

Chapter One

Introduction: Mammal Extinctions and Recovery in the Arid Zone

1.1 Species extinctions in the arid zone

The flora and fauna of Australia's arid zone have suffered badly in the 200 years since European settlement. There have been numerous extinctions and contractions of range, and in some places mere fragments of originally diverse communities now remain. Such a catastrophe demands interpretation and explanation, especially because improved understanding will lead to better management of these remnants.

Within the Northern Territory alone at least 15 species of arid zone vascular plants and vertebrate animals have become extinct since European settlement. A further 75 species are classified as either endangered or vulnerable. Additional species have declined to vanishingly small populations, and are dangerously close to extinction. Many were once widespread and abundant, and formed an important element in the diet of Aboriginal people. Spencer (1896) reported the Common Brush-tail Possum *Trichosurus vulpecula* to be"everywhere among the gum trees"...., and to be one of the most common marsupials. Finlayson (1935) reported large areas of shrubland to be dug over by the Bilby *Macrotis lagotis* in search of its food, and he had little trouble getting"a nice series of specimens".... of the Rufous Hare-wallaby or Mala *Lagorchestes hirsutus* during his expeditions of the early 1930s. On his return in the 1950s, just 20 years later, he took no specimens of these species and considered them to have become extinct or exceedingly rare in most of the country he visited (Finlayson 1961). Plants such as the Native Sweet Potato *Ipomoea polpha* were once important staple foods for desert Aborigines, but are now considered rare species.

The situation is obviously critical, and its improvement calls for innovative approaches and commitment from all sections of the community. This perception will undoubtedly grow in importance in a nation now increasingly interested in the conservation of its unique biological heritage.

1.2 Understanding the growing problem

Detailed appraisal of the patterns of decline and extinction within the flora and fauna of the arid zone fails to reveal a single cause or consistent combination of causes relating to European settlement. There are exceptions, inconsistencies and enigmas, and plainly the impact of certain factors has varied in relation to both the species and the areas involved.

The reasons advanced for these astonishingly swift declines are conjectural, but from the numerous reviews there is general agreement about the set of factors which have been involved in these declines and extinctions (Aslin 1983, Burbidge & McKenzie 1989, Morton 1990). The list below summarises those factors most often considered:

- destruction of habitat by European occupation and pastoral exploitation
- changes in fire regimes due to the decline in traditional Aboriginal land management practices
- competition from and/or predation by introduced species of plants and animals
- disease and parasites
- drought
- long-term climatic changes

Effective conservation and management of rare and endangered species relies on an understanding of the factors which have contributed to a species' present status. This type of information can only result from detailed studies of these rare species and the communities they occupy.

1.3 Opportunities to recover mammals of the arid zone

The apparently precarious survival of many arid zone mammal species has made it essential that research be undertaken urgently into their present status, distribution and habitat requirements. A profound ignorance of these attributes makes it impossible to institute conservation measures with any confidence. Highest priority must be given to species which

have suffered the greatest decline and which are confined to the arid zone. Active recovery programs are essential to secure and expand populations for many of the particularly vulnerable species.

Extensive surveys of central Australia conducted between the 1960s and the 1980s (Finlayson 1961, Gibson 1986) have provided the basis for determining the range and status of many species. Finlayson (1961) chronicled the apparent declines for many species like the mala which had been abundant during his previous surveys in the 1930s. Work by Gibson (1986) served to confirm the tenuous status of many arid zone species, and hence influenced the priorities for conservation and recovery action. The most positive outcome from recent surveys has been the rediscovery of species that were considered extinct, such as the Central Rock-rat, *Zyzomys pedunculatus* (Gibson pers. comm.) and Gilbert's Potoroo, *Potorous gilbertii* (Start *et al.* 1995).

The opportunity for recovery has been lost for those eleven mammal species of the Australian deserts that have become globally extinct. Opportunities do, however, exist for those species that survive in isolated pockets, either at the wetter periphery of their former ranges or on offshore desert islands. Conservation management to mitigate the impacts of threatening processes, and reintroduction/translocation programs represent key actions in the recovery of these species.

Work by the Conservation Commission of the Northern Territory (CCNT) to recover mammal species in central Australia has therefore targeted the mala and the bilby, two species that have declined substantially on mainland Australia but which remain, or remained until recently, in isolated pockets in the desert region.

1.4 The Rufous Hare-wallaby or mala

The Rufous Hare-wallaby or mala is a rabbit-sized wallaby which was once widespread and abundant in the central desert regions of Australia. Early reports indicate that the species was locally abundant and was an important food source for Aborigines (Finlayson 1961). The general fur colour of the mala, particularly on the hind quarters, chest and abdomen, is a rich sandy



Plate 1: Rufous Hare-wallaby or Mala, *Lagorchestes hirsutus*

buff (Gould 1844)(Plate 1). The pelage of the head and back has a greyish white tint and hair length increases towards the lower portion of the back, giving the animal a conspicuous "shaggy appearance" (Troughton 1965). The species name *hirsutus* refers to this characteristic.

The mala is the second smallest of the hare-wallabies, with an average head and body length between 300 and 400 mm. Finlayson (1943) judged *L. hirsutus* to be considerably larger than the Central Hare-wallaby *Lagorchestes asomatus* on the basis of his measurements of the aged type skull for the latter. The body weights for adult mala fall in the range between 700 g and 2 kg. Like the other members of its group, *L. hirsutus* is generally considered to be nocturnal and solitary.

The former distribution of *L. hirsutus*, as previously projected by a number of authors (Shortridge 1909, Newsome 1971, Burbidge and Johnson 1983), was through the interior areas of Western Australia, northern South Australia, and the central and southern regions of the Northern Territory. Some uncertainty, however, surrounds the exact limits of the species' former range, particularly its eastern and northern limits. Past location records for *L. hirsutus* extend from Macdonald Downs north east of Alice Springs to Beverly in south-west W.A., and from Banka Banka in the north to Everard in South Australia (Fig. 1.1). The absence of records from some areas within the presumed limits of the species may well be an artefact of inadequate sampling. It may also reflect the mode of occurrence of this species, which was reported by Finlayson (1961) during his extensive surveys through central Australia between 1931 and 1956, as being: "fluctuating and discontinuous and with isolated colonies widely sundered", a view also supported by Ride and Tyndale-Biscoe (1962). It could also reflect a persistently discontinuous distribution.

Over the past fifty years, however, it has suffered a severe decline. Recent extensive ground and aerial surveys throughout regions of the Northern Territory (N.T.) and Western Australia (W.A.) (Gibson 1986, Burbidge and Pearson 1988) have failed to locate additional populations. The mala is on the verge of extinction, with wild populations of mala currently known only from Bernier and Dorre Islands off the Western Australian coast. Genetic analyses confirm that these populations represent distinct subspecies of *L. hirsutus* (Courtney 1991, 1993, Lundie-Jenkins unpublished), *L. h. bernieri* and *L. h. dorrae*.

