlight kilometre (Figure 5.1). However, by May 1998 when rabbits had declined to a density of 3.0 per spotlight kilometre from a peak of 13.3 per spotlight kilometre seven months earlier, many shrubs had been severely defoliated. During monitoring in February 1999, much of the vegetation had recovered from the defoliation caused by rabbits during their peak in numbers over the summer of 1997/1998. This occurred after good rains had fallen in winter 1998, and a decline in rabbit numbers to a density of 0.7 per spotlight kilometre allowed regeneration of the vegetation.

5.3.3  **Percentage canopy cover**

In the analyses below, data used in the repeated measures analysis of variance did not differ significantly from a normal distribution.

5.3.3.1  *Acacia tetragonophylla*

There was a significant difference in the mean arcsine-transformed percentage canopy cover of fenced and unfenced *A. tetragonophylla* shrubs over time (Table 5.2). Fenced shrubs increased slightly in canopy cover between July and October 1997, while the canopy cover of unfenced shrubs almost halved over the same period, declining from a canopy cover of 50% to 30% (Figure 5.3). Between October 1997 and January 1998 the canopy of fenced shrubs continued to maintain cover (despite a lack of rainfall during this period; Figure 5.1) while unfenced shrubs continued to decrease slightly in the presence of the continued high rabbit density. Between January and May 1998 both fenced and unfenced shrubs decreased in canopy cover (with no rainfall and high, but declining rabbit density), then both increased from May to July 1998 (following the period of first substantial rainfall (> 20 mm) for the year in May and low, declining rabbit density). After July 1998 the canopy cover of fenced shrubs showed little change from 70% through to the last monitoring period in September 1999, while unfenced
shrubs continued to increase slightly over the same period to approach the cover level of the fenced control shrubs.

Table 5.2: Summary of single-factor, repeated measures analysis of variance comparing the difference in arcsine-transformed percentage canopy cover of fenced and unfenced (block) shrubs over time. *P* value corrected using Greenhouse-Geisser epsilon (GGε).

<table>
<thead>
<tr>
<th>Shrub species</th>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th><em>F</em> test</th>
<th>GGε</th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Acacia tetragonophylla</td>
<td>Time</td>
<td>5</td>
<td>1523.26</td>
<td>304.65</td>
<td>3.87</td>
<td>0.5006</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Block</td>
<td>9</td>
<td>10455.69</td>
<td>1161.74</td>
<td>14.76</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>45</td>
<td>3541.49</td>
<td>78.70</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. ligulata</td>
<td>Time</td>
<td>5</td>
<td>3048.61</td>
<td>609.72</td>
<td>6.26</td>
<td>0.5007</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Block</td>
<td>9</td>
<td>12152.30</td>
<td>1350.26</td>
<td>13.87</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>45</td>
<td>4381.48</td>
<td>97.37</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Melaleuca cardiophylla</td>
<td>Time</td>
<td>5</td>
<td>2059.0</td>
<td>411.8</td>
<td>4.05</td>
<td>0.5697</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Block</td>
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<td>4316.8</td>
<td>479.6</td>
<td>4.71</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>45</td>
<td>4579.4</td>
<td>101.8</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Final levels of canopy cover were slightly greater than the initial level for both fenced and unfenced shrubs. Unfenced shrubs suffered severe canopy losses and one of these shrubs died between July and October 1998. The most substantial losses occurred in the first three months after monitoring began, when rabbits were peaking in number. Rabbit damage included defoliation and bark stripping (Plate 5.6). Despite the severe and obvious impact of rabbit herbivory, the majority of shrubs managed to recover to ≥50% canopy cover, approximating their initial state in July 1997.

5.3.3.2 Acacia ligulata

*A. ligulata* shrubs were first measured in October 1997. At this stage, the shrubs chosen were similar in canopy cover (Figure 5.3). There was a significant difference in the mean arcsine-transformed percentage canopy cover of fenced and unfenced *A. ligulata* shrubs over time (Table 5.2). Fenced shrubs maintained a similar canopy cover of nearly 60% between October 1997 and January 1998, while the canopy cover of unfenced shrubs decreased to 23% over the same period when the rabbit population was at a high density and increasing. Between January and May 1998 the canopy cover of both fenced and unfenced shrubs decreased (with no rainfall and high, but declining rabbit density). In the following two months, the canopy cover of fenced shrubs
continued to decrease (despite low rabbit density), then increased slowly from July 1998 (after the first substantial rainfall for the year) through to September 1999. Beyond May 1998 the unfenced shrubs showed little change in canopy cover, generally at < 20%.

Plate 5.6: Rabbit damage to an *A. tetragonophylla* shrub in 1998, showing severe defoliation and bark stripping.

Final levels of canopy cover were less than the initial level for both fenced and unfenced shrubs, though canopy cover of fenced shrubs was significantly greater than that of unfenced shrubs. Two of the ten fenced shrubs died (despite no rabbit damage); one in May 1998 and one in September 1999, and all ten unfenced shrubs died (thought to be due to rabbit damage) between May 1998 and September 1999 (with seven deaths occurring in the last year of monitoring). The most substantial losses of canopy cover occurred in the first three months of monitoring, when rabbits were declining in number. Rabbit damage included severe defoliation and biting of branch tips (Plate 5.7). Canopy cover of unfenced shrubs was comprised only of branches after shrub death (Plate 5.8).
Figure 5.3: Change in mean ± SE percentage canopy cover over time in fenced and unfenced *Acacia tetragonophylla*, *A. ligulata* and *Melaleuca cardiophylla* shrubs.
Plate 5.7: Rabbit damage to an *A. ligulata* shrub in 1998, showing severe defoliation of the canopy and biting of tips of branches.

Plate 5.8: An example of an unfenced dead *Acacia ligulata* shrub, thought to have died due to severe rabbit damage over the summer of 1997/1998.
5.3.3.3  *Melaleuca cardiophylla*

*M. cardiophylla* shrubs were first measured in October 1997. At this stage, the shrubs chosen were similar in canopy cover (Figure 5.3). There was a significant difference in the mean arcsine-transformed percentage canopy cover of fenced and unfenced *M. cardiophylla* shrubs over time (Table 5.2). Fenced shrubs increased in canopy cover between October 1997 and January 1998, while the canopy cover of unfenced shrubs decreased over the same period. From January through to July 1998 the canopy cover of both fenced and unfenced shrubs decreased, reaching just 20% for unfenced shrubs. The canopy cover of both fenced and unfenced shrubs increased from July 1998 to September 1999.

Final levels of canopy cover were less than the initial level for unfenced shrubs but greater for fenced ones (45% compared to > 60%), and that of fenced shrubs was significantly greater than that of the unfenced shrubs. Unfenced shrubs suffered severe and long-lasting canopy losses. Two of the unfenced shrubs died; one in May 1998 and one in September 1998.

5.3.4  **Shrub height**

5.3.4.1  *Acacia tetragonophylla*

Despite being fenced in July 1997, no height measurements were taken for the *A. tetragonophylla* shrubs until October 1997. At this time, however, the mean height of fenced and unfenced shrubs was similar. There was no significant difference in the mean height of fenced and unfenced shrubs over time (Table 5.3), as evidenced by similar decreases and increases of paired shrubs throughout the study period (Figure 5.4). There was a decrease in the height of shrubs over the summer and autumn of 1997 to 1998, followed by a slow increase due to regrowth of foliage after rainfall in May 1998 through to 1999. The mean height of fenced shrubs was always higher than that of unfenced shrubs.
Table 5.3: Summary of single-factor, repeated measures analysis of variance comparing the difference in height (cm) of fenced and unfenced shrubs (block) over time. $P$ value corrected using Greenhouse-Geisser epsilon (GGε).

<table>
<thead>
<tr>
<th>Shrub species</th>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>$F$ test</th>
<th>GGε</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
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<td>Acacia</td>
<td>Time</td>
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<td>393.93</td>
<td>78.79</td>
<td>0.92</td>
<td>0.6892</td>
<td>0.45</td>
</tr>
<tr>
<td>tetragonophylla</td>
<td>Block</td>
<td>9</td>
<td>3112.93</td>
<td>3458.10</td>
<td>40.23</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>45</td>
<td>3868.07</td>
<td>85.96</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. ligulata</td>
<td>Time</td>
<td>5</td>
<td>4564.0</td>
<td>912.8</td>
<td>3.20</td>
<td>0.4289</td>
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<td>Block</td>
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<td>31737.6</td>
<td>3526.4</td>
<td>12.34</td>
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<td></td>
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<tr>
<td></td>
<td>Residual</td>
<td>45</td>
<td>12856.0</td>
<td>285.7</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Melaleuca</td>
<td>Time</td>
<td>5</td>
<td>88.68</td>
<td>17.74</td>
<td>0.39</td>
<td>0.6365</td>
<td>0.77</td>
</tr>
<tr>
<td>cardiophylla</td>
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<td>8508.02</td>
<td>945.34</td>
<td>20.74</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Residual</td>
<td>45</td>
<td>2051.48</td>
<td>45.59</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

5.3.4.2 Acacia ligulata

There was no significant difference in the mean height of fenced and unfenced A. ligulata shrubs over time, although a trend toward significance was evident (Table 5.3). The mean height of fenced shrubs was lower than the unfenced shrubs at the beginning of monitoring in October 1997 (Figure 5.4). The height of fenced shrubs increased between October 1997 and January 1998, while the height of unfenced shrubs decreased slightly during the same period and continued to do so until the end of monitoring in September 1999 due to loss of all foliage and death. The fenced shrubs maintained a similar mean height between January 1998 and October 1998, before increasing again in the following year through to September 1999. During the final period of monitoring, the heights of all shrubs were similar, despite the death of unfenced shrubs.

5.3.4.3 Melaleuca cardiophylla

There was no significant difference in the mean height of fenced and unfenced shrubs over time (Table 5.3; Figure 5.4). All shrubs increased in height slightly between October 1997 and January 1998 despite the high rabbit numbers, then decreased between January and May 1998. Fenced shrubs began to recover in May 1998 (at the time of the first significant rainfall for the year), and continued to gain height. Unfenced shrubs were slower to recover, not showing any height increase until
October 1998 and then decreasing slightly in the final year of monitoring through to September 1999.
Figure 5.4: Change in mean ± SE shrub height over time in fenced and unfenced *Acacia tetragonophylla*, *A. ligulata* and *Melaleuca cardiophylla* shrubs.
5.3.5 **Canopy height above ground**

5.3.5.1 *Acacia tetragonophylla*

The canopy height above ground was measured for only three *A. tetragonophylla* shrubs in July 1997.

There was no significant difference in the mean canopy height above ground of fenced and unfenced *A. tetragonophylla* shrubs over time (Table 5.4), with little fluctuation throughout the period of the study (Figure 5.5). The canopy height above ground of fenced shrubs did increase between July and October 1998 after rainfall, but declined in a similar fashion to unfenced shrubs thereafter.

**Table 5.4**: Summary of single-factor, repeated measures analysis of variance comparing the difference in height of canopy cover above ground of fenced and unfenced shrubs (block) over time. *P* value corrected using Greenhouse-Geisser epsilon (GGε).

<table>
<thead>
<tr>
<th>Shrub species</th>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>F test</th>
<th>GGε</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acacia tetragonophylla</em></td>
<td>Time</td>
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<td>1836.4</td>
<td>367.3</td>
<td>1.39</td>
<td>0.3511</td>
<td>0.28</td>
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<td>Block</td>
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<td>7558.5</td>
<td>839.8</td>
<td>3.17</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>45</td>
<td>11925.7</td>
<td>265.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. ligulata</em></td>
<td>Time</td>
<td>5</td>
<td>1829.7</td>
<td>365.9</td>
<td>1.48</td>
<td>0.4289</td>
<td>0.25</td>
</tr>
<tr>
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<td>Block</td>
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<td>9323.7</td>
<td>1036.0</td>
<td>4.19</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Residual</td>
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<td>11134.5</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Melaleuca cardiophylla</em></td>
<td>Time</td>
<td>5</td>
<td>142.39</td>
<td>28.48</td>
<td>1.12</td>
<td>0.5553</td>
<td>0.36</td>
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<td>Block</td>
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<td>983.28</td>
<td>109.25</td>
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<td></td>
<td>Residual</td>
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<td>1143.99</td>
<td>25.42</td>
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<td></td>
</tr>
</tbody>
</table>

5.3.5.2 *Acacia ligulata*

There was no significant difference in the mean canopy height above ground of fenced and unfenced *A. ligulata* shrubs over time (Table 5.4). Both fluctuated in a similar manner, with an initial period of decrease over the first three months, followed by an increase in early 1998 (Figure 5.5). Canopy height above ground of fenced shrubs increased to its highest level by September 1999, while that of unfenced shrubs hardly fluctuated at all from October 1998 to September 1999.
5.3.5.3 *Melaleuca cardiophylla*

There was no significant difference in the mean canopy height above ground of fenced and unfenced *M. cardiophylla* shrubs over time (Table 5.4). The canopy height above ground of fenced shrubs decreased between October 1997 and May 1998, while that of unfenced shrubs increased over the same period and continued to do so through to July 1998 (Figure 5.5). After a brief period of decrease between July and October 1998, the canopy height above ground of both fenced and unfenced shrubs increased through to September 1999. The canopy height above ground of fenced shrubs was always lower than that of unfenced shrubs, and for fenced shrubs was similar at the start and end of monitoring, but was higher at the end of monitoring than at the beginning for unfenced shrubs.
Figure 5.5: Change in mean ± SE canopy height above ground over time in fenced and unfenced *Acacia tetragonophylla*, *A. ligulata* and *Melaleuca cardiophylla* shrubs.
5.3.6 **Percentage ground litter cover**

5.3.6.1 *Acacia tetragonophylla*

No measurements of percentage ground litter cover were taken for *A. tetragonophylla* shrubs in July 1997. There was no significant difference in the mean percentage of ground litter cover of fenced and unfenced shrubs over time (Table 5.5). The percentage ground litter cover of fenced shrubs gradually increased by 10% throughout the period of monitoring, and was always greater than that of unfenced shrubs (Figure 5.6). Percentage ground litter cover under unfenced shrubs decreased slightly between October 1997 and January 1998, increased throughout the year until October 1998, then decreased again over the last year of monitoring to a level similar to that occurring in October 1997.

Table 5.5: Summary of single-factor, repeated measures analysis of variance comparing the difference in percentage ground litter cover (arcsine-transformed) of fenced and unfenced shrubs (block) over time. *P* value corrected using Greenhouse-Geisser epsilon (GG*ɛ*).

<table>
<thead>
<tr>
<th>Shrub species</th>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>F test</th>
<th>GG<em>ɛ</em></th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
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<td>221.9</td>
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<td>0.6720</td>
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<td>9</td>
<td>14338.5</td>
<td>1593.2</td>
<td>13.19</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>45</td>
<td>5436.0</td>
<td>120.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. ligulata</em></td>
<td>Time</td>
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<td>1762.1</td>
<td>352.4</td>
<td>2.03</td>
<td>0.5698</td>
<td>0.14</td>
</tr>
<tr>
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<td>7796.0</td>
<td>173.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Melaleuca cardiophylla</em></td>
<td>Time</td>
<td>5</td>
<td>398.8</td>
<td>79.8</td>
<td>1.06</td>
<td>0.6557</td>
<td>0.38</td>
</tr>
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<td>Block</td>
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<td>4804.5</td>
<td>534.2</td>
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</tr>
<tr>
<td></td>
<td>Residual</td>
<td>45</td>
<td>3373.1</td>
<td>75.0</td>
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<td></td>
</tr>
</tbody>
</table>

5.3.6.2 *Acacia ligulata*

There was no significant difference in the mean percentage of ground litter cover of fenced and unfenced *A. ligulata* shrubs over time (Table 5.5). The percentage ground litter cover of fenced and unfenced shrubs was similar at the beginning of the experiment in October 1997. However, while there was an increase in litter cover under fenced shrubs between October 1997 and May 1998, litter cover decreased slightly under unfenced shrubs over the same period, and continued to do so through to July
1998 (Figure 5.6). From this point onwards, both fenced and unfenced shrubs followed a similar trend, changing little until September 1999. The percentage ground litter cover under fenced shrubs was slightly greater, and under unfenced shrubs was lower in September 1999 than at the commencement of the study.

5.3.6.3 *Melaleuca cardiophylla*

There was no significant difference in the mean percentage of ground litter cover of fenced and unfenced *M. cardiophylla* shrubs over time (Table 5.5). Similar changes occurred in the percentage of ground cover under fenced and unfenced shrubs over time (Figure 5.6). After an initial period of slight increase in ground litter cover between October 1997 and January 1998, there were periods of decrease through to July 1998, increase between July and October 1998, and decrease in the following year until September 1999.
Figure 5.6: Change in mean ± SE percentage ground litter cover over time in fenced and unfenced *Acacia tetragonophylla*, *A. ligulata* and *Melaleuca cardiophylla* shrubs.
5.3.7  **Ground litter depth**

5.3.7.1  *Acacia tetragonophylla*

There was no significant difference in the mean ground litter depth under fenced and unfenced *A. tetragonophylla* shrubs over time (Table 5.6). Litter depth was similar in both fenced and unfenced *A. tetragonophylla* shrubs in October 1997 (Figure 5.7). However, mean litter depth under fenced shrubs increased through to October 1998, whereas litter depth under unfenced shrubs decreased slightly through to July 1998, with no signs of increase until October 1998. In the final year of monitoring, the litter depth under both fenced and unfenced shrubs decreased. Litter depth under fenced shrubs had increased by almost 2 cm from the initial depth in October 1997 of 2.8 cm to 4.7 cm in September 1999. However litter depth under unfenced shrubs remained similar.

Table 5.6: Summary of single-factor, repeated measures analysis of variance comparing the difference in litter depth (cm) of fenced and unfenced shrubs (block) over time. *P* value corrected using Greenhouse-Geisser epsilon (GGε).

<table>
<thead>
<tr>
<th>Shrub species</th>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>F test</th>
<th>GGε</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
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<td>Time</td>
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<td>25.73</td>
<td>5.15</td>
<td>2.14</td>
<td>0.6646</td>
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<td>12.93</td>
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<td>Residual</td>
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<td>108.16</td>
<td>2.40</td>
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<td>0.6031</td>
<td>0.06</td>
</tr>
<tr>
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<td>Time</td>
<td>5</td>
<td>28.62</td>
<td>5.72</td>
<td>2.75</td>
<td>0.6031</td>
<td>0.06</td>
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<tr>
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<td>0.14</td>
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<tr>
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<td>3.45</td>
<td>0.38</td>
<td>2.91</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>45</td>
<td>5.93</td>
<td>0.13</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

5.3.7.2  *Acacia ligulata*

Despite a strong tendency, there was no significant difference in the mean ground litter depth under fenced and unfenced *A. ligulata* shrubs over time (Table 5.6). Litter depth was similar under both fenced and unfenced *Acacia ligulata* shrubs in October 1997 (Figure 5.7). However, mean litter depth of fenced shrubs increased through to May 1998, whereas litter depth under unfenced shrubs decreased during the same period. There was a decrease in litter depth under fenced shrubs between May and July.
1998, followed by an increase between July and October 1998. Litter depth under unfenced shrubs was similar between May and July 1998, but increased between July and October 1998. Litter depth remained similar under both fenced and unfenced shrubs between October 1998 and September 1999, though the litter depth under fenced shrubs was 1.5 cm greater than that found under unfenced shrubs.

5.3.7.3 *Melaleuca cardiophylla*

There was no significant difference in the mean litter depth under fenced and unfenced *M. cardiophylla* shrubs over time (Table 5.6). Litter depth was similar under both fenced and unfenced *M. cardiophylla* shrubs in October 1997 (Figure 5.7). However, litter depth of fenced shrubs increased through to January 1998, whereas litter depth under unfenced shrubs decreased. Between January and July 1998 the litter depth of all shrubs decreased. Litter depth of both fenced and unfenced shrubs then increased in October 1998 and remained at a similar level through to September 1999. Litter depth under fenced shrubs remained similar between the beginning and end of the experiment, however under unfenced shrubs it decreased slightly during the same period.
Figure 5.7: Change in mean ± SE ground litter depth over time in fenced and unfenced *Acacia tetragonophylla*, *A. ligulata* and *Melaleuca cardiophylla* shrubs.
5.3.8 Penetration

5.3.8.1 Acacia tetragonophylla

The mean penetration score of fenced and unfenced *A. tetragonophylla* shrubs differed over time (Table 5.7). The mean penetration score was similar in both fenced and unfenced *Acacia tetragonophylla* shrubs in October 1997 (3.5; Figure 5.8). However, by January 1998, the penetration score of fenced shrubs had increased more than unfenced shrubs. The penetration score of both fenced and unfenced shrubs fluctuated in a similar manner by decreasing and increasing slightly until July 1998. Over the next three months to October 1998 the penetration score of fenced shrubs increased slightly, while that of unfenced shrubs decreased, and continued to do so until September 1999 to 2.8. The penetration score of fenced shrubs decreased slightly over the final year of monitoring, however, the score of 4.1 was greater than at the beginning of the trial. The final penetration score of unfenced shrubs was lower in September 1999 than at the outset in October 1997.

Table 5.7: Summary of single-factor, repeated measures analysis of variance comparing the difference in penetration scores of fenced and unfenced shrubs (block) over time. *P* value corrected using Greenhouse-Geisser epsilon (GGε).

<table>
<thead>
<tr>
<th>Shrub species</th>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>F test</th>
<th>GGε</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acacia tetragonophylla</em></td>
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<td>1.79</td>
<td>3.03</td>
<td>0.5704</td>
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<td>9.07</td>
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<tr>
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<td>0.35</td>
<td>0.4228</td>
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<td>2.98</td>
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<td>0.75</td>
<td>3.38</td>
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<tr>
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<td>9.93</td>
<td>0.22</td>
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</table>

5.3.8.2 Acacia ligulata

There was no significant difference in the mean penetration score of fenced and unfenced *A. ligulata* shrubs over time (Table 5.7). The penetration score of fenced shrubs tended to increase over time, while that of unfenced shrubs changed little over the same period (Figure 5.8).
5.3.8.3 *Melaleuca cardiophylla*

The mean penetration score of fenced and unfenced *M. cardiophylla* shrubs differed significantly over time (Table 5.7). The penetration score of fenced shrubs showed an initial period of increase from 2.1 to 2.6 in the first three months of monitoring to January 1998, and then declined slowly through to September 1999 (Figure 5.8). The penetration score of unfenced shrubs tended to decline slowly over time from 1.9 to 1.3, and was lower than that of fenced shrubs from January 1998 through to September 1999.
Figure 5.8: Change in mean ± SE penetration score over time in fenced and unfenced *Acacia tetragonophylla*, *A. ligulata* and *Melaleuca cardiophylla* shrubs.
5.3.9 Impact of rabbits on regeneration of *Acacia ligulata*

No *Acacia ligulata* seedlings were sighted on Heirisson Prong between October 1995 and May 1998, when rabbit density ranged from 2.4 – 13.3/spotlight km (Figure 5.1). The first signs of regeneration of *Acacia ligulata* on Heirisson Prong were noted in late 1998 when rabbit density was low (< 1/spotlight km) and after winter rainfall (Plate 5.9). There was little evidence of rabbit damage to these seedlings throughout 1999, with rabbit density remaining at < 2/spotlight km.

Plate 5.9: *Acacia ligulata* seedlings in February 1999, demonstrating regeneration on Heirisson Prong when rabbits were at low density (0.71/spotlight km).

5.4 Discussion

5.4.1 Variation in nest use between years

Western barred bandicoots displayed a high degree of flexibility in nest construction, using a wide variety of shrub species for nest sites at Heirisson Prong. In May 1997, prior to the peak in rabbit abundance when vegetation was in good condition, nine shrub species were chosen as nest sites, with *A. tetragonophylla* the preferred option (Section 4.3.4). In May 1998 immediately after the peak in rabbit
abundance when shrubs such as *A. tetragonophylla, M. cardiophylla, Pimelea microcephala,* and *Scaevola spinescens* had been defoliated by rabbits, there was a definite preference for *A. ligulata* shrubs, with no discrimination between those living or dead, as both offered good surface litter cover and canopy cover, whether it be foliage and branches, or branches alone. By February 1999 when much of the vegetation had recovered and rabbit abundance was low, 11 shrub species were chosen as nest sites, including *Thryptomene baeckeacea.* This specimen was then the most commonly used for nest sites, despite not having been recorded as a nest site in previous years.

When introduced predators were scarce, rabbit density was low, and the vegetation was in good condition, western barred bandicoots appeared to use almost any available shrub species, even those with limited canopy cover and ground litter. Grasses were used in nest construction when available and soil was used once under a *T. baeckeacea* shrub that offered little in the way of litter for nest construction. The use of soil may therefore have been an alternative to litter, providing protection from the heat of the day in summer. When vegetation was in poor condition, this flexibility was maintained, but the preference of bandicoots appeared to be narrowed to the larger *A. ligulata* shrubs with a more dense canopy and greater ground litter cover.

Eastern barred bandicoots at Hamilton, Victoria, used as nest sites the introduced plants wormwood *Artemisia absinthium,* blue agapanthus *Agapanthus orientalis,* Monterey cypress *Cupressus macrocarpa,* and gorse *Ulex europaeus,* along with a variety of artificial debris associated with the Hamilton rubbish tip (Dufty 1994). The nests were commonly constructed using grass, leaves and twigs (Dufty 1991). At Gellibrand Hill Park, Victoria, eastern barred bandicoots nested in dense thickets of native *Acacia paradoxa,* within grass tussocks, and in or at the edge of stands of *Eucalyptus melliodora* and *Bursaria spinosa* (Murphy and Serena 1993). Soil, leaves and twigs were used in nest construction by eastern barred bandicoots held in captivity in Tasmania, either in thick shrubbery or in open areas among grass, clover and weeds (Heinsohn 1966). This ability of eastern barred bandicoots to construct nests under a variety of plant species and in open areas amongst grass tussocks suggests that the species demonstrates a similar degree of flexibility in nest site location to western barred bandicoots at Heirisson Prong.
Nests of the long-nosed bandicoot at North Head in the Sydney Harbour National Park, New South Wales, were typically found in areas with a dense understorey and leaf litter of > 60% cover, and often in areas where introduced weeds such as lantana *Lantana camara* and pampas grass *Cortaderia selloana* were common (Chambers and Dickman 2002). The northern brown bandicoot in Brisbane constructed nests of plant litter collected from the vicinity of the nest, including grasses and *Eucalyptus* leaves, and these were situated amongst tall ground cover so that they were concealed from sight (Gordon 1974). Two nests found during wet weather had a layer of soil on the surface, possibly acting as a waterproof layer (Gordon 1974). The southern brown bandicoot constructs nests amongst thick grass and may use earth, grass and other vegetation in nest construction (Courtenay 1996). All these bandicoots demonstrate an ability to use a variety of plant species for nest sites, including a range of introduced species. However, all plants used offer a substantial degree of vegetative cover that does not appear to be essential for the western barred bandicoot, which can nest under shrubs with sparse cover, providing litter is available.

The western barred bandicoot at Heirisson Prong utilised rabbit burrows as nest sites on a number of occasions. Abandoned rabbit burrows were sometimes used by eastern barred bandicoots in Tasmania (Heinsohn 1966).

5.4.2 Impact of rabbits on vegetation at Heirisson Prong

The impacts of a period of very high rabbit density over the summer of 1997/1998 on components of the vegetation at Heirisson Prong were both obvious and severe. Changes in plant structure and species composition were evident during and after the period of high rabbit abundance. The most obvious effects during the peak in rabbit numbers were a decrease in canopy cover of shrubs and the death of mature *Acacia ligulata*. Vegetation exclosures around the three species of shrub commonly used by western barred bandicoots for nest sites in May 1997 (*A. tetragonophylla*, *A. ligulata* and *Melaleuca cardiophylla*) acted as controls, unaffected by rabbit impact, while paired unfenced shrubs were subject to the impact of rabbits over a two-year period of monitoring between July or October 1997, and September 1999.

There was a series of effects that tended to be common to all shrub species where significant differences in canopy cover and penetration score of fenced and unfenced shrubs were noted over time. There was an initial period of rabbit damage to unfenced
shrubs from July or October 1997 through to May 1998 when rabbit density was high, which in some cases, extended through to July 1998. The first substantial rainfall for 1998 occurred in May, along with a four-fold decline in rabbit density, continuing with a ten-fold decline by July. The subsequent period of low rabbit density and winter rainfall promoted the recovery of canopy cover and shrub height from July 1998 onwards, with the exception of the 10 unfenced *A. ligulata*, 2 *M. cardiophylla* and 1 *A. tetragonophylla* and 2 unfenced *A. ligulata* shrubs that had previously died. This vegetation recovery continued throughout the dry spring and summer months of 1998 and 1999 in the presence of the low rabbit density, despite limited rainfall. However, penetration scores did not follow this trend, increasing slightly in mid or late 1998, but then continuing to decline over time. It is possible that the period of increase was a result of the release of plant toxins as a defence mechanism against rabbit grazing.

Rabbits reduced the canopy cover of all unfenced shrubs, but the degree of impact of rabbits on all other shrub measurements taken was variable and not as obvious. The decline in canopy cover did not necessarily correspond with a decline in shrub height, litter accumulation under the shrub or penetration score, as twigs and branches contributed to shrub height, litter composition, and penetration score, in a similar fashion to the contribution made by foliage. Twigs and branches of *A. tetragonophylla* and *A. ligulata* offered suitable protection from the removal of ground litter by strong prevailing southerly winds in summer, and litter accumulation under *M. cardiophylla* shrubs was minimal, regardless of rabbit density or rainfall, due to the small size of its foliage.

By contrast, the fenced shrubs (where there was a significant difference in the mean shrub measurements with the paired unfenced shrubs over time) tended to show an increase in canopy cover and penetration score in the latter half of the year after winter rainfall, and a decline early in the year after drought conditions over summer, demonstrating a relationship with rainfall, but not with rabbit density. The shrub height of the fenced *A. ligulata* tended to increase over time, with no obvious relationship to rainfall.

The three shrub species appeared to possess different abilities to withstand heavy rabbit grazing. In general, unfenced *A. tetragonophylla* shrubs defoliated due to grazing by rabbits had tended to regain their former structure by September 1999 during the preceding period of low rabbit density. Unfenced *M. cardiophylla* shrubs tended not to
regain their former structure, and unfenced *A. ligulata* shrubs declined to such an extent that they were unable to recover, and all were dead by the end of monitoring in September 1999. Bark stripping by rabbits during extended dry conditions has been noted in *A. carnei*, *A. victoriae* and *Eremophila sturtii*, leading to mortality or dieback in established plants (Auld 1993).

The death of *A. ligulata* on Heirisson Prong did not appear to have any repercussions on the ability of bandicoots to use the shrubs as nest sites, at least over the short term. However, if there is little regeneration, the species will no longer be available to western barred bandicoots in future as sites for nest construction and foraging.

Robley (2000) found that the niche of rabbits and burrowing bettongs at Heirisson Prong was sufficiently different to allow their co-existence, suggesting that facets of the biology of bettongs, such as a broad and adaptable diet, and large foraging range to search for high quality food, diminished the potential impact of the rabbit on the population dynamics of the burrowing bettong. In a similar fashion, the western barred bandicoot may be buffered by differences in niche use and biology, from the impact of rabbits at Heirisson Prong. As bandicoots are omnivorous (Visser 2000) and appear to be flexible in their ability to use a variety of shrub species with vastly different structure, canopy cover and surface litter for nest sites, it is unlikely that some loss of *A. ligulata* would be entirely detrimental to the western barred bandicoot.

The spring of 1998 was the first time that *A. ligulata* seedlings and numerous grasses had been seen on Heirisson Prong since the reintroduction of the western barred bandicoot in 1995. Grasses dominated the winter diet of rabbits at Heirisson Prong in 1996 and 1997 (Robley, Short and Bradley 2001), and their grazing appears to keep grasses at low biomass. Both rabbits and bettongs made use of *A. ligulata* in their diet in the summer and winter of these years (Robley et al. 2001). The presence of grass in bandicoot nests in February 1999 reflected this increase in abundance of grass and decrease in rabbit abundance on Heirisson Prong after mid-1998. Grasses may be a preferred nesting material when available, and are utilised by other species of bandicoot including the eastern barred bandicoot (Dufty 1991) and long-nosed bandicoot (Scott et al. 1999).

Over 150 years of grazing by sheep and rabbits in the semi-arid zone has caused a major discontinuity in the size structure of shrubs, with the landscape devoid of
seedlings due to a lack of regeneration (Pickard 1991). For example, Woodell (1990) found that some populations of *A. burkittii* in South Australia had not regenerated for at least 75 years, under grazing pressure from rabbits and sheep. Auld (1993) found limited regeneration in *A. carnei* in only seven of 37 populations across its range, and caging experiments at Kinchega National Park indicated that rabbits were primarily responsible for the observed lack of regeneration for the last 20 - 50 years. Virtually all *A. oswaldii* seedlings exposed to rabbit grazing did not survive, and those that did, tended to be protected from grazing if they had established within the protective canopy of small shrubs such as *Maireana pyramidata* (Auld 1995). Rabbits have also caused the death of mature *A. carnei* by the construction of warrens near the roots, which result in collapse and death of shrubs (Auld 1993). Lange and Graham (1983) found that rabbits grazed with extreme selectivity, actively seeking out *Acacia* seedlings that represented a very small percentage of the biomass of the surrounding vegetation. Foran et al. (1985) found that rainfall had a greater influence on short-term changes in plant composition than the exclusion of rabbits during a two-year experiment on calcareous shrubby grassland in central Australia, where rabbit populations were reduced from up to 22 to less than 5 rabbits per kilometre of spotlight transect. However, Auld (1993) suggested that there was likely to be a long-term decline in many *Acacia* species in arid and semi-arid Australia due to the lack of regeneration caused by rabbit grazing unless active rabbit control was instigated.