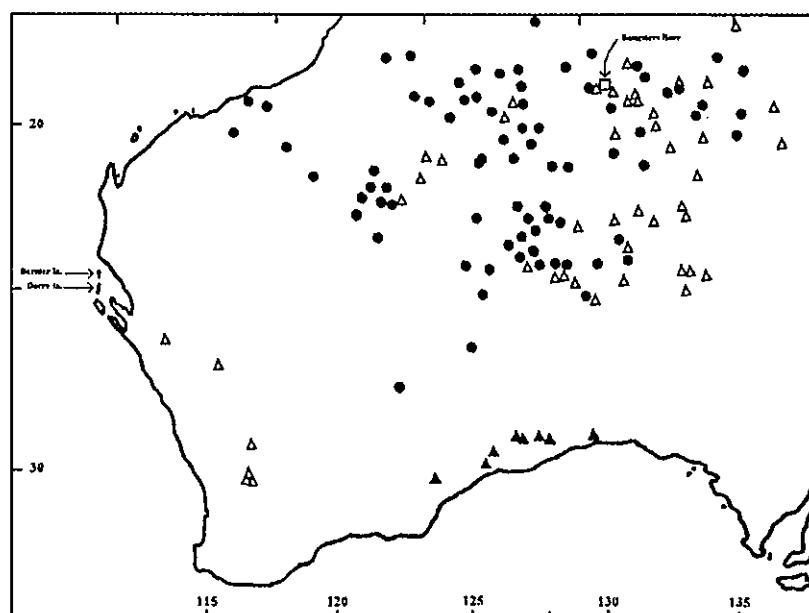


Figure 1.1 Historical records of the Rufous Hare-wallaby (mala)

- Δ Museum and historical records
- Aboriginal accounts
- ▲ Subfossil material

Prior to 1987 a population of mala was also known to persist on the Australian mainland in a region of the Tanami Desert, N.T. This population consisted of two discrete groups about 15km apart located some 30km south of The Granites. Sometime between September and early December, 1987 one of these colonies was driven to extinction by the impact of an introduced predator, the Red Fox *Vulpes vulpes*. The remaining colony remained undisturbed until November 1991 when wildfire destroyed most of the habitat supporting the colony. Subsequent surveys in this area suggest that the fire may have caused the local extinction of this last remaining wild colony. There was obviously an urgent need to expand the distribution and size of the hare-wallaby populations, if their long-term survival was to be secured.

It was the prescient realisation, soon after the Tanami population's discovery in 1974 (Parker 1973), that catastrophic events such as these could ultimately lead to the extinction of the mala on the mainland, which prompted the CCNT to establish a major conservation project aimed at securing the species by captive breeding and reintroduction.

1.5 The Mala Recovery Program

Efforts to recover and conserve the mala have been considerable, and predate the formation of the Australian Commonwealth's Endangered Species Program (ESP) and the protocol of developing formal recovery plans and teams. Such efforts commenced soon after rediscovery of the species. Direct conservation measures initiated by the CCNT to improve the status of the mainland populations of mala included fire management (Bolton and Latz 1978), population and habitat monitoring (Lundie-Jenkins 1993c), ecological research (Lundie-Jenkins *et al.* 1993a, 1993b), and establishment of captive populations and experimental reintroductions (Gibson *et al.* 1995, Lundie-Jenkins & Bellchambers 1995). While a coordinated approach had been taken to implementing these measures, no formal management/recovery plan for the species had been prepared prior to enactment of the Commonwealth *Endangered Species Protection Act* 1992.

1.5.1 The Recovery Plan

The first version of a "Recovery Plan for the Mala" was developed in 1992 (Johnson and Lundie-Jenkins 1992) and focussed on research and management actions related to the central Australian populations of mala. Consistent with the original format proposed by the Australian Nature Conservation Agency (ANCA), the plan was structured to contain separate sections detailing research and management actions. A total of four primary research actions and four primary management actions were identified; these are indicated in Table 1.1. The criteria listed in the recovery plan for measuring progress toward recovery of the mala were:

- a) Maintenance of mainland and island mala populations.
- b) Establishment of self-sustaining populations at two sites in the Tanami Desert.
- c) Maintenance of genetically diverse, self-sustaining captive populations in a number of zoological institutions
- d) Self-sustaining populations at a number of other mainland sites.

Table 1.1

Summary of actions in original Recovery Plan for the Mala
(from Johnson & Lundie-Jenkins 1992)

<u>Research Actions</u>	
1.1	Assess the ecological processes by which translocated mala establish new self-sustaining populations
1.2	Determine cost-effective methods for stress mitigation to optimise establishment of reintroduced mala.
1.3	Determine habitat management requirements in the post-establishment phase.
1.4	Clarification of the status of the 3 recognised subspecies and establish genetic relationships among individuals in the captive breeding colony.
<u>Management Actions</u>	
1.1	Maintenance of naturally occurring mainland and island populations and those reintroduced to Sangster's Bore and the Lander River.
1.2	Maintenance of captive breeding colony in Alice Springs.
1.3	Negotiation of conservation areas in the Tanami Desert with Aboriginal traditional owners.
1.4	Reintroduction of mala to 2 major central Australian National Parks.

No formal consultation process was initiated in the development of the original mala recovery plan, and hence ownership of the document was essentially limited to the Northern Territory. While some actions relating to Western Australian island populations of mala were incorporated in this plan, no accurate estimates of the resources, costs or commitment for these actions were included, since no direct input from the W.A. Department of Conservation and Land Management (CALM) was sought in developing these actions. Similarly, establishment and maintenance of captive populations were important management actions in the original recovery plan, but no consultation with the zoo community was undertaken to develop them. With the wisdom of hindsight it is now apparent that whilst the plan as a document indicated an array of recovery actions, the potential to implement many of these would have been greatly enhanced by broader stakeholder involvement in its development.

1.5.2 Implementation of the Plan

Formal implementation of the initial "Recovery Plan for the Mala" commenced in 1992 with ANCA funding to support 2 major actions, namely research action 1.1 and management action 1.1 (refer Table 1.1). Funding for research action 1.4 was received in 1993. Details of the specific programs initiated and their progress is summarised in Johnson *et al.* (1995). The major achievements of this recovery program to date have been:

- Establishment of a genetically diverse captive population of mala by the Conservation Commission in Alice Springs in 1981, from animals captured from the Tanami population. Over the 10 years since it was established the captive breeding program has successfully bred over 200 mala. At the time of writing, the Alice Springs breeding facility contains a total of 58 mala (24 M, 22 F, 12PY). Animals from this colony have been used to establish additional, but very small, colonies in Western Plains Zoo (Dubbo) and Monarto Zoological Park in South Australia.
- Successful translocation of captive-bred mala to remote sites in the Tanami Desert. Two experiments in reintroducing the mala were initiated: one at the site of the colony that went extinct in 1987 (reported in this thesis), and the other in a fresh-water palaeodrainage line that traditional Aboriginal owners selected on the basis of habitat suitability and use by mala in living memory (Lundie-Jenkins & Bellchambers 1995). Captive-bred animals have been used in each of these experiments designed to examine: techniques for re-establishment, and increased understanding of the factors influencing translocated populations, including introduced predators and fire.
- Development of equipment and techniques applicable to the translocation and conservation management of mala and other arid zone species.
- Cooperative conservation of an endangered species on Aboriginal land.
- Improved understanding of the biology/ecology of the mala and the arid ecosystems it previously inhabited.