The release and establishment of the rabbit calicivirus disease (RCD) in 1995 caused a decline of more than 80% in rabbit abundance in much of the rangelands (semi-arid and arid Australia), and led to a subsequent reduction in grazing pressure (Cooke 1999). Evidence of native vegetation recovery was found at a series of RCD monitoring sites across Australia, including increases in palatable grasses and moderately-palatable plants, increased seedling regeneration of *Acacia* spp. and woody perennials (e.g. *Bursaria spinosa*), increases in shrub and tree regrowth (especially chenopod shrubs and rosewood *Alectryon oleifolius*; Sandell and Start 1999). Edwards, Pople, Saalfeld and Caley (2004) recommended that damage by rabbits and other introduced pest species be monitored directly, noting that most managers monitor pest population size as an indicator of associated damage, and correlations between pest numbers and damage caused by those pests may not be concordant.
5.5 Conclusions

Even where some regeneration of vegetation is evident, rabbits need to be maintained at low densities for many years to allow the more palatable species of plants to regenerate (Williams et al. 1995). The impact of rabbits at high densities may result in a decrease in both survival and regeneration of susceptible plant species such as *A. ligulata*. However, the cost of rabbit control, the difficulty of controlling rabbits in the presence of western barred bandicoots (which are susceptible to 1080 poisoning due to their omnivorous diet and small size), and the apparent ability of bandicoots to co-exist with rabbits and show no obvious signs of a decrease in fecundity, may mean that rabbit control is neither desirable, nor necessary, from a management perspective.

There is currently a lack of adequate data on the impact of rabbit density on plant regeneration. Such information could allow managers to reduce rabbit density to levels that would allow regeneration and vegetation recovery to occur (Auld 1995). However, there is a need also to consider the range of fauna species within any ecosystem, and their food resources, if integrated management of introduced and native fauna is to be achieved (Newsome 1989). The management of an individual species such as the rabbit cannot be considered in isolation at Heirisson Prong.

Marshall (1966, p. 208) stated that “The key to the survival of wild animals and plants is the preservation of their habitats”. However, in the case of the western barred bandicoot, a preserved, or ‘unmodified’ habitat may be of far less importance than the eradication of introduced predators. Its flexibility in use of materials for nest construction and its omnivorous diet may enable the species to survive in the face of an environment modified by rabbit grazing, as long as predators are absent.

This chapter summarised the impact of rabbits and rainfall on three species of native shrubs used by bandicoots as nest sites, and examined the changes in choice of nest site with varying rabbit density. The following chapter describes the use of population viability analysis to determine the probability of extinction of the reintroduced bandicoot population on Heirisson Prong, where rabbits are present and occasional fox and cat incursions occur, compared with the wild population on Dorre Island where introduced mammal species are absent.
Chapter 6

Population viability analysis of remnant and reintroduced populations of the western barred bandicoot

6.1 Introduction

Many populations of threatened mammals in Australia persist as small and isolated populations, in the wild, at reintroduction sites, or both. The western barred bandicoot is one such mammal, which persists as two remnant island populations, and two small, reintroduced populations at Heirisson Prong (Chapter 2, 3, 4 and 5; Richards and Short 2003) and the Arid Recovery Project near Roxby Downs in South Australia (Arid Recovery 2003; Richards 2003). Friend and Orell (1997), Maxwell et al. (1996) and Richards (2003) outlined additional potential mainland reintroduction sites for the species, including Dragon Rocks Nature Reserve, Kalbarri National Park, Lake Magenta Nature Reserve, Dryandra Woodland and the Fitzgerald River National Park in Western Australia, and Yookamurra Sanctuary, Venus Bay Conservation Park, Lincoln National Park, Coffin Bay National Park, and Flinders Ranges National Park in South Australia.

The viability of the existing or any proposed populations over the long-term is uncertain. Factors that are likely to threaten their viability are: predation by introduced foxes and feral cats, the smallness of the populations, their isolation, environmental variability, lack of suitable refuges, loss of genetic variation, and interactions between these factors. A number of reintroductions of the endangered eastern barred bandicoot have taken place in Victoria but have had limited success, due to predation, drought and loss of habitat.

The viability of populations can be assessed by modelling, using population viability analysis (PVA), which provides a technique for modelling the chance of extinction or persistence of a population within a specified time frame into the future (Possingham and Davies 1995). Some indication of the likelihood of persistence of the reintroduced population of western barred bandicoots at Heirisson Prong prior to the establishment of additional populations may assist in determining whether these future
reintroduction sites are likely to sustain viable populations, and in making management decisions to improve the probability of their persistence. The more detailed the data that are available about a species, the more realistic a PVA will be (Shaffer 1990); however, all too often, the data used for input into models are limited and involve a substantial amount of estimation. At Heirisson Prong, we are able to use biological data collected from the wild and reintroduced western barred bandicoot populations for input into PVA software to compare the probability of extinction of bandicoot populations subjected to different management strategies, and reserve size. In turn, this may assist in determining best management practices, choice of reintroduction site, and minimum levels of management for this, and future bandicoot reintroductions.

The aim of this chapter is to briefly review the concept and use of PVA, and to examine some key management issues related to the reintroduction of the western barred bandicoot. These are: (1) reserve size, (2) loss of genetic variation in reintroduced populations, (3) founder size, and (4) impact of different levels of predation. I use the PVA software package VORTEX (Lacy, Borbat and Pollak 2003). Scenarios are explored for both the Dorre Island population and the small, reintroduced population on Heirisson Prong.

6.2 Population Viability Analysis (PVA)

The concept of population viability was formalised by Shaffer (1981) when he described a selection of the stochastic processes that impact on populations. These processes described by Shaffer (1981) and more recently by Morris and Doak (2002), include:

- Demographic stochasticity – random fluctuations in observed birth, death and growth rate, and sex ratio of a population even if probability of birth and death remain constant;
- Environmental stochasticity – fluctuation in probability of birth and death resulting from fluctuations in the environment (e.g. weather, disease, predator and prey abundance, availability of habitat);
- Catastrophic events – extreme environmental variation (epidemic disease, cyclone, fire, flood), which can often lead to extinction (Simberloff 1986, 1988);
• Genetic drift – "cumulative and non-adaptive fluctuation in allele frequencies resulting from the random sampling of genes in each generation" (Lacy 1993), including problems of inbreeding, loss of heterozygosity, and decline in ability to adapt to future environmental change;

• Spatio-temporal variation – when multiple populations are considered, birth, death and growth rates are unlikely to be equal across all sites and habitats, and metapopulations may be linked by movement of individuals; and

• Density dependence – a change in the performance of individuals, and therefore population growth rate, as the size or density of a population changes.

The term PVA was coined by Gilpin and Soulé (1986), and was regarded as a “structured, systematic and comprehensive examination of the interacting factors that place a population or species at risk”. Recent authors have opted to restrict PVA to quantitative modelling techniques (Ralls, Beissinger and Cochran 2002; Reed, Mills, Dunning, Menges, McKelvey, Frye, Beissinger, Anstett and Miller 2002).

Populations become increasingly vulnerable to extinction the smaller they become, as the processes within small populations are unpredictable (Lindenmayer, Clark, Lacy and Thomas 1993). The fate of these populations can be modelled, based on simulated probability distributions (Lacy 1993). PVA uses simulation modelling to explore the various deterministic and stochastic forces contributing to the dynamics of small populations and has been used increasingly to assist in the management of threatened species (Table 6.1; Lacy 1993; Soulé 1986). By adjusting parameters within the model (such as founder population size, carrying capacity, frequency of predation event) and choosing the best result, it has the potential to be used as a management tool in the field of conservation biology.

At its simplest, a ‘count-based PVA’ model may predict only the total number of individuals in a single population, treating all individuals within the population as identical, and not taking into account spatial locations or habitat suitability. At the more complex end of the PVA spectrum are the ‘multi-site’ spatially-explicit models that track the location of all individuals, through birth, reproduction and movements, to death (Morris and Doak 2002). Morris and Doak (2002) maintained a philosophy of keeping models simple, avoiding complex models that require more biological detail and ultimately lead to an illusion of more accurate estimates, which are undermined by
a considerable degree of guesswork. Caughley and Gunn (1996) highlighted the
difference between single-species population models and interactive ecological system
models. The single species models on which PVAs are usually based do little to take
into account interactions between a population and its environment, and do not integrate
the complex ecological interactions that are involved in the conservation of any species.
The more complex interactive models that involve the dynamics of an ecological
system, in its simplest form an herbivore and the plants it eats, may be closer to reality.

There are a wide variety of PVA software packages available, including RAMAS
(Akçakaya and Ferson 1992; Ferson 1990; Ferson and Akçakaya 1990), VORTEX
(Lacy 1993; Lacy et al. 2003); ALEX (Possingham and Davies 1995; Possingham,
Davies, Noble and Norton 1992), GRIER and SPGPC (Grier 1980), GAPPS (Downer
1993; Harris, Metzgar and Bevin 1986), SIMPOP (Lacy, Flesness and Seal 1989), and
INMAT (Mills and Smouse 1994), but the latter five of these programs have been less
widely used. There have also been a number of models developed for specific animals
such as the helmeted honeyeater (Menkhorst and Middleton 1991), African elephant
(Armbruster and Lande 1993), and the splendid fairy-wren (Brooker and Brooker
1994). The process of PVA has been examined in detail by Beissinger and McCullough
(2002), Boyce (1992), Lindenmayer et al. (1993), Morris and Doak (2002), and
Possingham, Lindenmayer and Norton (1993). Some authors have also compared the
various different PVA packages (Lindenmayer, Burgman, Akçakaya and Lacy 1995)
and the use of PVA packages for a single set of data (e.g. Brook, Cannon, Lacy,
Mirande and Frankham 1999; Brook, O'Grady, Chapman, Burgman, Akçakaya and
Frankham 2000; Lindenmayer et al. 1995). Generic PVA packages are particularly
advantageous as they are open to evaluation and iterative development (Brook, Lim,
Harden and Frankham 1997), and facilitate use by scientists with no specialist skills in
modelling. However, users need to be aware of the constraints of the simulation
software, and in particular, the lack of input data for endangered species and the
differences between the model and the ecology of real populations (Caughley and Gunn
1996).

PVA does not predict what will happen to a population; it only forecasts the likely
effects on a population of the factors incorporated in the model, and therefore the
possible fates of the population (Lacy 1993). McCarthy, Andelman and Possingham
(2003) and McCarthy, Possingham, Day and Tyre (2001) thought that the value of many
PVA models lay in the relative predictions that they made, and their ability to help choose between management strategies. The IUCN recommend the use of PVA for quantitative analysis of the probability of extinction of populations in the wild for use in classifying species at high risk of extinction in the IUCN Red List (IUCN 2003). However, Taylor (1995) thought that current PVA techniques were not adequate to use the estimations of extinction risk as a common metric between species. Lindenmayer et al. (1993) recommended the use of PVA in the process of policy formulation, implementation, and appraisal for endangered species restoration, as a means of improving management. Richards (2003) recommended the use of PVA in the process of recovery planning for threatened Shark Bay marsupials, including the western barred bandicoot. On a cautionary note, it must be remembered that any PVA model is only as good as the data and assumptions input into the model (Lindenmayer et al. 1993). The use of any PVA has an inherent risk of making incorrect assumptions about biological data relating to the population under study.

As with all models which require the estimation of some input values, there has been constant debate over the usefulness of PVA in conservation biology since its inception. Numerous authors tout its usefulness as a management tool (e.g. Brook et al. 2000; Brook, Burgman, Akçakaya, O'Grady and Frankham 2002a; Reed et al. 2002), but many others suggest that the outcomes of PVA are usually too imprecise to be worthwhile, particularly where data are sparse or of low quality (e.g. Caughley 1994; Coulson, Mace, Hudson and Possingham 2001; Ellner, Fieberg, Ludwig and Wilcox 2002), and where confidence intervals, observation errors and possible catastrophes are not included (Ludwig 1999). Brook et al. (2002a) suggested that the alternatives to PVA are subjective decisions, often made by politicians with little scientific input, or “ecosystem-based” methods that are usually regarded as poorly developed and vague. However, Caughley (1994) and Caughley and Gunn (1996) offered alternative methods based on the diagnosis and treatment of population decline, and noted that determining which agent or agents are causal factors in the decline is pivotal to conserving a threatened species, rather than treating the problem of small population size. This logical series of actions to aid in endangered species recovery was outlined in Section 1.3, and was used by Short (1999) in relation to the burrowing bettong. Ralls et al. (2002) outlined a number of alternatives to PVA, with the choice of methods depending primarily upon management objectives and the quality and quantity of available data.
Brook et al. (2002a) suggested that one of the most important uses of PVA is to bring clarity to a problem, and that its predictive component is relatively unimportant. Lindenmayer et al. (1993) listed a number of strengths of PVA, which included:

- The production of a summary of the ecology of the species and identification of missing data;
- Providing a synthesis of the relative impact of interacting factors on population extinction and trends in population behaviour;
- Identification of threatening processes;
- Identification of minimum reserve size, providing assistance in reserve design;
- Clarification of management needs; and
- Enhancement of on-ground management techniques and decision-making.

Conversely, Lindenmayer et al. (1993) and Morris and Doak (2002) listed a number of limitations in the use of PVA, which include:

- PVA is a data-intensive technique and few data tend to be available for rare species;
- Observation errors will compromise the usefulness of data sets;
- PVA models omit too many factors that are likely to affect the viability of a population, and thus are highly simplified representations of the population dynamics and interactions between parameters of true biological populations;
- Does not examine the functional role (the interdependence of organisms) of a species within an ecosystem (Conner 1988);
- There is no single generic model applicable for all species; and
- PVA models are rarely validated.
### Table 6.1: Selected examples of the use of PVA in a range of studies, adapted from Lindenmayer et al. (1993) and Morris and Doak (2002).

<table>
<thead>
<tr>
<th>Use of PVA</th>
<th>Species</th>
<th>Primary causes of risk identified for the species</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
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<td>Assessing extinction risk of a population</td>
<td>Northern spotted owl <em>Strix occidentalis caurina</em></td>
<td>Habitat loss</td>
<td>Forsman, Sovern, Seaman, Maurice, Taylor and Joseph 1996; Lande 1988a</td>
</tr>
<tr>
<td>Choice of reserve size to maximise population persistence</td>
<td>Yellowstone grizzly bear <em>Ursus arctos</em></td>
<td>Habitat destruction, poaching</td>
<td>Pease and Mattson 1999</td>
</tr>
<tr>
<td>Choice of reserve size to maximise population persistence</td>
<td>Eastern barred bandicoot <em>Perameles gunnii</em></td>
<td>Habitat loss, predation, drought</td>
<td>Lacy and Clark 1990</td>
</tr>
<tr>
<td>Choice of reserve size to maximise population persistence</td>
<td>Yellow-bellied glider <em>Petaurus australis</em></td>
<td>Habitat alteration and reduction</td>
<td>Goldingay and Possingham 1993</td>
</tr>
<tr>
<td>Choice of reserve size to maximise population persistence</td>
<td>African elephant <em>Loxodonta africana</em></td>
<td>Habitat loss, poaching</td>
<td>Armbruster and Lande 1993</td>
</tr>
<tr>
<td>Choice of reserve size to maximise population persistence</td>
<td>Greater glider <em>Petauroides volans</em></td>
<td>Habitat loss, fire</td>
<td>Possingham, Lindenmayer, Norton and Davies 1994</td>
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<td>Level of culling/ poaching/ predation/ sustainable harvesting to maintain population persistence</td>
<td>African elephant <em>Loxodonta africana</em></td>
<td>Habitat loss, poaching</td>
<td>Armbruster and Lande 1993</td>
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<td>Determination of minimum viable population size</td>
<td>Sooty shearwaters <em>Puffinus griseus</em></td>
<td>Predation by introduced mammals</td>
<td>Hamilton and Moller 1993</td>
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<tr>
<td>Determination of minimum viable population size</td>
<td>Cape mountain zebra <em>Equus zebra</em></td>
<td>Hunting, habitat loss, grazing competition</td>
<td>Novellie, Millar and Lloyd 1996</td>
</tr>
<tr>
<td>Determination of minimum viable population size</td>
<td>Bighorn sheep <em>Ovis canadensis</em></td>
<td>Habitat loss, grazing competition</td>
<td>Berger 1990</td>
</tr>
<tr>
<td>Determination of minimum viable population size</td>
<td>Yellow-bellied glider <em>Petaurus australis</em></td>
<td>Habitat alteration and reduction</td>
<td>Goldingay and Possingham 1993</td>
</tr>
<tr>
<td>Determination of minimum viable population size</td>
<td>Sooty shearwaters <em>Puffinus griseus</em></td>
<td>Predation by introduced mammals</td>
<td>Hamilton and Moller 1993</td>
</tr>
<tr>
<td>Use of PVA</td>
<td>Species</td>
<td>Primary causes of risk identified for the species</td>
<td>Authors</td>
</tr>
<tr>
<td>--------------------------------------------------------------------------</td>
<td>---------------------------------------------</td>
<td>--------------------------------------------------</td>
<td>-------------------------------------------------</td>
</tr>
<tr>
<td>Planning of reintroductions and translocations, e.g. number of animals</td>
<td>Red-cockaded woodpecker <em>Picoides borealis</em></td>
<td>Habitat loss due to logging</td>
<td>Haig, Belthoff and Allen 1993</td>
</tr>
<tr>
<td>required, number of sites chosen, key parameters for long-term monitoring</td>
<td>Greater bilby <em>Macrotis lagotis</em></td>
<td>Predation by introduced mammals, drought</td>
<td>Southgate and Possingham 1995</td>
</tr>
<tr>
<td></td>
<td>Gray wolf <em>Canis lupus</em></td>
<td>Landscape fragmentation</td>
<td>Carroll, Phillips, Schumaker and Smith 2003</td>
</tr>
<tr>
<td>Identification of factors that represent risks to population survival</td>
<td>Leadbeater’s possum <em>Gymnobelideus leadbeateri</em></td>
<td>Logging, habitat loss</td>
<td>Lindenmayer <em>et al.</em> 1993</td>
</tr>
<tr>
<td>and at what life stage risks are greatest</td>
<td>Loggerhead turtle <em>Caretta caretta</em></td>
<td>Fisheries by-catch</td>
<td>Crouse, Crowder and Caswell 1987</td>
</tr>
<tr>
<td></td>
<td>Sooty shearwaters <em>Puffinus griseus</em></td>
<td>Predation by introduced mammals</td>
<td>Hamilton and Moller 1995</td>
</tr>
<tr>
<td>Determination of number of populations required to minimise extinction</td>
<td>Leadbeater’s possum <em>Gymnobelideus leadbeateri</em></td>
<td>Logging, habitat loss</td>
<td>Lindenmayer and Possingham 1996</td>
</tr>
<tr>
<td>risk</td>
<td>Fender’s blue butterfly <em>Icaricia icarioides fenderi</em></td>
<td>Habitat destruction</td>
<td>Schultz and Hammond 2003</td>
</tr>
<tr>
<td></td>
<td>Mountain brushtail possum <em>Trichosurus caninus</em></td>
<td>Habitat fragmentation</td>
<td>Lacy and Lindenmayer 1995</td>
</tr>
<tr>
<td>Analysis and synthesis of monitoring data</td>
<td>Gulf Coast beach mice <em>Peromyscus polionotus</em></td>
<td>Habitat loss and fragmentation</td>
<td>Oli, Holler and Wooten 2001</td>
</tr>
<tr>
<td></td>
<td>Leadbeater’s possum <em>Gymnobelideus leadbeateri</em></td>
<td>Logging, habitat loss</td>
<td>Lindenmayer and Possingham 1994</td>
</tr>
</tbody>
</table>
PVA is merely a modelling process. The result of a PVA is only an ‘estimate’ of the probability that a population will persist over time. The result is based on available information, the nature of which can range from very little to high quality long-term population data collected in the field. However, data are never available for all input parameters. PVA should be used to assess the improved probability of survival that would result from each possible management action (Lacy and Clark 1990).

Lindenmayer et al. (1993) recommended that PVA be integrated with a range of other approaches to wildlife management, and not be used in isolation. PVA is a single-species approach to conservation biology (Possingham et al. 1993) and it does not take into consideration aspects of community ecology, such as interactions between species and the functional role of species within an ecosystem (Conner 1988).

It has been recommended that researchers develop a new program that is tailored to the specific requirements of a particular species and management problem (e.g. Lindenmayer et al. 1995; Morris and Doak 2002); however, this requires a sound knowledge of programming and biostatistics, and may be better left to professionals in those fields, rather than ecologists. Generic packages have several advantages, including being relatively error-free, and preventing potentially inconsistent interactions between input parameters, which may affect results of viability analyses (Lindenmayer et al. 1995). Morris and Doak (2002) provided eight recommendations and cautions for practitioners conducting a PVA, which included:

1) Avoid conducting a PVA if data are sparse;
2) Estimates of population viability should be accompanied by confidence intervals;
3) View probability of population extinction as estimates only;
4) Do not try to project population viability for many centuries into the future;
5) Consider how potential determinants of population viability that have been omitted from the model might result in more optimistic or pessimistic model outcomes;
6) Do not base management on estimates of the probability of absolute extinction; rather, use a higher “quasi-extinction threshold”, where the population has declined to a point that is certain to lead to extinction;
7) Consider multiple models as a method of addressing model uncertainty; and
8) Regard a PVA as a work in progress, by incorporating additional data as it becomes available.

These issues should be considered by all practitioners of PVA prior to the commencement of modelling, and taken into consideration where applicable. While detailed knowledge of the demography of a population (rates of fecundity, mortality and dispersal, and major environmental variables) is preferred when using PVA, sensitivity analyses have been advocated as a means of isolating life history parameters that are influential in determining the probability of extinction of the population, and may pinpoint additional information that should be collected before the analysis may be regarded as reliable (Mills and Lindberg 2002). Sensitivity analysis involves repeating the analysis with variation in the value of individual parameters that may be critical to the outcome of the PVA. This aids in assessing the effect of uncertainty within the data used (Possingham et al. 1992), and provides insights into the factors that most affect population growth or the probability of quasi-extinction (Reed et al. 2002). One of the advantages of PVA modelling is that it can reveal the instability of a population long before it would be noticed through field observations during monitoring (Miller and Lacy 2003).

Brook et al. (1997) and Lindenmayer et al. (1993) reasoned that PVA is quantitative and objective by nature, and Brook et al. (2002a) concluded that PVA is not a useless tool, providing that data adequately capture the distribution of population growth and vital rates. However, they doubted that PVA can be used to reliably predict the future status of wild populations, due to the dynamic nature of ecological systems, and likelihood that population growth and vital rates will change in the future, as a result of environmental, anthropogenic or intrinsic processes. Finally, Lindenmayer et al. (1993) considered that the benefits of PVA outweigh the limitations, and Ralls et al. (2002) tabulated a list of questions as a first attempt at evaluation of PVA models and output.
6.3 A review of two PVA models – VORTEX and ALEX

As detailed above, there are a variety of models available for PVA, differing in capability, assumptions and ease of use. Two programs commonly used are VORTEX, an individual-based simulation model, and the Analysis of the Likelihood of Extinction (ALEX), a population-based simulation model. Lindenmayer et al. (1995) compared earlier versions of these software packages, but later versions have been updated and modified to address a variety of deficiencies within the early models. Both models provide default values for many parameters, to allow for missing data for some factors, such as environmental variation. The following brief description of each of these models current at February 2004, with primary strengths and limitations, provides a basis for the selection of PVA software to model the viability of wild and reintroduced western barred bandicoot populations.

6.3.1 VORTEX

The PVA model VORTEX Version 9.21 (Lacy et al. 2003) is a Monte Carlo simulation and has been described in detail by Lacy (1993) and Miller and Lacy (2003). It has been used extensively by the Conservation Breeding Specialist Group of the Species Survival Commission, IUCN, on a wide variety of threatened fauna, and because of this, is probably the most widely used PVA simulation program (Lacy 1993). The model was first developed as SIMPOP and later modified to VORTEX (Lacy 1993; Lacy and Clark 1990; Miller and Lacy 2003).

6.3.1.1 Strengths of VORTEX

- Models the impacts of inbreeding depression (reduction of fitness of individuals resulting from matings between related individuals, causing increased homozygosity in individuals and decreased heterozygosity of the population; Allendorf and Ryman 2002) and genetic drift on small, isolated populations.
- Provides opportunity to model density dependence in reproductive rate, although survival probabilities are density independent when population size is lower than the carrying capacity.
- Models catastrophes as sporadic random events that reduce survival and reproduction for one year.
• Allows harvesting or supplementing of population.
• Allows tracking of multiple sub-populations.
• Is applicable to species with low fecundity and long lifespan such as mammals, birds and reptiles.
• Can model monogamous or polygamous mating systems.
• Is user-friendly and able to be used by those with limited understanding of population biology and extinction processes.

6.3.1.2 Limitations and assumptions of VORTEX

• When examining the relationship between changes in population size and genetic variability, it can examine only one locus.
• All animals of reproductive age have an equal probability of breeding.
• Life-history attributes of a population (birth, death, migration, but also including harvesting and supplementation) are modelled as a sequence of discrete, seasonal events. The model ignores the possibility that they may be aseasonal or only partly seasonal.
• Genetic effects of inbreeding (loss of heterozygosity and a decrease in fitness of offspring) are based on one of two models: the unmasking of recessive lethal alleles (which become homozygous and result in death) or the loss of heterosis (loss of fitness resulting from loss of heterozygosity; Pusey and Wolf 1996), but impacts may fall between these two models. Inbreeding is assumed to affect first-year survival only.
• Assumes that animals continue to breed until they die, i.e. probability of reproduction and mortality is constant from age at first breeding till death.
• Migration rates are independent of age and sex.
• Catastrophe will have an effect on a population only in the year that the event occurs.
• Community dynamics, including interspecific interactions, cannot be modelled (e.g. cyclic predator-prey interactions).
• Does not model interactions among variables, e.g. if loss of habitat causes secondary changes in reproduction and mortality - VORTEX cannot simulate trends in these parameters.
6.3.2 **ALEX**

The Analysis of the Likelihood of Extinction (ALEX) Version 2.2 is a Monte Carlo simulation model and was developed by Possingham *et al.* (1992; 1993; 1994) for use in the management of Leadbeater's possum *Gymnobelideus leadbeateri* in Victoria. Its use has since been discussed by Ball, Lindenmayer and Possingham (2003), Lindenmayer and Possingham (1994), and Possingham and Davies (1995) and has been used by a variety of researchers in Australia. It is a spatially explicit metapopulation model, in which the population is assumed to exist in a number of isolated patches, and as such is regarded as best suited to the study of populations with greater than 100 individuals that are distributed in a number of locations (Possingham *et al.* 1992).

6.3.2.1 **Strengths of ALEX**

- A population-based generic model, applicable to most vertebrates;
- Incorporates metapopulation dynamics involving analysis of many sub-populations of varying size;
- Incorporates complex spatial structures of habitat patches that may differ in quality, and may be connected by corridors;
- For each patch, ALEX can follow several dynamic habitat variables that may affect or be affected by the likelihood of catastrophes;
- Allows the user to specify a variety of environmental processes, which can vary annually, and act on each patch independently, or globally on all patches simultaneously;
- Incorporates two kinds of movements by animals between patches - diffusion along corridors with zero mortality, and migration with a specific probability of dying; and
- Ability to compute a large number and wide variety of simulations rapidly.
6.3.2.2 Limitations and assumptions of ALEX

- It ignores the possible effects of genetic factors on population viability;
- Only one sex (females) is modelled;
- There are only three age classes – newborn, juvenile and adult, which are based on an annual time period;
- There is no provision for differences in mating systems and social structure; and
- There is no provision for reproduction to occur at less than one year of age.

6.4 Reasons for the choice of model

Lindenmayer et al. (1995) suggested that selection of a PVA model should be based on a range of criteria, including: (1) the key questions and objectives of the study, and (2) the strengths, limitations and assumptions that underpin the program, and how these compare with the life history parameters and data available for the species. VORTEX was chosen as the preferred model for use with the western barred bandicoot for a variety of reasons, which included its:

- Ability to examine single, isolated populations;
- Ability to take into account levels of genetic variation;
- Ability to account for supplementation of a population; and
- Ability to model catastrophes.

In addition, VORTEX has been used to model small populations of other species of *Perameles* (Banks 2004; Patrick and Myroniuk 1990 in Humphries and Seebeck 1995).

A spatially explicit model such as ALEX was not required, due to the isolation of the Dorre Island and Heirisson Prong populations where exchange between populations was limited to low levels of managed harvest and supplementation. The habitat quality parameters required by ALEX are unknown for the western barred bandicoot and may not be particularly significant for the species due to its apparent adaptability to changes in vegetation (Chapter 5). Thus VORTEX was chosen to minimise uncertainty in data input. ALEX has the potential to poorly represent the dynamics of small populations, due to the lack of effects of inbreeding depression and ignoring the possibility that males may be limiting or absent (Ball et al. 2003).
Ludwig (1999) demonstrated that estimates of parameters that are important in population dynamics are likely to have large confidence intervals. VORTEX does not include any confidence intervals for the probability of extinction, which Ludwig (1999) believed casts doubt upon the reliability of point estimates. However, the wide use of VORTEX (and its predecessor SIMPOP), particularly by the IUCN, and for a variety of species including the eastern barred bandicoot (Lacy and Clark 1990) and long-nosed bandicoot (Banks 2004), provided a good source of information for comparison with the PVA for the western barred bandicoot.

6.5 Methods

The PVA computer program VORTEX (Lacy 1993; Miller and Lacy 2003) was used to assess population viability by projecting population persistence over 100 years for populations of the western barred bandicoot at Dorre Island and Heirisson Prong. One thousand simulation runs for each scenario were conducted. VORTEX tracked the fate of each population and produced summary statistics that included an estimation of:

- Probability of population extinction;
- Median time to extinction;
- Mean final population size with standard error across iterations;
- Mean expected and observed heterozygosity (or “gene diversity”) remaining in the extant population, with standard error;
- When inbreeding depression was included, the number of lethal alleles remaining per diploid individual, with standard error;
- Final age-sex composition of the population; and
- Mean population growth rate, with standard error across iterations.

6.5.1 Input Data

The population biology of the western barred bandicoot at Dorre Island and Heirisson Prong has been detailed by Richards and Short (2003), Short et al. (1998), and in Chapters 2 and 3 of this thesis. These data were used as the basis for input values to VORTEX, along with additional unpublished data from 2000 to 2002 to
calculate the number of offspring per female per year and the average adult mortality rate (Table 6.2).

**Table 6.2:** Values for key life-history and environmental parameters input into VORTEX for population viability analysis of the ‘best estimates’ of wild Dorre Island and reintroduced Heirisson Prong western barred bandicoot populations. Data are from Richards and Short (2003), Short *et al.* (1998), Chapters 2 and 3, and this chapter. EV = environmental variation, SD = standard deviation, K = carrying capacity.

<table>
<thead>
<tr>
<th>Life-history parameters</th>
<th>Parameter estimates for western barred bandicoots</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>Dorre Island</em></td>
</tr>
<tr>
<td></td>
<td><em>Heirisson Prong</em></td>
</tr>
<tr>
<td>Inbreeding depression</td>
<td>Not included</td>
</tr>
<tr>
<td></td>
<td>3.14 lethal equivalents</td>
</tr>
<tr>
<td></td>
<td>50% due to recessive lethals</td>
</tr>
<tr>
<td>Definition of quasi-</td>
<td>20 animals remaining in population</td>
</tr>
<tr>
<td>extinction</td>
<td></td>
</tr>
<tr>
<td>Type of mating system</td>
<td>Polygynous</td>
</tr>
<tr>
<td></td>
<td>Polygynous</td>
</tr>
<tr>
<td>Age at first reproduction</td>
<td>1</td>
</tr>
<tr>
<td>Age at last reproduction</td>
<td>4</td>
</tr>
<tr>
<td>Maximum number of</td>
<td>12</td>
</tr>
<tr>
<td>progeny/year</td>
<td></td>
</tr>
<tr>
<td>Sex ratio at birth</td>
<td>54% male</td>
</tr>
<tr>
<td>Reproduction parameters:</td>
<td></td>
</tr>
<tr>
<td></td>
<td>51% male</td>
</tr>
<tr>
<td>% adult females breeding</td>
<td>85% (64% @ K)</td>
</tr>
<tr>
<td>EV in % breeding</td>
<td>7%</td>
</tr>
<tr>
<td>Average # offspring/female (SD)</td>
<td>Normal distribution</td>
</tr>
<tr>
<td>Mortality</td>
<td>5.3 (2.0)</td>
</tr>
<tr>
<td>Mortality from age 0 to 1 (SD due to EV)</td>
<td>35% (5%)</td>
</tr>
<tr>
<td>Mortality after age 1 (SD due to EV)</td>
<td>30% (5%)</td>
</tr>
<tr>
<td>Mortality from age 0 to 1 (SD due to EV)</td>
<td>35% (5%)</td>
</tr>
<tr>
<td>Mortality after age 1 (SD due to EV)</td>
<td>30% (5%)</td>
</tr>
<tr>
<td>Mortality from age 0 to 1 (SD due to EV)</td>
<td>35% (5%)</td>
</tr>
<tr>
<td>Mortality after age 1 (SD due to EV)</td>
<td>30% (5%)</td>
</tr>
<tr>
<td>Catastrophe - drought Frequency</td>
<td>10% of years, with rainfall &lt; 123 mm</td>
</tr>
<tr>
<td>Effect on reproduction</td>
<td>20% reduction</td>
</tr>
<tr>
<td>Effect on mortality</td>
<td>50% increase</td>
</tr>
<tr>
<td>Catastrophe – cat predation Frequency</td>
<td>N/A</td>
</tr>
<tr>
<td>Effect on reproduction</td>
<td>N/A</td>
</tr>
<tr>
<td>Effect on mortality</td>
<td>N/A</td>
</tr>
<tr>
<td>Mate monopolization</td>
<td>100% males breeding</td>
</tr>
<tr>
<td>Initial population size</td>
<td>2400 with stable age distribution</td>
</tr>
<tr>
<td>Carrying capacity (K)</td>
<td>2400</td>
</tr>
<tr>
<td>SD in K due to EV</td>
<td>240 (10%)</td>
</tr>
<tr>
<td></td>
<td>550</td>
</tr>
</tbody>
</table>
The values for quasi-extinction (where the population has declined to a point that is
certain to lead to extinction) are estimates based on the ability of male bandicoots to
move up to 4 km within two weeks (Section 2.3.3), extrapolated to the minimum
number of bandicoots that might be required to meet another bandicoot within the
population area (i.e. 20 bandicoots on 53 km$^2$ Dorre Island and one of each sex on 12
km$^2$ Heirisson Prong).