The prime setback of the recovery program has undoubtedly been the loss of the only known "naturally occurring" mainland population of mala in 1991, when wildfire destroyed approximately 90% of its habitat (Johnson *et al.* 1995). Without planning to establish captive

populations and initiate translocation/reintroduction experiments, this single event might have resulted in the extinction of the mainland form of the mala. Whilst these actions might well have been initiated without the development of a formal recovery plan, the situation highlights the necessity for a broad and flexible approach to recovery of a species.

1.5.3 The Recovery Team

The inaugural meeting of a National Mala Recovery Team was convened in April 1993, in conjunction with a Reintroduction Biology Conference in Healesville. This action was initiated by officers of the Conservation Commission of the Northern Territory as the lead agency involved in mala research and conservation activities. Invitations were circulated to 16 different organisations, seeking their involvement in the recovery planning process. To ensure a balanced approach was made to the process, equal representation was sought from all the former range states of the mala. Table 1.2 lists the organisations invited to participate on the Mala Recovery Team.

Table 1.2
Organisations invited to participate on the Mala Recovery Team

Organisation/Individual
Australian Nature Conservation Agency
Conservation Commission of the Northern Territory
Western Australian Department of Conservation and Land Management
South Australian Department of Natural Resources
World Wide Fund for Nature (Australia)
CSIRO Division of Wildlife and Ecology (Perth)
Threatened Species Network (Arid Zone and N.T.)
Western Plains Zoo (N.S.W.)
Monarto Zoological Park (S.A.)
Perth Zoo (W.A.)
Central Land Council (N.T.)
National Farmers Federation (N.T.)
Chamber of Mines (N.T.)
University of New England
Independent Publicist

The initial Recovery Team meeting endorsed a proposal to establish a small core group of people actively involved in research on or conservation of the species, and a larger outer

group who would be invited to be corresponding members of the team. The Australia-wide spread of Recovery Team members has made frequent meetings difficult, and hence only one other full Recovery Team meeting has been held, in November 1994 in conjunction with the National Rock-wallaby Conference. Although there have been few meetings, formation of the Recovery Team has acted to formalise the contacts between organisations with interests in the mala, and has greatly improved the exchange of information on the species.

1.6 Aims of this thesis

The elements discussed in the preceding section are all components of the overall recovery strategy for the mala. There is a desire to re-establish populations on the mainland; but in order to successfully achieve this aim we must first understand the factors that have affected the species' survival, develop means to identify and mitigate these factors, and devise means for reintroducing captive animals to the wild. This thesis attempts to address these issues both from a purely management perspective and also from pragmatic and conceptual perspectives. In investigating these issues in such a manner this project sought to achieve four broad aims :

- 1. To review the past applications of reintroduction as a conservation strategy and introduce a framework for planning, hypothesis testing and evaluation within reintroductions.**

The history of attempts to reintroduce mammals in Australia is relatively short and in general early attempts were poorly researched and documented (Copley 1995, Short *et al.* 1992). In many cases the failures have been apportioned to single factors, and little attention was paid to ecological theory or experimental design. Whilst recent reviews have highlighted the deficiencies of past attempts at reintroduction (Griffith *et al.* 1989, Short *et al.* 1992, Beck *et al.* 1994), they have only provided lists of the factors which should be examined in a reintroduction, and have not attempted to establish a sound model for planning, hypothesis testing and evaluation.

This aim is not simply to undertake another critical review of past reintroductions, but to examine the many phases of a reintroduction in order to suggest an approach to reintroductions which refine and improve the process. These phases include logistics and planning, captive

breeding, selection of release sites, development of release techniques and habitat management, as well as a monitoring phase. If the relationships between the various phases of a reintroduction can be better understood, then repeats of the reintroduction failures of the past can be avoided and the information and conservation outcomes derived from such programs can be significantly improved.

- 2. To conduct an “experimental” reintroduction of mala into an area of the Tanami Desert in the Northern Territory examining the factors which affect the survival and establishment of captive-bred mala during a reintroduction.**

Whilst the word “experimental” has often been used in the context of a reintroduction program, such programs have seldom in the past been conducted within an experimental framework (Armstrong *et al.* 1995). Whilst there will inevitably be some limitations to the degree to which strict experimental designs can be employed, due to the inherently small numbers involved in endangered species projects, significant improvements can be made to our approach to reintroductions. Significant information in relation to the population dynamics of mala will also be derived which will have direct relevance to future management of the species.

- 3. To explore the implications of the results from this “experimental” reintroduction with regards to future management, reintroduction and recovery of the mala.**

As a component of the overall recovery strategy for the mala the project will have significant bearing on the future direction of management, reintroduction and recovery of the species.

- 4. To critically evaluate the performance of the proposed reintroduction framework in relation to both its application in this project and its extrapolation to other future programs.**

The process of applying the proposed framework for reintroductions to a specific case study and critically reviewing its performance is intended to lead to further refinement of the process. This will involve examining the relative strengths and weaknesses of the proposed framework for reintroductions; firstly in relation to its application in the case study conducted

within this project, and secondly its extrapolation to reintroductions involving other species and sites. Given the poor record of Australia's arid zone in relation to species' extinctions, it is hoped that the results will provide a solid basis for progressing future recovery of a range of species.

Chapter Two

Reintroduction as a Conservation Strategy

2.1 Introduction

The reintroduction of species to the wild, with the ultimate aim of re-establishing populations, has become an area of keen interest in conservation management. In the Action Plan for Australian Marsupials and Monotremes (Maxwell *et al.* 1996), reintroductions have been implemented or are planned for 16 of the 53 species listed as endangered or vulnerable. Whilst the focus of most such programs is on individual species, reintroduction is also seen as a means of restoring ecosystems or communities to near natural states. More recently the value of reintroduction as a means of investigating the status and functional ecology of ecosystems has also been recognised (Armstrong *et al.* 1995, Soderquist 1995).

The growing interest in reintroduction has led to significant review of the process and projects past and present (Griffith *et al.* 1989, Stanley Price 1991, Short *et al.* 1992, Beck *et al.* 1994, Wilson and Stanley-Price 1994, Copley 1995). With such review has come the realisation that reintroductions should not be viewed as singular management actions, but as complex experiments that should be deliberately planned and monitored. The approach to such reintroductions needs to be sufficiently rigorous to validate any conclusions that can be drawn from them relating to ecosystem function, extinction forces and threatening processes. The high costs associated with reintroductions demand that such an approach be adopted.

Whilst there is broad agreement that a more rigorous approach is required for reintroductions, there remains some division in relation to the extent to which an experimental approach can, or should be, adopted. Of course, there will be practical constraints which will impinge on the fully replicated experimental approach proposed by some purists. As well as the biological aspects, reintroductions frequently contain non-biological elements, and hence adherence to experimental principles may need to be compromised by realism and practicality.

Reintroductions might therefore be better described as exercises in “Adaptive Management” with protocols subject to change in the light of ongoing experience (May 1991). This does not discount the value of fully replicated and controlled reintroductions where they can be conducted, but recognises that circumstances may dictate adoption of alternative approaches.

The other contentious issue associated with reintroductions relates to measuring success and failure (Griffith *et al.* 1989, Beck *et al.* 1994). In general terms the ultimate aim of all reintroduction programs will be the establishment of a new self-sustaining population of a species, but should this be the only measure of success? The application of generic measures of success in terms of population size and rates of increase, as attempted in some recent reviews, does not translate easily between different taxa. Whilst measures of success are needed, it may be more appropriate to measure them as milestones rather than singular achievements. If reintroductions are rigorously planned and monitored significant information can be derived from the process, even if the ultimate aim is not recognised.

There is scope for development of a conceptual approach to reintroductions which provides a basis for planning, implementation and evaluation. The remaining sections of this chapter will review the processes associated with a reintroduction, and in doing so introduce a theoretical framework for planning, implementation and evaluation of reintroductions. This approach is intended to provide an experimental basis for reintroductions that enables valid hypotheses, in relation to population processes and ecosystem function, to be examined and tested.

2.2 What is a reintroduction ?

Within the literature reviewing reintroductions and translocations, a range of definitions have been adopted. For the purposes of this review I shall use the following definitions adopted from the position statement on translocation of living organisms (IUCN 1987) :

Reintroduction: The deliberate release of individuals of a species into an area from which it has been lost, with the aim of establishing a self-sustaining and viable population.

Restocking: The release of individuals to reinforce an existing population, usually with the aim of increasing population viability.

Introduction: The deliberate or accidental dispersal of individuals of a species into an area outside its historically known native range.

Translocation: The movement of individuals of a species from one area, with free release in another. Translocation includes introductions, reintroductions and restocking.

2.3 Why reintroduce ?

Reintroduction is increasingly being seen as a means of reversing the alarming trends in extinction and decline of species. Species which persist in small remnant populations are extremely vulnerable to extinction through demographic or genetic stochasticity, simply because of their population size. If a population is declining in numbers, and no action is taken, then extinction is inevitable. Whilst reintroduction is not the only management action at the disposal of wildlife managers, it is a key component of the recovery planning for species whose populations have declined to critically low levels. Planning, to reduce the risk of extinction and secure the status of such species in the long term, must include programs of range extension (Johnson *et al.* 1989). This may be achieved by either:

- Natural extension of the boundaries of existing populations by manipulating components of the environment; or
- Reintroduction of the species to parts of its former range.

Of these two, a successful reintroduction offers the better opportunity for greatly extending a species' range through the establishment of new self-sustaining populations. As previously mentioned, reintroduction programs also provide an opportunity to examine the responses of the released species to environmental stresses under controlled conditions. Work of this sort provides useful insights into the factors which originally contributed to the species becoming locally extinct, and thus supplies information essential to the formulation of effective management prescriptions, for both naturally occurring "wild" populations and for reintroduced populations. For critically endangered species like the mala, the alternatives to reintroduction are the establishment of captive and semi-captive populations, neither of which provide long-term security for the species.

As intimated in the introduction to this chapter, decisions to reintroduce will also include both biological and non-biological considerations. The non-biological considerations will vary greatly between species and political and economic backgrounds. The draft guidelines for reintroductions produced by the IUCN/SSC Reintroduction Specialist Group list the following goals or objectives for reintroductions:

- (a) To enhance the long-term survival of the species;
- (b) To re-establish a keystone species (in either the ecological or cultural sense);
- (c) To increase or maintain diversity;
- (d) To provide long-term economic benefits to local people;
- (e) To achieve a combination of all of the above.

Whilst most attention within a reintroduction program is focussed on the target species, there are a number of examples where major benefits have resulted from a reintroduction that are external to the species. The reintroduction of the Arabian oryx *Oryx leucoryx* in Oman was a very costly exercise in terms of the support per oryx, but the project played an important role in the development of a large area of desert and its tribal inhabitants (Stanley-Price 1989, 1991). The government of Oman, in fact, saw the reintroduction as an effective way of creating long-term employment opportunities where there were few alternatives. Likewise, the return of the Golden Lion Tamarin *Leontopithecus rosalia* to Brazil acted as the vehicle for a major education campaign highlighting the value of, and threats to, the forests of the region (Kleiman *et al.* 1991).

There are numerous benefits to derive from reintroduction, in addition to those relating to the particular species involved. This being the case and bearing in mind the high costs of such programs, it will be important to have a logical basis for establishing the suitability/acceptability of species for reintroduction.

2.4 What factors affect decisions to reintroduce?

The most fundamental premise that should underpin any decision to reintroduce an endangered species is that there is a discoverable cause for the species going extinct at a site in the first place. Without knowing this cause and implementing some remedial action to remove or mitigate its effect, any attempt to reintroduce will surely be destined for failure. The very complex

nature of the reintroduction process dictates that many other factors need also to be considered before the decision is made to proceed with a reintroduction. In an ideal world we might hope that such decisions were pragmatic, and based on biological imperatives; however, in reality political, legal, logistical and economic considerations will also influence decisions regarding reintroduction.

Kleiman *et al.* (1994) suggested that there are 13 criteria that should be considered prior to implementing a reintroduction. These criteria, summarised in Table 2.1, relate to the condition of the species, environmental conditions, biopolitical considerations and biological and other resources. Whilst many of the criteria are self-evident, a number could be disputed as their relevance is likely to be influenced by the desired aim of a reintroduction. For instance, a reintroduction program initiated using a reasonably abundant species would be opposed under the first of these criteria. However, such a program would be a priority action if the reintroduction of the abundant species were being used as a surrogate, to evaluate reintroduction techniques for a critically endangered con-specific. In a similar sense, the criterion requiring that we have sufficient knowledge of a species' biology prior to implementing a reintroduction, may prejudice conservation efforts against rediscovered or poorly known species, for which there may be little or no knowledge of the species' biology. In such cases managers may need to implement reintroductions using available biological information on closely related species, and incorporating methods that enable them to learn more about the biology of the target species.