**Inbreeding depression**

Frankham (1998) found that many island populations were significantly inbred,
and suggested that these populations may have lower reproductive fitness, and be at
greater risk of extinction than their mainland counterparts. Similarly, Eldridge, King,
Loupis, Spencer, Taylor, Pope and Hall (1999) found evidence of inbreeding depression
in a small population of 150 black-footed rock-wallaby on Barrow Island in Western
Australia. However, inbreeding is generally assumed to be a rare event in populations
greater than 250 (Miller and Lacy 2003) or with an effective population size ($N_e$) of >
100 individuals (census population sizes of 500 – 1000; Frankham 1995; Waples 2002),
and was therefore assumed to have no impact on the fitness of the Dorre Island
bandicoot population because of its size (2,400 ± 480 SD). Reed et al. (2002) regarded
genetic factors as important components of PVA where the population was “historically
large”. Inbreeding depression may be of greater concern when large populations
become rapidly small (such as the translocation from Dorre Island to Heirisson Prong;
Chapter 2), compared to those that have been small for an extended period and have lost
deleterious alleles by natural selection during slow inbreeding. Beissinger and
Westphal (1998) recommended not including genetics within PVA until the relationship
between inbreeding depression and demographic variables is better understood, but
Allendorf and Ryman (2002) suggested using PVA to examine the loss of genetic
variation over time. They recommended retaining at least 95% of population
heterozygosity over 100 years.

VORTEX models inbreeding depression as a loss of viability (causing mortality)
of inbred juveniles during their first year only (Miller and Lacy 2003). The cost or
severity of inbreeding is expressed by VORTEX as the “average number of lethal
equivalents per diploid individual”, where lethal equivalents are the number of single
alleles which cause death when homozygous (Reed et al. 2002). “The number of lethal
equivalents per diploid individual estimates the average number of lethal alleles per individual in the population if all deleterious effects of inbreeding were due entirely to recessive lethal alleles” (p. 116, Miller and Lacy 2003). In the absence of any genetic data for the western barred bandicoot, the median value of 3.14 lethal equivalents for 40 captive mammal populations reported by Ralls, Ballou and Templeton (1988) was used for the Heirisson Prong population. The only Australian marsupial for which results have been reported is the parma wallaby Macropus parma, with a value of 3.38 lethal equivalents. Ralls et al. (1988) regarded the costs of inbreeding in natural populations as likely to be greater than their estimates for captive juveniles, thus it should be emphasised that the inclusion of inbreeding depression in the western barred bandicoot VORTEX simulation is used only as a tool to examine the possible effects of inbreeding. For the few species in which inbreeding depression has been adequately studied, Miller and Lacy (2003) reported that about 50% of the effects of inbreeding are due to recessive lethals alleles and 50% due to loss of heterosis. This value was used for the western barred bandicoot VORTEX simulation model.

Nothing is known of the mating system of the western barred bandicoot, however the mating system of bandicoots is generally regarded as polygynous (Lee and Cockburn 1985; males mate with several females, and females usually provide the parental care).

**Environmental variation**

Environmental variation was assumed to impact all individuals in the population simultaneously and to affect both reproduction and mortality; that is, good years for reproduction were also regarded as good years for survival.

**Dispersal**

There was no exchange of animals between populations of the western barred bandicoot due to geographical isolation.

**Reproduction**

The average age ± standard deviation at first reproduction on Heirisson Prong for bandicoots monitored between 1996 and 1999 on a regular basis and of approximate
known age was 11.2 ± 3.3 months (n = 19). The age at first reproduction was therefore assumed to be one year, and as such, one VORTEX year was equivalent to 12 months.

A female may have up to three young per litter and up to four litters per year, hence the maximum number of progeny per year may be as high as 12 per female. However, the average litter size on Dorre Island was 1.77 (Short et al. 1998) and on Heirisson Prong was 1.94.

Projections based on density-independent PVA models were regarded as optimistic and unrealistic by Brook et al. (1997). However, incorporating density dependence into PVA models has resulted in large differences in results between models, thus Mills, Baldwin, Wisdom, Citta, Mattson and Murphy (1996) recommended that: multiple PVA programs be used; at least one scenario with density dependence be used; and that qualitative results be emphasised, rather than quantitative predictions. There was no evidence for a density-dependent decline in reproductive rate (litter size and percentage of adult females breeding during the peak breeding season) on Dorre Island, however there was some indication that reproductive rate declined within the predator-free refuge on Heirisson Prong (Sections 3.3.2 and 3.4.2), possibly due to a shortage in food resources. Reproduction was therefore modelled as both density-independent and density-dependent for the Dorre Island and Heirisson Prong populations, and the outputs compared. The baseline model included density-independent reproduction.

For the density-dependent model, the percentage of females breeding when the population was small (no Allee effect) was estimated at 85% on Dorre Island and 82% on Heirisson Prong (taken as the maximum percentage of females breeding during the peak breeding season). The percentage of females breeding at carrying capacity was estimated to be 64% on Dorre Island and 62% on Heirisson Prong, based on a decline of 25% per annum in pouch young production within the predator refuge at high density, assuming a shortening of the breeding season by approximately three months over the summer. Fowler (1981) suggested that density dependence in reproductive success can often be modelled with a quadratic function. This model was used for the western barred bandicoot population, with a steepness parameter $B = 2$. There was considered to be no Allee effect at low population size on Heirisson Prong.

The environmental variation in reproduction was estimated by calculating the standard deviation of a distribution, calculated as the observed range (best – worst
years) divided by the expected range (from Table 26 in Rohlf and Sokal (1981)). From five years of observation on Dorre Island (1989, 1990, 1991, 1992 and 1995) the percentage of females breeding was 93% in the best year and 77% in the worst year during the peak winter breeding season between June and August (Short et al. 1998). The observed range of 16% divided by the expected range of 2.33 standard deviations (for 5 years of observation), produced a standard deviation of 7%. From three periods of observation of the free-range population on Heirisson Prong in July 1998 and June and August 1999 the percentage of females breeding was 100% at best and 73% at worst during the peak winter breeding season (Figure 3.2). The observed range of 27% was divided by the expected range of 1.69 standard deviations (for 3 years of observation) to produce a standard deviation of 16%.

The number of offspring per female per year on Dorre Island was modelled as 5.3, which is based upon a normal distribution and three average litters per year, during a nine-month breeding season between March and November (Short et al. 1998). The standard deviation was unknown, so was modelled as 2.0 as for Heirisson Prong below. The distribution of the number of offspring per female per year on Heirisson Prong was based upon a normal distribution, with an average of 6.7 pouch young per year and standard deviation of 2.0, calculated from the average fecundity of females (n = 23) trapped at regular intervals over one-year periods on Heirisson Prong between 1997 and 2002 (Table 6.3).
Table 6.3: Calculation of annual fecundity of adult females on Heirisson Prong. Dates in italics and estimated average litter size in brackets (2) refers to periods during which bandicoots were not trapped but production of a litter was thought to be likely, based on examination of nipples at a later capture date. *Average litter size ± standard deviation.

<table>
<thead>
<tr>
<th>Female</th>
<th>Trapping dates</th>
<th>Litter size</th>
<th>Total # PY</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>February, May, July, October 1997, January 1998</td>
<td>0, 0, 1, 1, 1</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>October 1996, February, May, June – September 1997</td>
<td>2, 0, 2, (2)</td>
<td>6</td>
</tr>
<tr>
<td>3</td>
<td>July, October 1997, January, March, May 1998</td>
<td>2, 2, 1, 0, 0</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
<td>August, September, October 1999, December 1999 – April 2000, May 2000</td>
<td>2, 0, 2, (2), 2</td>
<td>8</td>
</tr>
<tr>
<td>4</td>
<td>August, October 1996, February, May, July 1997</td>
<td>2, 2, 0, 1, 2</td>
<td>7</td>
</tr>
<tr>
<td>14</td>
<td>February, June, August, October 1999</td>
<td>2, 3, 1, 1</td>
<td>7</td>
</tr>
<tr>
<td>18</td>
<td>July, October 1998, February, June 1999</td>
<td>1, 2, 2, 2</td>
<td>7</td>
</tr>
<tr>
<td>20</td>
<td>October 1998, January, March, May, July, September 1999</td>
<td>2, 0, 1, 2, 2</td>
<td>7</td>
</tr>
<tr>
<td>24</td>
<td>October 1998, February, June, August 1999</td>
<td>2, 2, 2, 2</td>
<td>8</td>
</tr>
<tr>
<td>33</td>
<td>July, October 1998, February, June 1999</td>
<td>2, 3, 3, 2</td>
<td>10</td>
</tr>
<tr>
<td>34</td>
<td>November 1997, January, March, May, July, October 1998</td>
<td>0, 0, 0, 0, 2, 3</td>
<td>5</td>
</tr>
<tr>
<td>34</td>
<td>February, June, August 1999, September 1999 – January 2000</td>
<td>2, 2, 2, (2)</td>
<td>8</td>
</tr>
<tr>
<td>42</td>
<td>October 1998, February, June, August 1999</td>
<td>0, 0, 1, 2</td>
<td>3</td>
</tr>
<tr>
<td>46</td>
<td>June, August, October 1999, February, May 2000</td>
<td>3, 3, 2, 0, 2</td>
<td>10</td>
</tr>
<tr>
<td>50</td>
<td>February, March – May, June, October 1999</td>
<td>2, (2), 1</td>
<td>5</td>
</tr>
<tr>
<td>55</td>
<td>March – May, June, August, September, December 1999, February 2000</td>
<td>(2), 2, 2, 0, 0, 0</td>
<td>6</td>
</tr>
<tr>
<td>64</td>
<td>February, May, July, October 1997, January 1998</td>
<td>0, 2, 2, 2</td>
<td>6</td>
</tr>
<tr>
<td>64</td>
<td>March, May, July, October 1998, February 1999</td>
<td>0, 0, 2, 2, 2</td>
<td>6</td>
</tr>
<tr>
<td>121</td>
<td>October 1999, February, May, July 2000, August – September 2000</td>
<td>1, 0, 2, 2, (2)</td>
<td>7</td>
</tr>
<tr>
<td>275</td>
<td>January, May, July, October 1996</td>
<td>2, 2, 2, 3</td>
<td>9</td>
</tr>
<tr>
<td>1375</td>
<td>October 1996, February, May, July 1997, August – September 1997</td>
<td>2, 0, 1, 3, (2)</td>
<td>8</td>
</tr>
<tr>
<td>1375</td>
<td>February, June, August 1999, September 1999 – January 2000</td>
<td>2, 2, 3, (2)</td>
<td>9</td>
</tr>
<tr>
<td>1DB0A19</td>
<td>July, October 1998, February, June 1999</td>
<td>1, 1, 0, 2</td>
<td>4</td>
</tr>
</tbody>
</table>

*6.7 ± 2.0
Chapter 6: Population viability analysis

Mortality

The mortality rate for juvenile and adult western barred bandicoots at Dorre Island is unknown, but was assumed to be similar to the rates within the predator refuge on Heirisson Prong. Data from the free-range population on Heirisson Prong were not used, due to the suspicion that sub-adults were suffering a high risk of mortality due to cat predation and potential diffusion from the core 12-km² conservation reserve to the buffer zone. The average mortality rate for adults at Heirisson Prong was therefore estimated to be 30% \((n = 21)\), based upon no further capture of adult \(\geq 200\) g animals within the predator refuge during the 12-month period after first capture between 1996 and 2002 (additional unpublished data from J. Richards was used from 2000 – 2002). The standard deviation was represented as 5% due to small sample sizes and a lack of opportunity to sample between-year variation, and was elevated during sensitivity analyses to account for the possibility of greater variation (Section 6.6.7).

Data from the predator refuge during the period between June 1997 and May 1998 were not used to calculate juvenile mortality due to a lack of recruitment and high mortality rate, thought possibly to be caused by a combination of an unusually high density of rabbits throughout the year, low rainfall, and an increase in the sighting of tawny frogmouths from 0 per spotlight kilometre between 1995 and 1997 to 0.02 – 0.05 per spotlight kilometre through 1998, and 0.02 - 0.03 in 1999 (J. Short, B. Turner and J. Richards unpublished data). Tawny frogmouths were often sighted perched on the fence of the predator refuge and are known to consume small mammals (Higgins 1999). Tawny frogmouths may therefore have preyed upon juvenile western barred bandicoots, particularly within the predator refuge at a time when prey abundance was probably higher within the predator refuge than the surrounding habitat, and with the first increase in abundance and prior to bandicoots becoming wary of a novel predator not previously experienced. For example, barn owls *Tyto alba* and wedge-tailed eagles *Aquila audax* have been responsible for the decline of captive populations of greater stick-nest rats *Leporillus conditor* (J. Stelmann pers. comm.) and banded *Lagostrophus fasciatus* and rufous hare-wallabies *Lagorchestes hirsutus* (Friend and Beecham 2003). The mortality rate for juveniles at Heirisson Prong was estimated to be 35%, based upon the average ratio of observed to expected number of pouch young produced within the predator refuge over two periods of one year (Table 6.4; June 1996 - May 1997 and June 1998 – May 1999). The standard deviation was represented as 5% due to small
sample sizes and a lack of opportunity to sample between-year variation, and was elevated during sensitivity analyses to account for the possibility of greater variation (Section 6.6.7). Variation in the number of litters potentially produced was due to the attainment of sexual maturity at different times during the year of monitoring (so that the expected 6.7 pouch young per female per year recorded above, was not achieved). The numbers of new recruits observed (captured) in subsequent 12-month periods (lagged by eight months to allow for typical non-capture of bandicoots until at least eight months of age; Section 3.3.2) were tallied. For example, nine adult females capable of producing pouch young between June 1996 and May 1997, produced 15 known new recruits, and an additional 14 pouch young are likely to have been produced during periods when no monitoring was conducted (expected). During trapping between February 1997 and January 1998, 13 new recruits were captured (observed; Table 6.4).

**Table 6.4:** The mortality of juvenile western barred bandicoots, based on the estimated observed number of new recruits produced per year compared with the expected number of new recruits produced per year. Observed number of new recruits included those recorded as present.

<table>
<thead>
<tr>
<th>Year</th>
<th># Adult females</th>
<th>Expected # pouch young</th>
<th>Observed # new recruits</th>
<th>% Mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 1996 – May 1997</td>
<td>9</td>
<td>29</td>
<td>13</td>
<td>55</td>
</tr>
<tr>
<td>June 1997 – May 1998</td>
<td>8</td>
<td>13</td>
<td>1</td>
<td>92</td>
</tr>
<tr>
<td>June 1998 – May 1999</td>
<td>16</td>
<td>49</td>
<td>41</td>
<td>16</td>
</tr>
</tbody>
</table>

**Catastrophes**

Long-term rainfall datum from the Bureau of Meteorology for Denham between 1894 and 2003 was used. Drought years were assumed to be those in the lowest 10th percentile with an average rainfall of 87 – 123 mm per annum, and therefore occurring on average, once in every ten years. The impact of drought was included in all simulations due to its known probability of occurrence and likely impact. An increase in the frequency of drought to two and three times every ten years was modelled, mimicking extended dry periods for 2 – 3 years that have occurred within the historic rainfall records, and may occur again in the future.
During monitoring on Dorre Island in March 1991 and October/November 1995 at the beginning and tail end of the breeding season during dry conditions, 43% of adult females were breeding. The impact of drought was therefore modelled as reducing reproduction by 57%, both on Dorre Island and Heirisson Prong. The severity of a drought was modelled as causing 50% mortality (spread across age classes) at each location, based upon an estimated increase in the western barred bandicoot populations on Dorre and Bernier Island from a combined minimum population size of 2,200 in 1988/89 after a severe drought (112 mm rainfall in 1988), to 4,400 in 1991/92 during a period of average to above-average rainfall (Short et al. 1997a).

The home range of three feral cats at Heirisson Prong varied from 55 ha (female), to 370 and 1080 ha (males; Parsons and Cane unpublished data), suggesting that males may range over the entire 12 km$^2$ peninsula. The impact of predation by cats on western barred bandicoots is unknown, but is suspected to be high, due to the high fecundity of bandicoots but lower than expected recruitment at Heirisson Prong (Chapter Two), and the potential for cats to act globally on the western barred bandicoot population. Predation of bandicoots by cats was modelled as a catastrophe, causing an increase in mortality of 25% and 50% (spread across age classes), and occurring once every two, four or ten years. The impact of cat predation on a reintroduced population was also modelled for a larger reserve size of 50 km$^2$ (equivalent to a carrying capacity of 2,400), to mimic Dorre Island, occurring once every two or four years, and increasing mortality by 25%.

The impact of predation by foxes at Heirisson Prong was unknown and therefore not modelled, though it may be similar to cat predation. For example, Banks (2004) modelled fox predation as a catastrophe resulting in a reduction in adult long-nosed bandicoot Perameles nasuta survival of 20%. Any direct impact of rabbits on the western barred bandicoot is probably minimal (Chapters Three, Five), and was not included within the PVA. It is possible that rabbits could support both cat and fox populations as dietary items during periods when bandicoot numbers are low, thus exacerbating predatory impacts on bandicoots, but such interactions cannot be modelled by VORTEX.
Chapter 6: Population viability analysis

Mate monopolization

All males were regarded as potential breeders within the polygynous mating system. VORTEX assumes that some males are excluded from the breeding pool and that a Poisson distribution describes breeding success among available males. This translated to 55% of males successfully siring offspring.