Kleiman *et al.* (1994) attempted to extend the application of their criteria by incorporating a scoring system, by which the managers could assess whether appropriate conditions existed for reintroducing a particular species. Whilst such an approach ensures that a range of important criteria are considered, it assumes that these criteria have equal weighting for all species in the decision-making process, and does not accommodate departures from the thinking used to derive them (as illustrated in the previous paragraph.)

Whilst reintroductions are most often implemented as a means of securing the survival of a threatened species, they are often not the most cost-effective strategy for achieving this end (Kleiman 1989, Stanley-Price 1991). As such, the range of alternative conservation strategies and their respective probabilities of success will strongly affect the decision to implement a reintroduction program.

Table 2.1
Criteria for assessing if appropriate conditions exist for implementing a reintroduction
(adapted from Kleiman *et al.* (1994))

Criteria
<i>Condition of the species</i>
1. Need to augment the population
2. Available stock for reintroduction
3. Reintroduction poses no threat to the wild population
<i>Environmental conditions</i>
4. Causes of decline removed
5. Sufficient protected habitat for reintroduction
6. Available habitat is unsaturated
<i>Biopolitical considerations</i>
7. No negative impacts on local human population
8. Local community support for the reintroduction
9. All relevant Government and non-government organisations should support the program
10. Any action should conform with relevant laws and regulations
<i>Biological and other resources</i>
11. Techniques for reintroduction should be known or in development
12. Sufficient knowledge of the species' biology
13. Sufficient resources exist for the program

2.5 Alternatives to reintroduction

In evaluating the appropriateness of implementing reintroduction as a conservation strategy for a species, it is important that alternative approaches are given equal consideration. There is growing criticism of the focus on single species and the enormous costs associated with programs involving captive breeding and reintroduction. In light of the growing competition for access to limited financial resources, there is increasing support for the focus to shift to *in situ* conservation management in areas of high biological diversity (Magin *et al.* 1994), or where several endangered species might be reintroduced or conserved sympatrically.

Efforts to recover endangered species need to be multifaceted, and the worldwide movement towards the development of individual species recovery plans is aimed at ensuring that a comprehensive and balanced approach is taken to recovery of endangered species (ESP 1995). Reintroduction should therefore be seen as one element of the recovery strategy for a species. Other elements might include:

- The establishment of national parks and protected areas to reduce loss of habitat and protect important habitat features. Whilst establishing protected areas is a key element in recovery, the altered equilibriums which exist in natural systems due to the disturbances wrought by humans dictate that other action is required. Species have gone, and will continue to go extinct in national parks without mitigation of threatening processes.
- Adaptive management of remaining populations based on current knowledge. This approach represents a sensible compromise between continuing research and reactive management. This enables managers to measure responses to management actions, and hence improve their ability to achieve conservation gains.
- Ongoing research to identify the causes of species' decline and extinction, and developing means for managing these agents to benefit both the target species, and biodiversity values in general.
- Community education and legislation, in that order, to promote protection of endangered species and critical elements of their environment. Education and community support provide better long-term prospects for a conservation program, but laws need to be put in place as a backstop.
- Biological survey is an element often overlooked in the recovery planning for an endangered species. Recovery effort often focuses on remnant populations when some potential exists that other extant populations may remain. Recent rediscoveries of populations of species such as the Central Rock-rat *Zyomys pedunculatus* (Gibson pers. comm.), and the Golden Bandicoot *Isodon auratus* (Woinarski pers. comm.) on the Australian mainland have greatly altered the known conservation status of these species. Whilst discovery of new populations does not ensure the survival of a species, it may dramatically alter the priorities assigned to recovery actions.

It is apparent that whilst both captive breeding and reintroduction programs enjoy significant popularity as high profile strategies for the recovery of endangered species the top priority for most species is, and must remain, management of the environment to conserve wild populations *in situ*. Primary amongst this management is protection of habitat and resources, including freedom from diseases and excessively heavy predation. The fact also remains that for some species, whose populations have declined to critically low levels, captive breeding and

reintroduction will be the prime strategies for effecting some long-term recovery . The shift in focus towards conservation programs which produce broader biodiversity benefits is further evidence for the need to improve the rigour of reintroductions, and hence the quality of information on species and ecosystems that can be derived from them.

2.6 Reintroduction vs translocation of wild animals

It would seem logical to assume that wild-bred animals will possess certain survival skills which have either been lost, diminished or not learnt by animals born and reared in captivity. The logical extension of this would be an expectation that wild-born animals might have enhanced probabilities of survival when translocated, compared with captive-bred animals. In a recent review of the use of translocations, predominantly for game species, Griffith *et al.* (1989) noted that translocations involving the movement of wild animals from one site to another had a higher success rate (75%) than the release and establishment of captive-bred animals (38%). In a program initiated to reintroduce the Swift Fox *Vulpes velox* to Alberta in Canada (Carbyn *et al.* 1994), wild caught foxes translocated to a release site had significantly higher survival rates (47%) during the first 12 months compared with the most successful captive reared group (33%). Short *et al.* (1992) found no evidence of such a trend in macropod reintroductions in Australia, but few direct comparisons were made in the studies reviewed. Reintroductions of the Numbat *Myrmecobius fasciatus* detailed by Friend (1990) included successful establishment of both wild and captive-bred animals in areas of south-western Western Australia.

Whilst there have been a number of successful reintroductions involving both wild and captive-bred animals, in the few documented cases where direct comparisons have been conducted for a species, the wild animals have generally fared better. However, the opportunity to utilise wild animals has been lost for many critically endangered species. For species that remain in single remnant populations, or in some cases in captivity, captive breeding and release will be the only option for future reintroductions.

2.7 Histories of success and failure

There have been a number of recent reviews documenting the successes and failures of

reintroductions on a global scale (Griffith *et al.* 1989, Beck *et al.* 1994). In the more recent of these, Beck *et al.* (1994) examined the characteristics and relative success of 145 distinct reintroductions involving the use of 126 different species of captive-born animals. In their review, they applied a criterion for measuring the success of a reintroduction requiring either: (i) The establishment of a wild population of at least 500 individuals which were free of provisioning or other human support, or (ii) A formal genetic/demographic analysis predicting the population to be self-sustaining. Not surprisingly, less than 11% of the 145 programs they reviewed were able to satisfy these criteria for success. In their review, Griffith *et al.* (1989) used the judgement of project managers as the basis for comparing the success of reintroductions involving captive-bred animals to those using wild-born animals. They estimated that only 38% of projects reintroducing captive-bred animals were successful, while 75% of projects translocating wild animals were successful. In both these major reviews the success or failure of a project was determined entirely in terms of the population size and rates of increase for the reintroduced animal.