Population carrying capacity

The carrying capacity of Dorre Island (53 km$^2$) was determined by line transect spotlight surveys conducted during 1991/2 that estimated a population density of 45.5 bandicoots/km$^2$ at a time when the population was assumed to have recovered after a period of drought between 1987 and 1989 (Short et al. 1997a). Based upon this value, the carrying capacity for Dorre Island was assumed to be 2,400 and for Heirisson Prong it was 550 bandicoots, with standard deviations set at 10%.

Harvest and supplementation

The Dorre Island population was initially modelled with no harvest or supplementation, and then with a harvest rate of 50 animals per year, mimicking translocation to established, and future reintroduction sites. The Heirisson Prong population was initially modelled with no harvest or supplementation, and then with supplementation of 20 animals per year for years 2 – 5, to gauge the effect of adding genetic diversity to the reintroduced population.

6.6 Scenarios and results

6.6.1 ‘Best estimates’ wild Dorre Island population

The ‘best estimates’ VORTEX simulation based on the initial data in Table 6.2 and with drought, indicated that the Dorre Island population would survive for 100 years with 0% extinction probability, and a stochastic rate of increase ($r$) of 0.59 ± 0.00 SE. A harvest rate of 50 individuals per annum for translocation similarly produced a 0% probability of extinction, and $r$ of 0.57 ± 0.38 SD. A change to density-dependent reproduction did not affect extinction probability, but lowered $r$ to 0.42 ± 0.40 SD.
6.6.2  ‘Best estimates’ reintroduced Heirisson Prong population

The ‘best estimates’ VORTEX simulation based on the initial data in Table 6.2, with a founder population of nine and with drought but without cat predation, indicated that the reintroduced Heirisson Prong population had a 3% extinction probability over 100 years, \( r \) of 0.74 ± 0.01 SE, and final gene diversity (expected heterozygosity) of 0.76 ± 0.00 SE (declining from 0.91 ± 0.00 SE). All extinction events occurred within the first seven years, and of those simulated populations going extinct, mean time to first extinction was 2.03 years ± 0.23 SE. A change to density-dependent reproduction did not affect the extinction probability. Population supplementation of 20 animals per year in years 2 – 5 resulted in a decrease in extinction probability to 0% and increase in gene diversity to 0.85 ± 0.00 SE.

6.6.3  Scenario One: impact of reserve size

Size of reserve was adjusted from 53 km\(^2\) (Dorre Island), to 25 km\(^2\), 12 km\(^2\) (equivalent to Heirisson Prong), 5 km\(^2\) and 1 km\(^2\), by adjusting carrying capacity from 2400, to 1100, 550, 230 and 50 respectively. These decreases in carrying capacity may also represent decline in habitat quality, which is particularly associated with the more arid areas of the former range of the western barred bandicoot, such as the Arid Recovery Project near Roxby Downs. The effects of a decrease in reserve size to 25 km\(^2\), 12 km\(^2\) and 5 km\(^2\) (using the Dorre Island ‘best estimates’ simulation) produced no change in the probability of extinction, but a decline in gene diversity from 0.97 to 0.74 (Table 6.5; Figure 6.1). At smaller reserve sizes of 2 km\(^2\) and 1 km\(^2\) the probability of extinction increased to 2% and 9% respectively, and gene diversity declined further. The value of \( r \) was similar for each simulation. The addition of inbreeding depression saw a further decline in gene diversity (Figure 6.1; Section 6.6.4).

For the Heirisson Prong simulation (using inputs from Table 6.2), decreases in reserve size to 5 km\(^2\) and 2 km\(^2\) did not alter the probability of extinction, however a 1 km\(^2\) size produced a slight increase to 4% (Table 6.5). The decline in reserve size corresponded to a decline in gene diversity and again, the value of \( r \) was similar for each simulation.
Table 6.5: Probability of extinction (%), gene diversity ± SE and stochastic rate of increase \((r)\) ± SE after 100 years for a simulated population of western barred bandicoots in different sized reserves.

<table>
<thead>
<tr>
<th>Reserve</th>
<th>Reserve size</th>
<th>Probability of extinction</th>
<th>Gene diversity</th>
<th>Growth rate ((r))</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dorre Island</strong></td>
<td>53</td>
<td>0</td>
<td>0.97 ± 0.00</td>
<td>0.59 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>0</td>
<td>0.94 ± 0.00</td>
<td>0.58 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>0</td>
<td>0.88 ± 0.00</td>
<td>0.58 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0</td>
<td>0.74 ± 0.00</td>
<td>0.58 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2</td>
<td>0.46 ± 0.01</td>
<td>0.58 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>9</td>
<td>0.25 ± 0.01</td>
<td>0.58 ± 0.00</td>
</tr>
<tr>
<td><strong>Heirisson Prong</strong></td>
<td>12</td>
<td>3</td>
<td>0.76 ± 0.00</td>
<td>0.74 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>3</td>
<td>0.64 ± 0.00</td>
<td>0.74 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>3</td>
<td>0.42 ± 0.01</td>
<td>0.73 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>4</td>
<td>0.22 ± 0.01</td>
<td>0.73 ± 0.00</td>
</tr>
</tbody>
</table>

Figure 6.1: The relationship between reserve size and gene diversity, modelled by VORTEX using Heirisson Prong data, with and without the effects of inbreeding depression for the western barred bandicoot.
6.6.4 Scenario Two: impact of inbreeding depression

The Heirisson Prong population was modelled with and without inbreeding depression. The inclusion of inbreeding depression increased the extinction probability from 3% to 4%. The initial year one gene diversity was 0.91 ± 0.00 SE, the number of extant alleles was 15.08 ± 0.09 SE, and the number of lethal alleles per diploid was 1.58 ± 0.02 SE. The final gene diversity was 0.76 ± 0.00 SE, the number of alleles was 7.83 ± 0.07 SE, and the final number of lethal alleles per diploid was 0.10 ± 0.00 SE.

The interaction of inbreeding depression with reserve size saw a further decline in gene diversity with decreasing reserve size, particularly in reserves of 5 km² or less (Figure 6.1). There was an associated increase in the probability of extinction, from 3% for reserve sizes between 2 km² and 53 km², to 10% in reserves sizes of 1 km².

6.6.5 Scenario Three: founder population size

The initial population size at Heirisson Prong was modified from 9 (baseline), to 20, 50 and 100, to examine the effect of larger founder size, particularly on gene diversity. All three produced a decrease in the probability of extinction to 0% and increased gene diversity ± SE from 0.76 ± 0.00 (Table 6.5) to 0.83 ± 0.00, 0.86 ± 0.00, and 0.87 ± 0.00 respectively.

6.6.6 Scenario Four: impact of catastrophes (drought and cat predation)

An increase in the frequency of drought from 10% to 20% and 30% of years, to simulate reintroductions to areas with a harsher climate, such as the Arid Recovery Reserve in South Australia, produced an increase in the probability of population extinction from 3%, to 6% and 11% respectively.

Several scenarios for the possible frequency and impact of cat predation events on the western barred bandicoot population at Heirisson Prong were modelled, and the results displayed in Figure 6.2. Cat incursion once every ten years increased the probability of extinction to 8-18%, while increasing the frequency to once every four or two years resulted in extinction probabilities of 41-78% and 99-100% respectively, with little chance that the population would be extant after 100 years.
Figure 6.2: Modelled responses of the Heirisson Prong western barred bandicoot population to different levels of cat predation (influencing the mortality of bandicoots and occurring at varying frequencies in time) on (a) the probability of population persistence, (b) gene diversity, and (c) population size over a 100-year period.
An increase in the frequency of cat incursion and the impact on the mortality of western barred bandicoots resulted in a decrease in growth rate ± SE of the population, from 0.61 ± 0.00 when cat predation occurred in 10% of years and caused a 10% decrease in the probability of persistence of the bandicoot population, to -0.07 ± 0.01 when cat predation occurred in 50% of years and caused a 50% increase in bandicoot mortality.

An additional scenario to examine the impact of cat predation at a larger reserve size of 50 km$^2$ was modelled. Cat incursion once every two and four years (increasing bandicoot mortality by 25%) reduced the extinction probability to 6% and 3% respectively, with no change in growth rate.

6.6.7 Sensitivity analysis

The modelled Heirisson Prong population showed minimal sensitivity to changes in adult mortality rate increases of 10%, 20%, 30% and 40% from the Heirisson Prong ‘best estimates’ model, and environmental standard deviation of mortality increases of 5% and 15% (from 5% to 10% and 20%), on the mean probability of population persistence, gene diversity and mean population size (Figure 6.3). For example, an increase in adult mortality from 30 ± 5% to 60 ± 20% produced an 8% decrease in the mean probability of population persistence, an average of 8% of gene diversity was lost, and the average population size declined by 12%.

The modelled population showed greater sensitivity to changes in juvenile mortality rate increases of 10%, 20%, 30%, and 40%, and environmental standard deviation of mortality increases of 5% and 15% (Figure 6.4). An increase in juvenile mortality from 35 ± 5% to 65 ± 20% produced an 18% decrease in the mean probability of population persistence, an average of 9% of gene diversity was lost, and the average population size declined by 33%.

The population showed far greater sensitivity to combined increases in adult and juvenile mortality rates and environmental standard deviation of mortality (Figure 6.5). The modelled population was not sustainable with combined mortality rates of 60 ± 20%. An increase in the environmental standard deviation of mortality from 10% to 20% produced a greater decrease in mean probability of population persistence, gene diversity and population size than did an increase in mortality rate from 40% to 50%. All increases in mortality produced some decline in mean probability of population persistence, gene diversity and population size.
Figure 6.3: The effect of increases in adult mortality and environmentally-induced variation (EV) in adult mortality on (a) the probability that the western barred bandicoot population will persist, (b) gene diversity, and (c) population size over a 100-year period at Heirisson Prong.
Figure 6.4: The effect of increases in juvenile mortality and environmentally-induced variation (EV) in juvenile mortality on (a) the probability that the western barred bandicoot population will persist, (b) gene diversity, and (c) population size over a 100-year period at Heirisson Prong.
Figure 6.5: The effect of increases in both juvenile and adult mortality and environmentally-induced variation (EV) in mortality on (a) the probability that the western barred bandicoot population will persist, (b) gene diversity, and (c) population size over a 100-year period at Heirisson Prong.
Decreases in the percentage of females breeding by 5%, 10%, 15% and 20% from the Heirisson Prong ‘best estimates’ model, produced an increase in the probability of extinction from 3% to 4%, 4%, 5% and 8% respectively.

6.7 Discussion

Although the reintroduced western barred bandicoot population at Heirisson Prong was studied for a period of four years, it was still necessary to make numerous assumptions within the PVA model to facilitate its use (Table 6.6). For a complete data set to be obtained for PVA, data collection would have required more focus on rates of survival, mortality and reproduction, and genetic diversity, and this would have necessitated more intensive monitoring by monthly trapping and radio tracking and genetic analyses, at both Dorre Island and Heirisson Prong. It is important to stress that the results discussed below should be used only in a relative manner, and should not be considered absolute. Data collection to improve the PVA model should be ongoing.

Table 6.6: Summary of the PVA parameters for which data were known, and for which assumptions were made.

<table>
<thead>
<tr>
<th>Parameters known</th>
<th>Parameters missing or incomplete</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population size</td>
<td>Lethal equivalents per diploid</td>
</tr>
<tr>
<td>Carrying capacity</td>
<td>EV in reproduction</td>
</tr>
<tr>
<td>Sex ratio</td>
<td>EV in mortality rates</td>
</tr>
<tr>
<td>Age at first and last reproduction</td>
<td>EV in carrying capacity</td>
</tr>
<tr>
<td>Reproductive output</td>
<td>Effect of drought on reproduction</td>
</tr>
<tr>
<td>Mortality rate</td>
<td>Density dependence</td>
</tr>
<tr>
<td>Frequency and impact of drought</td>
<td>Impact of cat predation</td>
</tr>
</tbody>
</table>

The VORTEX simulation for the Dorre Island western barred bandicoot population produced a model that was thought to provide the ‘best estimate’ of long-term population dynamics, based on the knowledge of the species provided by Short et al. (1998), Richards and Short (2003) and within this thesis. The stochastic rate of population increase of 0.59 predicted by the VORTEX ‘best estimate’ simulation for the population is similar to the 0.64 estimated during a period of population recovery after drought by Short et al. (1998), suggesting that the data input may be adequate.
Parameters from the Dorre Island population provided an estimate of data for use in the Heirisson Prong simulation where information about population parameters was sometimes limited. The intrinsic rate of increase when external factors are not limiting \((r_m)\) for the western barred bandicoot, according to Sinclair’s (1996) formula \(r_m = 1.375W^{-0.315}\) (where \(W\) = mean adult female body weight; 0.244 kg for captured western barred bandicoots at Bernier and Dorre Islands and Heirisson Prong) is far greater at 2.144. Species with smaller body size respond to environmental variability by increasing reproduction, so survivorship is low and the annual rate of population change is depressed; thus conservation is reliant on the maintenance of large populations, or several small interconnected populations that allow for dispersal (Sinclair 1996).

The harvest of 50 animals per year from Dorre Island appeared to have no impact on population persistence, providing support for the continuation of Dorre Island as a source of animals for future translocations to reintroduction sites. Island populations are regarded as having a much greater risk of extinction than mainland populations, through over-exploitation, habitat loss, loss of genetic variation and consequent inbreeding, and introduced species (e.g. Eldridge et al. 1999; Frankham 1997; Smith, May, Pellew, Johnson and Walter 1993). Disease may be a significant causal factor also, though there has been little evidence of this. Frankham (1997) found that the majority of island populations (165 of 202 comparisons) were correlated with lower levels of genetic variation than corresponding mainland populations. Inbreeding depression may be common (Pusey and Wolf 1996), and affect the susceptibility of island populations to extinction (Mills and Smouse 1994).

The results of the analyses for the reintroduced western barred bandicoot population on Heirisson Prong indicate that the population is robust and faces a low risk of extinction in the absence of introduced predators, even with factors such as low founder number, and inbreeding depression. An increase in the frequency of drought increased extinction risk, highlighting the need for refuges during periods of extended drought, and suggesting that population persistence may be affected by future climatic changes. The majority of extinction events appeared to occur within the first ten years of the modelled reintroduction, highlighting the susceptibility of small populations to demographic and environmental stochasticity. Once the population is larger, these factors are less important. There have been no signs of inbreeding depression at Heirisson Prong, such as reduced fecundity, decreased resistance to disease or skewed
sex ratio, although heterozygosity is known to be low in both the reintroduced and source populations (S. Smith unpublished data). Gene diversity declined by 15% over the 100-year simulation period, representing a considerable loss of what little heterozygosity may have been present within the small founder population. A single population bottleneck is predicted to reduce heterozygosity by $1/2N_e$, where $N_e$ is the effective population size at the time of the bottleneck (James 1971). Therefore, the heterozygosity of the reintroduced population at Heirisson Prong is expected to have been immediately reduced by at least 5%.

A modelled change to density-dependent reproduction did not appear to affect either the Dorre Island or Heirisson Prong population probability of extinction, despite suggestions that modelling density-independent reproduction may produce optimistic and unrealistic results (Brook et al. 1997).

Decreases in reserve size that might be comparable to future reintroduction sites corresponded with a decrease in gene diversity, however the risk of extinction did not increase substantially until reserve size was decreased to 1 km$^2$, or a carrying capacity of 50. These results suggest that the minimum reserve size for a sustainable western barred bandicoot population is probably of this magnitude, provided that habitat quality is good, there are no introduced predators, and that there is little consequence of loss of genetic diversity. However, inbreeding depression was of greater concern in these smaller populations. To retain genetic diversity, reserves larger than 2 km$^2$ and with a carrying capacity of over 100 would be preferable.

Reading, Clark, Seebeck and Pearce (1996) proposed that existing reserves (1 – 4 km$^2$) for mainland eastern barred bandicoots were too small to support long-term genetically viable populations, and argued for sites of > 10 km$^2$ and populations of > 1200 bandicoots, or alternatively, management of populations as metapopulations, with artificial migration between subpopulations to meet the criteria for population size. Ulbrich and Kayser (2004) thought that even large habitat area was not sufficient for survival of the common hamster Cricetus cricetus in Western Europe, and that habitat connectivity may be of greater importance for the species. The only opportunities for establishing exchange between western barred bandicoot populations is through ongoing translocation to reintroduced populations, or perhaps by cross-breeding of Bernier and Dorre Island animals, which are able to produce fertile F1 offspring (Friend and Beecham 2003).
6.7.1 Are genetic issues of concern for the western barred bandicoot?

An increase in the founder population size from nine to 20 animals produced a decline in the probability of extinction from 3% to 0%, and a 7% increase in gene diversity. Once again, this result highlights the risk associated with very small founder populations, and while it corroborates the importance of larger founder populations (Fischer and Lindenmayer 2000; Griffith et al. 1989), an order of magnitude less than the 100 individuals suggested by Fischer and Lindenmayer (2000) may be adequate for successful reintroductions where threat abatement is in place. Any supplementation of the population once established has benefits in terms of increasing population size and genetic diversity.

The inclusion of inbreeding depression in modelled populations produced a decrease in gene diversity and an increase in the probability of extinction, particularly for small populations in the order of 50 individuals in 1 km² reserves. Genetic issues such as inbreeding depression are regarded as more important in the dynamics of small, isolated, and historically large populations, with a low intrinsic growth rate (Allendorf and Ryman 2002). In these populations even small amounts of gene flow can improve genetic diversity. Bottlenecked populations, such as that of the western barred bandicoot at Heirisson Prong, probably show reduced evolutionary potential due to the loss of genetic variation (Frankham 1997). However, populations that have recovered from bottlenecks may be less sensitive to inbreeding due to the purging of deleterious recessive alleles (Brook, Tonkyn, O'Grady and Frankham 2002b). There are many populations that have survived bottlenecks, suggesting that inbreeding does not always affect recovery. However, we need also to know how many populations have become extinct after bottlenecks, and this information is not available (Allendorf and Ryman 2002). The addition of any available genetic diversity from the Dorre Island population to Heirisson Prong would reduce the rate of loss of heterozygosity, and is therefore recommended as a future management action.

The cost of inbreeding has been quantified in some species for survival, reproduction, shifts in sex ratio, and ability to tolerate environmental perturbation (e.g. Frankham 1995; Lacy 1993; Lacy and Horner 1997; Wilmer, Melzer, Carrick and Moritz 1993). However, the link between traits that are affected by inbreeding depression and those that cause a reduction in population viability is not clear. The Serengeti cheetah Acinonyx jubatus is a prime example of a population that was thought
to be endangered due to low heterozygosity (O’Brien, Wildt, Goldman, Merril and Bush 1983; O’Brien, Roelke, Marker, Newman, Winkler, Meltzeer, Colly, Evermann, Bush and Wildt 1985). Instead, predation by lions *Panthera leo* and spotted hyenas *Crocuta crocuta* was found to be responsible for low densities in the wild (Laurenson 1994), and poor husbandry for the lack of success in captive breeding (Wielebnowski 1996). As a result, Kelly and Durant (2000) opted not to include genetic data within their PVA model for the Serengeti cheetah, due to the species’ survival and increase through a bottleneck, the lack of signs of inbreeding depression, and the argument that the relationship between genetic variability and population viability is poorly understood (Dawson, Ligon, Murphy, Myers, Simberloff and Verner 1987).

Frankham (1997) found that the majority of island populations had lower levels of genetic variation than mainland populations. Sherwin, Murray, Marshall Graves and Brown (1991) found no genetic variation at 27 presumptive loci in either Tasmanian island or Victorian mainland populations of the eastern barred bandicoot, and the average heterozygosity, based on these loci, was estimated to be zero. However, Robinson (1995) and Robinson, Murray and Sherwin (1993) examined VTNR loci and mitochondrial DNA respectively for the same species, and found that despite population reduction, the mainland Hamilton population displayed a higher level of heterozygosity than the relatively intact Tasmanian population.

Frankham (1995) predicted high susceptibility of island populations to extinction on genetic grounds (inbreeding depression, loss of genetic variation, accumulation of mildly deleterious mutations, genetic adaptations to island environments), but others have stressed the importance of demographic and environmental stochasticity acting upon small island populations (Caughley 1994; Lande 1988b). Eldridge *et al.* (1999) found very low levels of genetic variation in the black-footed rock-wallaby population on Barrow Island in Western Australia. The population of about 150 animals represented only 8.5% of the variation, based upon 14 microsatellite loci, that was found in a mainland population of the same species at nearby Exmouth. In addition, signs of inbreeding depression were noted (reduced female fecundity, skewed sex ratio, increasing levels of fluctuating asymmetry), providing evidence that it is possible for genetic factors to influence the persistence of small, isolated populations, as well as factors related to demographic and environmental stochasticity. In reality, demographic, environmental and genetic stochasticity may all interact to increase the
risk of extinction for island populations (Allendorf and Ryman 2002; Frankham 1997), but the other threats may often be greater than genetic factors. Genetic factors alone probably do not often cause extinctions (Caughley 1994), although genetic problems may contribute to extinction risk once populations become small and isolated (Boyce 2002). Despite isolation, a bottleneck, and preliminary data that suggest low levels of heterozygosity (S. Smith and J. Richards *unpublished data*), the western barred bandicoot population at Heirisson Prong has shown no signs of inbreeding in the short-term.

Few published PVAs have included genetics (Allendorf and Ryman 2002). For example, Banks (2004) did not include inbreeding when modelling a small population of the long-nosed bandicoot in Sydney, because “data on the genetic health of the population are lacking”. Brook *et al.* (2002b) carried out PVAs for 20 species of bird, mammal, reptile, amphibian, fish, invertebrate and plant, and found that inbreeding depression decreased median times to extinction by 25 – 31% for founder populations of 50 – 1000. Where data were not available, these authors modelled inbreeding depression as 3.14 lethal equivalents per diploid based on data from Ralls *et al.* (1998) and as used in this PVA for the western barred bandicoot. They suggested that inbreeding depression should not be ignored as the extinction risk may be underestimated, particularly for isolated populations (Allendorf and Ryman 2002). However, the robust nature of the modelled Heirisson Prong population and lack of signs of inbreeding in the field support lowering the relative importance of genetic information in the decision-making process for the management of the endangered western barred bandicoot.

### 6.7.2 The impact of predation

All the previous scenarios for Heirisson Prong were modelled in the absence of predation. However, where predators such as feral cats are present, even infrequently, there is a substantial risk of extinction. There is little doubt that this risk is real, with mounting suspicion that the slow growth in the reintroduced western barred bandicoot population at Heirisson Prong (Chapter 2) was attributable to the presence of a small number of feral cats.

Based on the modelled impact of cat incursions and VORTEX predictions, the likely level of sustainable predation was no more than a cat incursion once in every four
years at Heirisson Prong. In reality, a ‘cat incursion’ may occur for a few days or a few months; it may be a single female cat with a home range of 55 ha that has little impact on the bandicoot population, or multiple male cats each with home ranges of 1100 ha that cover the entire peninsula and that work in concert to quickly eliminate the bandicoot population. Any increase in the frequency or combination of cat and fox incursions in the same year would greatly increase the probability of population extinction. Similarly, if cat predation causes a decrease in both juvenile and adult mortality, a population would be far more susceptible to extinction than if cat predation acted upon adults alone. Both juvenile and adult western barred bandicoots fall within the preferred range of prey size for cats (Paltridge et al. 1997). If little else, these results highlight the susceptibility of western barred bandicoot populations to cat predation, at all but minimal levels.

Larger reserve size may reduce the impact of low levels of cat predation on western barred bandicoots, however an increase in reserve size is likely to be coupled with an increase in cat numbers. The difficulty of controlling feral cats in the presence of threatened mammals is unlikely to change with an increase in reserve size, other than to compound the logistics involved. Cat control was difficult at Heirisson Prong (12 km$^2$; Section 2.4.4; Short and Turner 2000), and has proved even more problematic at nearby Peron Peninsula (1,000 km$^2$; Morris et al. 2003). Shortridge (1909) thought that bandicoots had become rare on Bernier Island “Probably owing to the introduction of a number of cats”, and recorded a single skull as the only specimen collected. By comparison, 18 burrowing bettongs were collected at the same time. An excerpt from one of Shortridge’s unpublished letters from 1906 said that “there is a man on the island looking after a flock of about 60 sheep - he had five cats there and on a small island like Bernier they have perhaps thinned them [western barred bandicoots] out” (Short in press). While a larger reserve size may offer some protection from cat predation, provided any reintroduced bandicoot population is large, and the impact of cat predation is low or confined, Shortridge’s comments suggest that western barred bandicoots are vulnerable even to low levels of cat predation. Sinclair, Pech, Dickman, Hik, Mahon and Newsome (1998, p. 572) suggested that the “near-total” removal of predators was required for species such as the burrowing bettong and brush-tailed phascogale where the net rate of increase of these prey species in the presence of predators was highly negative. Western barred bandicoots are likely to follow suit.
There are examples of PVAs used to make management decisions without sufficient data incorporated into the model. For example, Lacy and Clark (1990) used the PVA SIMPOP to estimate the probability of extinction of the small, remnant mainland population of the eastern barred bandicoot at Hamilton, Victoria, concluding that the population had a 91% probability of extinction in 10 - 25 years without any active management being undertaken. However, they did not include predation as a catastrophe within their model, preferring to model any impact of predation within estimated rates of mortality. There was no statement about the proportion of mortality that may have been attributed to cats. As a consequence, possibly the most important management issue was overlooked, despite stating, that “By understanding the risks faced by a population, we can determine the urgency of action to change those parameters” (p. 143, Lacy and Clark 1990). This omission was highlighted when the remnant wild eastern barred bandicoot population at Hamilton declined rapidly with the removal of the introduced weed gorse *Ulex europaeus*, which had formerly provided the dense habitat required by the eastern barred bandicoot as a refuge from introduced predators (J. Seebeck *pers. comm.*).

Lacy and Clark (1990) and Maguire, Lacy, Begg and Clark (1990) suggested that large increases in habitat, improvement of existing habitat, reduction in mortality, protection from catastrophic events (drought, flood, fire), and captive breeding would be necessary to decrease the probability of extinction of the eastern barred bandicoot over a moderate time frame. Almost 15 years on, the Hamilton population has persisted, albeit with a reduction in number and distribution. Management actions have included captive breeding, continued reintroductions to Woodlands Historic Park and the Hamilton Community Parklands, and the establishment of five additional populations, with varying levels of predator control (Watson 2001; Watson and Halley 1999). Sinclair *et al.* (1998) predicted that modest control of predators combined with a larger population size of over 1200 eastern barred bandicoots would provide a good chance of recovery, due to the ability of the species to tolerate some predation and thereby achieve a positive rate of increase. This figure of 1200 has never been achieved, due to a combination of inadequate predator control and drought (Watson and Halley 1999).

More recently, Todd, Jenkins and Bearlin (2002) conducted PVAs of the reintroduced population of the eastern barred bandicoot at Woodlands Historic Park,
Victoria, and similarly ignored the impact of predation, suggesting that the removal of animals for translocation to other reintroduction sites may have been one of the primary factors contributing to the decline of the population. Habitat loss through overgrazing by eastern grey kangaroos *Macropus giganteus* and predation are listed as other factors that could not be “explicitly identified and parameterised”. Predation was included within sensitivity analyses as a 10% reduction in adult survival, which resulted in a large increase in quasi-extinction risk from 0 to 55% (Todd *et al.* 2002). It is more likely that predation by foxes and feral cats, combined with the loss of vegetative cover due to grazing by kangaroos, were responsible for the rapid decline of what was formerly regarded as a robust population, and may certainly have accounted for more than a 10% decrease in mortality. The majority of animals (61 of 120) were removed for translocation to other sites in 1994 when the population was estimated to be at least 400 in the previous year (Todd *et al.* 2002; Watson and Halley 1999). The major population decline did not appear to occur until 1996 (Long, Robley and Lovett *submitted*), well after the majority of removals, and at a time when eastern grey kangaroos *Macropus giganteus* had increased in abundance, drought conditions had prevailed in 1996/97 (Watson and Halley 1999), the predator-proof fence was ineffective, and regular predator control was not implemented (J. Seebeck *pers. comm.*). The removal for translocation undoubtedly contributed to population decline, but loss of cover and predation are more likely to have been the primary forces that drove the formerly robust population to extinction.

Similarly, Southgate and Possingham (1995) used PVA to model the reintroduction of the greater bilby and to assess a range of reintroduction techniques and population parameters such as founder population size, and catastrophes (drought, big rain, fire). They produced a series of extinction probabilities for the range of scenarios, and recommended that populations should be spatially separated to reduce the risk of experiencing similar environmental catastrophes that would result in increased extinction risk. However, they neglected to model predation as a catastrophe, even though it was regarded as the primary reason for the decline of the species (Southgate 1990) and the cause of failure of the bilby reintroduction. The authors noted, moreover, that “the mortality of radio-tracked bilbies…was primarily from predation, and the decline of the entire population was associated with an increase in predator activity” (p. 155, Southgate and Possingham 1995).
This lack of focus on the threat of predation within these models is likely to severely underestimate extinction risk, and creates the additional concern that management priorities will be directed away from the critically important measure of controlling predators. Watson (2001) suggested that “fences are not vital to reintroduction success” for the eastern barred bandicoot, yet also stressed that sustained, intensive predator control is the primary element for successful reintroductions of the species. Research at Heirisson Prong and the Arid Recovery Project, both fenced reintroduction sites, has illustrated the importance of both fences and other sustained techniques for controlling predators (Moseby and O’Donnell 2003; Richards and Short 2003; Short and Turner 2000).

The majority of PVAs model catastrophes such as habitat loss, fragmentation or degradation, fire, and poaching by humans. Very few model predation as a catastrophe (e.g. Banks 2004), and a few include predation as an increase in mortality, due to the interpretation of predation as continuous, rather than catastrophic, in nature (e.g. Todd et al. 2002). This apparent oversight of the impact of predation may be an artefact of the development of PVA in the northern hemisphere, where predators are typically an integral component of ecosystems. PVA models do not adequately represent the Australian situation where novel introduced predators have a far different impact within an ecosystem and on individual species. Predation by feral cats is likely to be continuous in nature, rather than episodic (e.g. foxes, which can be eradicated quickly with 1080), and PVA models do not currently model such an impact. This oversight of predation may also arise from an historic commitment to the small population paradigm. For example, Lacy and Clark (1990, p. 143) stated that the goal of recovery of the eastern barred bandicoot “must be to pull a population out of the extinction vortex”; to stop the population being small, rather than ameliorating predation. The inclusion of predation as a component of mortality would address this issue, providing the role of predators is emphasised as a component of mortality that is not a fixed value and can be subject to management actions.
6.7.3 **Sensitivity analyses**

A common conclusion of PVA analyses is to recommend reduction of mortality in the study population (e.g. Lacy and Clark 1990; Ulbrich and Kayser 2004). The lack of impact of increases in the adult mortality rate on the extinction probability of the Heirisson Prong western barred bandicoot population is likely to be due to the high fecundity of the species, which may act as a buffer to poor survival. Lacy and Clark (1990) estimated adult mortality of eastern barred bandicoots to be 42% over a six-month period, and made “plausible guesses” to determine juvenile mortality rates of 50% pre-weaning and 69% juvenile to sub-adult. These mortality rates included the impact of predation, and were therefore much higher than those modelled for the ‘best estimates’ model at Heirisson Prong, but were mimicked in sensitivity analyses for the western barred bandicoot.

6.7.4 **Why use PVA for the western barred bandicoot?**

The eastern barred bandicoot population at Hamilton, Victoria, was declining at a rate of 25% per annum through the 1980s (Brown 1989; Dufty 1988), prior to the use of PVA by Lacy and Clark (1990) to project the likely fate of the population. Simple logic was enough to determine that the population was destined to continue to decline without management action, so why use PVA? The authors maintained that they used PVA to highlight the risk of extinction, to identify factors that were the primary sources of risk for the population, and to assess the efficacy of possible management actions. However, the extinction from predation risk was already known (Seebeck 1979), and as previously mentioned, the omission of such an important process from models may affect best management and reduce the chance of avoiding extinction.

Burgman and Possingham (2000) highlighted the role of PVA in organising information, engaging stakeholders, and making decisions, insisting that any model has its uses, even with limited data, provided that all assumptions are clearly stated. Banks (2004) provided a good example of how PVA can be used to forecast the consequences of different management decisions, such as changes in the quantity of available habitat, instigation of predator control, and increased traffic flow, for the small population of long-nosed bandicoots in Sydney. Possingham et al. (1993) suggested that PVA enables management options to be ranked according to their impact on the viability of populations, and Dreschler and Burgman (2004) and Possingham, Lindenmayer and
Tuck (2002) recommended the use of PVA as one step in decision analysis for management of endangered species. According to Clark, Gibbs and Goldstraw (1995), the process of PVA has benefited the long-term conservation of the eastern barred bandicoot, as it has done for many other single species for which the IUCN’s Conservation and Breeding Specialist Group Population and Habitat Viability workshops are run throughout the world (Seal 1992). However, I would argue that the plight of the eastern barred bandicoot and the bilby do not appear to have been altered by the use of PVA.

The use of PVA for the western barred bandicoot in this study has decoupled PVA from the small population paradigm. It has highlighted the critical need for predator eradication and suggested that additional populations of the western barred bandicoot may be viable in areas the size of Heirisson Prong or smaller, and with low founder population sizes. However, I believe the PVA has done little more to improve our knowledge and ability to make management decisions about future conservation actions for the species, beyond adding support to some of the recommendations outlined in a draft recovery plan for the species produced by Richards (2003), without the aid of PVA. Perhaps PVA is not an appropriate tool for examining the impact of predation on a population?

6.8 Conclusions and recommendations

Coulson et al. (2001) concluded that PVAs may be used as a tool to predict extinction risk of populations where data adequately capture the distribution of population growth rates. As the long-term collection of such a large amount of data is rare, the predictions of PVAs should be treated with extreme caution. However, they may be used as a means of comparing management strategies, for “exploring theoretically the implication of model assumptions on extinction probabilities and population dynamics” (Coulson et al. 2001), and as a decision-support tool (Burgman and Possingham 2000), rather than a decision-making tool (Possingham et al. 1993).