Beck *et al.* (1994) also examined several characteristics of reintroductions within their review with respect to their influence on success. They found five notable differences in the characteristics of the “successful” and “other” projects. Successful projects used medical screening and post-release provisioning less often than the other projects. They interpreted this as either a counter-intuitive outcome resulting from a small sample, or indicating that such measures are not essential to the success of a reintroduction. Successful projects were found to have more frequently provided local employment and community education programs. They also released animals in an average of 11.8 years whilst other projects released animals in an average of 4.7 years. The overall conclusion they were able to draw from their work was that successful reintroduction projects seem to extend over many years and release large numbers of animals. They also invested more heavily in the involvement of local people through employment opportunities and community education. This serves to highlight the significance of non-biological factors, particularly the need for adequate long-term funding and commitment.

Whilst there are several different yardsticks which can be used to measure the success of a reintroduction, the true success of any program can only ever be measured in terms of its goals and objectives. Generic measures based on target population sizes and the absence of management suggested by Beck *et al.* (1994) do not accommodate the significant differences between species or

systems. A reintroduction program can achieve a number of successful outcomes, despite not reaching its ultimate goal of a new self-sustaining population. The extent to which these outcomes are recognised or measured is completely dependent on the approach taken to planning and implementing the reintroduction.

2.7.1 Australian experiences

The history of attempts to reintroduce mammals in Australia is short and in general early attempts were poorly researched and documented (Copley 1995 , Short *et al.* 1992). In 1994 Healesville Sanctuary played host to a major conference to review the “Reintroduction Biology of Australian and New Zealand Fauna” (Serena 1995). This publication provides an excellent summary of past and present reintroductions being conducted in Australia. The reported failures of many such reintroductions have been blamed on single factors, primarily introduced predators, and little attention has been paid to ecological theory.

A review of macropod reintroductions by Short *et al.* (1992) again highlighted a high failure rate for reintroductions to sites where eutherian predators were present (Table 2.2). Interestingly this review by Short *et al.* (1992) focussed on reintroductions of species which fall within the critical weight range defined by Burbidge *et al.* (1989), and ignored the many translocations/reintroductions of large macropods which have occurred within Australia and overseas. Wodzicki and Flux (1967) detail the successful establishment of 6 different wallaby species to parts of New Zealand.

From review of past attempts to reintroduce macropods in Australia, two clearly discernible patterns emerge:

1. The most common factor blamed on the failure of the reintroduction attempts is predation, and,
2. A great many of these past attempts were poorly documented and not conducted in a rigorous/scientific manner.

Table 2.2
Reintroduction of macropods to the Australian mainland
(after Short *et al.* 1992)

Species	Year(s) of Reintroduction	Site	Number Reintroduced	Survival	Factors limiting success of reintroduction	Source
Red-bellied pademelon	1911-14	Wilsons Prom.	?	?	?	Menkhorst & Mansergh (1977)
Quokka	1972-88	Jandakot, WA	c. 700	Some >3 year most < 1 year	?Foxes	Algar (1986)
Tammar Wallaby	1971-88	Jandakot, WA	85	< 2 years	?Foxes	Short et al 1992
Brush-tailed bettong	1977	Yendicup Block, Perup, WA	52	13 years +	Foxes (controlled by 1080 baiting 1979, 1980 and 1981),	P. Christensen (pers. comm.)
Brush-tailed bettong	1982-83	Collie, WA	52	< 2 years	Foxes (baited at release) low ground cover, ? native cats	P. Christensen (pers. comm.)
Brush-tailed bettong	1983	St Johns Brook, WA	67	< 6 months	Foxes (no 1080 baiting)	P. Christensen (pers. comm.)
Brush-tailed rock-wallaby	1980-81	Wombeyan Caves, NSW	4 + 6	10+ years	?Foxes, cats	Short et al 1992
Rufous hare-wallaby	1984-85	Lake Surprise, NT	12 + 15	c. 16 months	?Drought, cats, dingos	Lundie-Jenkins (1989)
Rufous hare-wallaby	1990	Lake Surprise, NT	11	< 4 months	Cats	K. Johnson (pers. comm.)
Parma wallaby	1988	Robertson, NSW	47	< 4 months	Foxes	Short et al 1992

2.8 Developing a model for the reintroduction of endangered species

2.8.1 A conceptual model

Whilst re-establishment of a species in the wild is arguably the prime aim of most reintroduction programs, the previous discussion has examined the potential of these programs to answer substantial questions related to the ecology and population dynamics of a species. This relationship has been lost to many previous reintroduction attempts, and in some cases little information could be extrapolated from the failures or successes of reintroduction programs. The model introduced here is designed to illustrate the processes involved in a reintroduction, the benchmarks against which the success of such a program can be assessed, and the biological and management information that can potentially be generated by it. Although originally

designed for application in assessing the design and progress of the mala reintroduction program, the model does have general applicability for reintroduction of animal species and, with modification, for plants.

2.8.2 Why develop a model ?

With the rapid development of computer technology, the word “model” now strikes fear into the hearts of many wildlife managers. The application of “black box” modelling approaches, sometimes involving complex algorithms, to wildlife management problems has been a source of growing concern. In reality, however, a model can simply be a means of representing or abstracting a system or process (Starfield & Bleloch 1988). The advantages of building even the simplest of models are:

- To define goals, problems and resources;
- To organise available information on a system or process;
- To assist in the interpretation of data;
- To communicate and test our understanding of a system or process; and
- To make predictions about systems or processes.

In short, a model is simply an intellectual tool that can be used by managers in decision making, planning, evaluation and communication. Many experienced managers unconsciously apply simple models as a basis for decision making (Starfield & Bleloch 1988). Such experience-based decision making, like other forms of models, relies on a process including data input by observation, some type of logical sorting based on previous experience, and a final output. The unfortunate flaw to such an approach is that because the model used is not explicit there is no way of validating the process, or testing its application under different circumstances. This is very much the same scenario that exists for poorly designed and monitored reintroductions. Whilst they may either fail or succeed in their ultimate aims, the lack of a structured experimental approach means there is no way of evaluating or validating the approach they have taken such that future programs may benefit. This is not to belittle the value of such experienced decision-makers, as development of more explicit models can benefit greatly from such individuals. The reintroduction model presented here draws substantially on the extensive literature regarding management of endangered species, and has

as its major input the accumulated ecological information on a target species.

2.8.3 Relevance of ecological setting of Australia's arid zone to model development

Australia's arid zone is typified by both the scarcity and uncertainty of its rainfall. Equally important, however, is the infertility of the ancient soils that dominate this region of Australia. The combined influence of these two factors creates an environment in which productivity is highly patterned both spatially and temporally (Morton 1990). This patterning is thought to have contributed to the high level of extinctions that have occurred in the arid zone. It also complicates the process of extrapolating from the results of ecological investigations conducted in the region.

The number of extinct and endangered species known from the arid zone is relevant when considering the justification for developing a model to describe and control one of the important processes in species recovery. With a high level of decline there is both an ample requirement for species recovery and a need to derive significant information from programs for one species that can be applied to others. The highly patterned nature of the arid zone environment also heightens the need for a rigorous framework, as interpretation of the results from any reintroduction in the arid zone will be influenced by environmental factors that vary significantly in space and time.

2.8.4 Developing a model

Unlike a simulation, a basic model is not intended as a replication of a process but rather as a simplification. For this reason models are frequently developed with imperfect information in order to "explore the consequences of what we believe to be true" (Holling 1978). In this way we develop an understanding of the processes, by monitoring the performance of experiments, in this case an experimental reintroduction. The model itself is not the final product, but is merely a tool for evaluating and re-evaluating the process. It is only by manipulating our modelled systems, questioning the relevance of particular elements and comparing their behaviour with what we already know about the system that we can ultimately progress our understanding. Improved understanding will undoubtedly lead to the

development of better models.

Holling (1978) presents a diagram representing the classification of modelling problems, which is relevant to development of the elements of a model for use in reintroductions (Fig 2.1). The horizontal axis represents how well we understand the problem we are trying to model, whilst the vertical axis represents the quality and/or quantity of relevant data. Holling divides the quadrant between the two axes into four areas, which essentially partition the elements of our modelling problem.

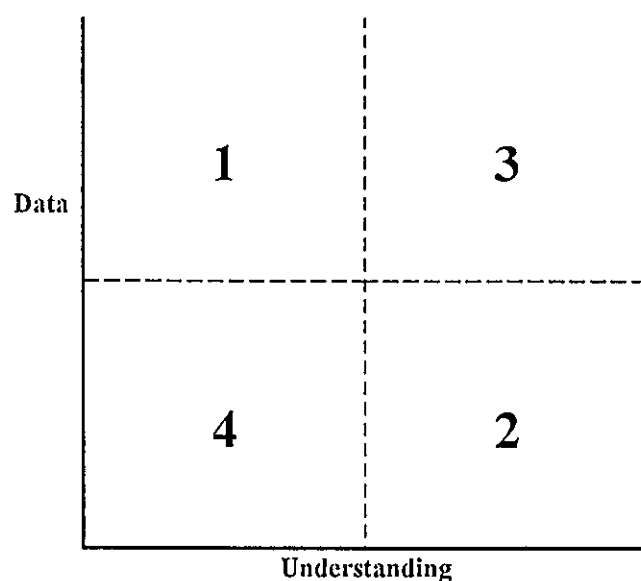


Figure 2.1 Holling's (1978) classification of modelling problems.

Area 1 is the region of good data but little understanding. In the context of reintroductions this could include information on historical distribution, preferred habitats, genetic composition of source populations and predator effects, where reasonable data sets may exist but our understanding of the population's demographic and ecological processes is poor. For elements within this region there is scope for further analysis of available data to search for patterns, and construct and test hypotheses (Starfield & Bleloch 1988). The process of identifying these elements for a species will ultimately enhance the development of a reintroduction program and the hypotheses it will seek to address.

In contrast, area 3 is the region of both good data and good understanding, and as such elements that fall within this region can effectively act as controls within an experimental reintroduction. Such elements might include aspects of captive breeding and husbandry, translocation and monitoring techniques. Typically, however, there are fewer components of a biological system which reside in this region compared with disciplines such as engineering and the physical sciences (Starfield & Bleloch 1988). The few aspects of an experimental reintroduction that fall within this region will be important in terms of the predicability they provide in relation to modelling the process.

Unfortunately, many of the elements of biological systems that are relevant to experimental reintroductions lie in regions 2 or 4. In region 2 there is some understanding of the structure of problems, but there is limited data to validate this understanding or extrapolate it to other situations. This is essentially similar to the dilemma of decision-making based purely on experience, described in section 2.4.2. For elements that fall in region 4 even the understanding of the problem is weak, and it is only through an experimental approach to reintroduction that both information and understanding of these elements will be gained. The consignment of modelling problems to regions within this framework will obviously change greatly in relation to species and situations.

In the vernacular of modellers the process of developing a model for reintroductions is one of "boot-strapping". We commence with little data and understanding in the bottom left-hand corner of Holling's diagram and utilise the model to help navigate the path towards the upper right. Such an approach is far more efficient than the alternative of simply collecting data haphazardly. Without a structured rigorous approach, such programs run the real risk of discovering that they have collected the wrong data, and answered the wrong questions (Starfield and Bleloch 1988).

2.8.5 The model

The process of reintroduction has been applied to a wide array of species in a variety of environments, and for this reason few of the major concepts combined in the model presented here are original. The approach of combining them into a structured framework is,

however. The sections below will briefly describe the various elements of the model, and how they fit into the model in both a spatial and temporal context.

The model is essentially a “Decision Tree”, and is intended to be used for pre-planning a reintroduction program. This structured approach provides both a basis for examining hypotheses relating to re-establishment of populations, and a stepwise process for evaluating project milestones (Figure 2.2). Essentially the model provides a graphical depiction of the transitional stages (depicted by circles) passed through by a source population towards establishment of a new self-sustaining population. Hence the principal flow within the model is the movement from one population state to another (indicated by the bold solid arrows between the circles). This transition includes passage through a number of distinct management processes or decisions (depicted by diamonds). The other flows within the model relate to the action of particular intrinsic and extrinsic factors on various population states (depicted by solid arrows flowing into the population states) and the information/knowledge flows, which act as the feedback loops within the model (and are depicted by the broken lines). These later flows, which provide the basis for adaptive management of the reintroduction process, are where interpretation of some aspect of the reintroduction leads to a decision or action to modify some aspect of the source population, the site, management regime or the actual process. Whilst there is not graphical representation of the likelihood of a population moving to extinction, it is implicit within the model that during any of the transitional population states depicted in the model the population could move to extinction.

There are two distinct phases to the proposed reintroduction model: a Cognitive or Planning phase and an Experimental or Release phase. The discussion below will examine the components of each phase, and the manner in which the structuring of these elements can lead to improved planning, implementation and evaluation of reintroductions. Where possible examples will be used to enhance interpretation of the model.