Caughley (1994) pointed out that the majority of population extinctions have been a result of steady population decline, rather than chance events. However, PVA has been used within the small population paradigm to predict population persistence of populations that are already small and at risk due to demographic and environmental
stochasticity, thereby confirming the risk of being small. PVA may present an opportunity to merge the small population paradigm with the declining population paradigm, to aid in management actions for threat abatement and therefore to assist in halting population decline. However, to examine threatening processes within a PVA requires knowledge of the impact of the threat, which is seldom available, and as Caughley (1994) pointed out, PVA does not identify the cause of a problem. It is not a diagnostic tool, and is no replacement for Caughley’s process of diagnosis and treatment of population decline.

Shaffer, Watchman, Snape and Latchis (2002) outlined three important contributions of PVA to the conservation of threatened species: (1) PVA has highlighted the importance of population size and in turn, led to greater conservation efforts, (2) PVA provides a framework for organising what is known and unknown of the biology of a species and the threats that face that species, and (3) PVA has also made conservation decisions more transparent. Important future directions for the advancement of PVA in conservation biology include the development of standards for model structure and data suitability, long-term field studies of population dynamics, including a cross-section of species that represent major life-history types, and experiments and validation of PVA models (Belovsky, Mellison, Larson and Van Zandt 1999; Ralls et al. 2002; Shaffer et al. 2002). Another direction may be to develop structural changes to PVA models that allow the incorporation of an additional component of mortality associated with predation, or to use an interactive model described by (Caughley and Gunn 1996), which is structured around the interaction of predators and their prey.

The information gathered from the first reintroduction of the western barred bandicoot to mainland Australia (Chapter Two), the biology of the species (Chapter Three), and the potential impact of feral cats and rabbits (Chapters Three, Four and Five), provided the basis for the construction of the PVA outlined in this chapter. The results from the PVA provide additional information that can be used to aid the management and conservation of the western barred bandicoot. In particular, this information may be useful in assisting with future decision-making for the species, on such matters as the estimation of the minimum size for reintroduction sites, management to maximise genetic diversity of populations through supplementation of populations with a small founder size, and facilitation of cross-breeding between
reintroduced populations as suggested by Eldridge et al. (1999). In particular, the PVA has emphasised the low importance of genetic issues, the viability of small reserves (2 – 20 km²), and the need for exclusion of introduced predators at reintroduction sites. Sites such as Heirisson Prong are likely to play an important role in the conservation of threatened species in the immediate future and beyond, until broad-scale control of feral cats is firmly established.
Chapter 7

General discussion

Research at Heirisson Prong, Shark Bay, has facilitated both the recovery of threatened species (this thesis), and the preservation of an area of high conservation value (Richards and Short 2003; Short and Turner 2000; Short et al. 1994), achieving these dual aims, which were suggested by Dickman (1996), to stem the loss of species. The site has combined single species and threat-based approaches to conservation biology, by re-establishing a community of threatened species, actively conserving their habitat, and ameliorating the impact of diagnosed threats. The site acts as a working model for threatened species management.

The steps to address the conservation of threatened species suggested by Caughley (1994), Dickman (1996) and Ride (1970), and outlined in Section 1.3, influenced the design of the research outlined in this thesis to address the recovery of the endangered western barred bandicoot. The components of this research included:

1. Surveys to assess population distribution, abundance, habitat and past decline of the western barred bandicoot (Chapter One; Short et al. 1997a; Short et al. 1998);
2. A compilation of possible causes of the decline of the species on mainland Australia (Chapter One);
3. A comparison of reintroduced mainland and remnant island populations with and without three possible agents of decline (foxes, feral cats and rabbits; Chapters Two and Three);
4. Studies of the ecology of the species at Bernier and Dorre Islands and Heirisson Prong (Chapters Two, Three and Four; Short et al. 1998);
5. An experimental reintroduction to Heirisson Prong to test the hypothesis that the removal of introduced predators, but not rabbits, would allow the re-establishment of the western barred bandicoot (Chapters One, Two; and Three); and
6. Recommendations for future reintroduction and management of the western barred bandicoot, based upon the need to ameliorate the threat of predation by feral cats and foxes, but not rabbits (Chapters Two, Five and Six; Richards 2003).
The reintroduction of the western barred bandicoot from Dorre Island to Heirisson Prong (Chapter Two) was relatively straightforward, suggesting that future translocations of the species are unlikely to be problematic, provided: a predator eradication program is in place; suitable good quality habitat with substantial cover is available at the reintroduction site; and radio collars are not used, or if they are, for short periods only. A successful reintroduction of threatened mammals such as the western barred bandicoot on mainland Australia consists of: threat abatement (identify, remove); adequate site selection (good habitat, accessible for management, appropriate size for fencing, management and population persistence); and enough resources in the long-term (secure tenure, ongoing funding) to provide for effective management. Post-release monitoring is particularly important for any reintroduction, to diagnose any problems that may arise, to understand the causes of any population decline, and to put management actions in place to ameliorate threats as they arise.

The threat of fox and feral cat predation was controlled at Heirisson Prong, and the site chosen consisted of good quality habitat ungrazed by livestock, with plentiful cover and food resources. Heirisson Prong was conducive to both monitoring of bandicoots and the control of predators due to an extensive track system, and its size and shape. The site has an estimated carrying capacity of over 500 bandicoots, which appears adequate to alleviate the problems associated with small populations (Chapter Six). Resources for ongoing management are provided by the local mining company Shark Bay Salt Joint Venture, who have been investigating the possibility of changing the land tenure of the peninsula to conservation estate, thereby ensuring the continuation of the site as a sanctuary for threatened species.

Predictors of translocation success have included habitat quality at the release site, large numbers of animals being released over the duration of a translocation program, and release within the historical range of a species; there is also some evidence that omnivorous species are more successful in translocations than herbivores or carnivores (Wolf et al. 1998). Reintroduction of the western barred bandicoot at Heirisson Prong was to an area of good quality habitat, and within the historical range of the species. A small number were released, which is often the case for threatened species (e.g. Copley 1994; Wolf et al. 1998). Despite the potential problem of small founder size, the western barred bandicoot may be a good candidate for reintroduction elsewhere within its historical mainland range, due to its omnivorous diet, the highly flexible nature of the nesting biology of the species, and ability to cope with high rabbit density. In the
absence of threats such as predation by foxes and feral cats, the high fecundity of western barred bandicoots should ensure that populations increase rapidly and become large enough to avoid the adverse effects of demographic and environmental stochasticity.

Prior to the research by Short et al. (1997a; 1998) and this project, very little was known of the biology of the western barred bandicoot, and the reasons for its extinction from mainland Australia were unclear (Chapter One). The reintroduced population at Heirisson Prong provided an opportunity to study the biology of this endangered species, and to contribute to management decisions about future conservation actions. As outlined in Chapter Three, biological attributes of the remnant island and reintroduced populations were similar, suggesting that the reintroduction site at Heirisson Prong was suitable for the persistence of the species. The species is similar to other species of Australian bandicoots in that females mature earlier than males, juvenile mortality appears to be high, animals are solitary, the difference in home range size between sexes is similar, and habitat requirements are broad. However, notable differences include smaller body size, larger females, smaller litter size, larger testes size in males relative to body size, larger home range size relative to other species of Australian bandicoots, and equal sex ratios. The factors that have contributed to these differences were discussed in Section 3.5, and may be due to the competing pressures of island dwarfism, the lactational needs of females, and nest defence, if it is indeed necessary for females to defend nest sites from males. Whatever the reasons, the western barred bandicoot is a unique species, and in need of conservation actions to ensure its future survival. An increase in the knowledge of the ecology of the western barred bandicoot will facilitate informed decisions about additional reintroductions of the species elsewhere on mainland Australia.

An increase in the western barred bandicoot population during the control of foxes and cats (Chapter Two) supported the diagnosis of fox and cat predation as a limiting factor for the species, and this predation is likely to have been influential in the decline to extinction of the western barred bandicoot on mainland Australia in the 1930s and preceding years. While research at Heirisson Prong between 1995 and 1999 did not provide any direct evidence of the impact of foxes on population establishment, there was some suggestion that even low densities of feral cats led to a higher than expected mortality rate for re-established western barred bandicoots and a lower than expected population increase. To increase the probability of successful mainland reintroductions
Chapter 7: General discussion

of the species, the complete eradication of these introduced predators should always be a priority.

The role of the rabbit in the decline of native mammals in Australia remains largely unknown despite 100 years of speculation (Robley 2000). Rabbits were present on Heirisson Prong at densities of up to 38 per hectare, but did not appear to affect the re-establishment of the western barred bandicoot (Chapter Two), nor its ability to construct nests and utilise a variety of shrub species when vegetation was in poor condition due to rabbit grazing (Chapters Four and Five). The western barred bandicoot was reintroduced to the Arid Recovery Reserve at Roxby Downs in South Australia in 2001 in the absence of rabbits (and foxes and cats), yet the population has not increased at a rate any greater than that of the Heirisson Prong population (Arid Recovery 2003). This suggests that the removal of rabbits is not a necessary condition for population increase and establishment, and that population persistence and increase is more likely to be due to the absence of introduced predators. Robley (2000) came to a similar conclusion with regard to another threatened species, the burrowing bettong. The Arid Recovery Reserve has sparse vegetation and had been heavily grazed for over 100 years. By comparison to Heirisson Prong, the site appears to be one of poor habitat quality. Yet the reintroduction of the western barred bandicoot to the Arid Recovery Reserve has been successful, at least in the short-term (Arid Recovery 2003). Loss and degradation of habitat throughout the former range of the western barred bandicoot is therefore unlikely to have directly affected a species that appears to have high flexibility in habitat requirements, but is likely to have indirectly contributed to the demise of the species by reducing cover for predator avoidance. Rabbits support larger populations of predators, contributing to an indirect “hyperpredation” effect on smaller populations of native mammals (Smith and Quin 1996) like bandicoots.

Possingham et al. (1993) described a framework for the management of threatened species, based on PVA, that was proposed as a tool to assist with the choice of management options. Their five steps for improved management included (1) collation of existing information on the species, (2) listing and costing of management options, (3) assessment of management options using PVA, (4) sensitivity analyses, and (5) population monitoring. The PVA outlined in Chapter Six provided a means of collating information on the biology of the western barred bandicoot described in Chapters Two and Three, as well as the threat of cat predation, an assessment of management options for reintroduction sites, and sensitivity analyses of a number of parameters within the
PVA model that might have been influential in determining population persistence. A listing and costing of management options formed part of a draft recovery plan for the species by Richards (2003). However, it is hoped that the results of the PVA in Chapter Six, plus additional population monitoring should the opportunity arise, will contribute to the final national recovery plan for the endangered western barred bandicoot that is soon to be produced by the Western Australian Department of Conservation and Land Management.

The focus of a number of PVAs (e.g. Armbruster and Lande 1993; Goldingay and Possingham 1993; Possingham et al. 1994), and an issue often discussed by proponents of reintroduction biology, has been the scale of reintroductions. Reserve size must be large enough to cater for an effective population size to maintain genetic diversity and evolutionary potential, and to allow natural movement and dispersal, yet small enough to be managed for the control of introduced predators, particularly feral cats, which remain problematic (Section 2.4.4; Short, Turner and Risbey 2002). The 12 km\(^2\) Heirisson Prong Project appears to be of adequate size to balance these requirements, as does the 60 km\(^2\) Arid Recovery Project in South Australia (Arid Recovery 2003). The larger 1050 km\(^2\) Project Eden at Peron Peninsula, Shark Bay, has made a leap in reserve size, which has not been conducive to the adequate management of introduced predators. The presence of feral cats has prevented the successful establishment of species such as the banded and rufous hare-wallaby, and has led to the indefinite postponement of translocation proposals for species such as the western barred bandicoot and Shark Bay mouse *Pseudomys fieldi* (Morris, Sims, Himbeck, Christensen, Sercombe, Ward and Noakes 2003).

Boyce (2002) regarded the resolution of current conservation issues surrounding threatened species management as reliant upon the integration of the small and declining population paradigms (Caughley 1994). While PVA has been clearly entrenched within the small population paradigm, the addition of habitat quality and its effect upon the vital rates of a species is thought to provide an avenue for the contribution of the declining population paradigm to PVA (Boyce 2002). However, habitat quality may not be so important for the western barred bandicoot. In this thesis, I suggest that feral cats limited the growth of the reintroduced western barred bandicoot population, rather than the small population size itself, and this sits firmly within the declining population paradigm. An attempt was made to meld this information with PVA by the impact of cat predation as a catastrophe. However, the outcome did little
more than to emphasise the suspected impact of predation, and highlighted the difficulty
of including catastrophes that are episodic by nature, rather than continuous. Future
refinement of the way in which the impact of predation, and other threatening processes
are modelled within PVA, may assist in producing a more accurate representation of the
role of threatening processes in the decline of species such as the western barred
bandicoot. An interactive model, as outlined by Caughley and Gunn (1996), which
includes western barred bandicoots, rainfall and feral cats, is another alternative that
requires further exploration.

The question remains, is the cost of single species conservation worth the effort
and expense? The research at Heirisson Prong has been based around threat-based
conservation, consisting of the diagnosis and amelioration of threatening processes,
which has benefited a number of species, including the western barred bandicoot. PVA
is very much reliant upon single species ecology, emphasising the need for long-term
studies of individual species (Beissinger 2002; Possingham et al. 1993). Multi-species
and landscape-scale conservation approaches are popular alternatives (e.g. biodiversity
hotspots, landscape scale planning for conservation and ecosystem conservation;
Beissinger 2002; Recher and Lim 1990), however, there is no substitute for the basic
ecological data required for even the most basic of PVA models. There has yet to be
any generalisation made from the multitude of PVAs of single species, and any attempt
to do so, perhaps using indicator, keystone or umbrella species approaches (Simberloff
1998), will no doubt be fraught with uncertainty, and require considerable testing for
accuracy.

Future research on threatened mammals such as the western barred bandicoot
should continue to concentrate on the impact of foxes and feral cats, and the role, if any,
that dense cover plays in offering a refuge from predation by these predators. A more
comprehensive data set for the western barred bandicoot through ongoing monitoring,
including detailed information on mortality rates and environmental variation in
mortality and reproduction, may contribute to refining a PVA. Whether there would be
any substantial improvement in effective management with a more accurate PVA is
unclear.

An additional option is an adaptive management approach (Goodman 2002;
Holling 1978). This might proceed by conducting whole ecosystem experiments and
revising management intervention according to the new information gained from
experimentation (Ludwig and Walters 2002). For the western barred bandicoot, this
could be an experiment designed to monitor population growth and demography in the presence of a low-density feral cat population, followed by a change in management practice to either decrease or increase feral cat density and continue bandicoot population monitoring. The outcomes would assist in determining the maximum level of cat predation that would still allow a sustainable bandicoot population. While conceptually possible, this approach is not practicable because of our inability to manage cats with this degree of precision. The field of adaptive management is in its infancy as a practical approach to the conservation of threatened mammals. McCarthy et al. (2001) described a process to test PVA models by employing different management strategies in different areas to test the relative predictions under the different management strategies. The number of populations required to suitably replicate such an experiment is likely to make this process impossible for the majority of threatened species, and certainly impossible for the western barred bandicoot in the short-term.

There are also a number of theoretical and practical questions surrounding the long-term future of the reintroduced western barred bandicoot population on Heirisson Prong. These include: whether the population is genetically viable with such a small population size; whether predator control can be maintained at a suitable level that enables the population to persist at such a remote mainland site; and what level of predator incursions, if any, can the population cope with without succumbing to extinction? The PVA outlined in Chapter Six does not shed light upon these issues that are firmly entrenched in reality, and for which there is no substitute for long-term monitoring.

Management recommendations for the western barred bandicoot include the establishment of additional populations to continue to aid in the conservation of the species. Frankham (1998) suggested that island populations might be less suitable as sources for reintroductions due to greater inbreeding and lower reproductive fitness compared to their mainland counterparts. This is an irrelevant issue for the western barred bandicoot and similar species where the only remaining populations are those on islands. Dorre Island remains as a good source of western barred bandicoots for future translocation. The removal of animals appeared to have little impact on the persistence of the Dorre Island population.

PVA suggested that reintroduction to reserves of more than 2 km$^2$ is desirable to maximise the probability of long-term population persistence, as is maximising founder
size. However, experience on Heirisson Prong suggests that reintroductions should still go ahead, even if the founder population is as small as 20 individuals. Genetic issues are likely to remain a low priority for the western barred bandicoot, other than to attempt to maximise genetic diversity by maximising founder population size and carrying capacity (reserve size) at reintroduction sites. Addition of genetic variation through population supplementation is recommended also.

The primary concern for reintroductions of the western barred bandicoot, and other bandicoot species within Australia, remains the eradication of introduced predators. The impact of introduced predators on western barred bandicoots and other threatened mammals (e.g. burrowing bettong: Christensen and Burrows 1994; Short and Turner 2000) is typically immediate and catastrophic, and so must be managed in such a way as to prevent population extinction within the first few years of reintroductions. If this can be done and this management maintained, reintroduced populations are more likely to persist. The inclusion of threatening processes or catastrophes that are likely to affect the persistence of threatened mammal populations is a key issue for PVAs and the future management of species such as the western barred bandicoot, that require positive and ongoing human intervention to ensure their preservation.
Chapter 8

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