2.8.6 Cognitive or planning phase

The Cognitive phase of a reintroduction incorporates those logistical and research aspects of a program which occur before actual release of animals (labelled 1-7 in Fig 2.2), and is underpinned by the body of knowledge on a species and the system it exists in. For this reason, the certainty with which decisions are made during this phase will be greatly influenced by the

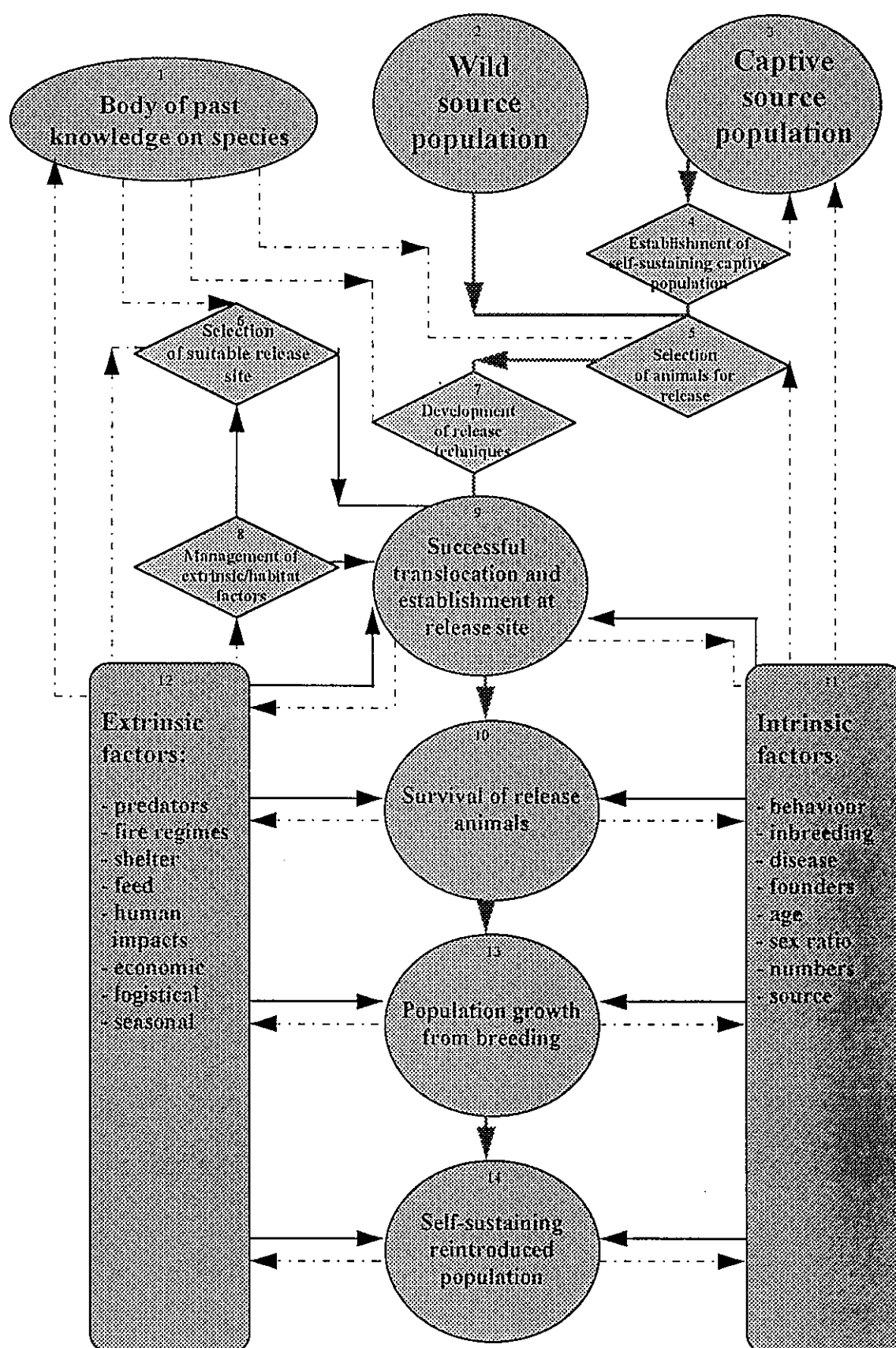


Figure 2.2 Theoretical framework for planning, decision-making and evaluation in an experimental reintroduction

quality of past information. In some cases, the Experimental phase of the reintroduction will provide a test of the assumptions and decisions made during this phase, and also the quality of this past information.

Elements 2-3-4: *Source Populations*

A fundamental concern in implementing a reintroduction program for a species will be determining the source of those animals intended for release. As indicated in the previous discussion, there have been few studies comparing the relative survival of reintroductions using captive-bred animals versus direct transfer of wild animals. Where potential exists to undertake such an approach it can be used to confirm experimentally which source population should be used in future reintroductions. A range of factors, including the status of remaining populations of the species, the time frames and costs involved in developing a captive population, and the logistics of moving animals to a release site, will all need to be considered in deciding an appropriate source for animals to reintroduce.

From a biological perspective, the major concern in removing individuals from a source population for reintroduction, regardless of whether it is a captive or wild population, is the impact this removal will have on the viability of the remaining population. The act of removing animals for reintroduction should not threaten the viability of the source population. For this reason, source populations need to be both self-sustaining and sufficiently large to sustain the removal of a number of animals over the period of the proposed program. Where alternative source populations exist, some consideration needs to be given to regional differences between populations that may potentially confer some advantage to the proposed release site for one selected group. For instance, animals sourced from an area with similar potential shelter resources as the release site might be expected to adapt better to the shelter conditions. As will be the case with many decisions made during this phase of a reintroduction program, the ultimate test of such decisions will only come through the act of reintroduction, where the alternatives can be experimentally compared.

If captive-bred stock are seen as the preferred alternative, then methods of husbandry and population management would be developed, both from information from ecological studies of the species and from similar programs using related species. The primary aim of the breeding program would be to become self-sustaining, and thus provide animals for

reintroduction to the wild. Doing so reduces the need for any further input of animals captured from the wild, and hence eliminates any potential impact on the wild source population. This goal can be achieved only through effective husbandry of the population including genetic management, elimination of disease, refinement of handling and containment techniques. These processes distinguish captive reintroduction programs from translocation experiments using wild stock. More details of the protocols and approaches to captive breeding, including founder representation, inbreeding effects and measures of self-sustainability, are provided in Chapter 3.

Element 5: *Selection of animals for release*

In selecting animals for release, consideration needs to be given both to which individuals from a source population should be used and also to how many. In selecting individual animals, significant caution should be exercised if attempting to predict that certain characteristics will favour survival and establishment. The ultimate test of such selection will only come by monitoring an experimental release. There is no evidence in recent reviews (Beck *et al.* 1994) to suggest that genetic screening has contributed to the success of reintroductions. However, a conservative approach would be to utilise as genetically diverse a release stock as possible. Genetic theory suggests that the long-term prospects of a population coping with environmental variation are enhanced by higher levels of heterozygosity. Our current understanding of the relationships between genetic differences at the molecular level and population processes for higher vertebrates is essentially poor.

The question of how many individuals should be released has been modelled for various species using both deterministic and stochastic (PVA) modelling approaches. McCallum (1995) modelled hypothetical translocation strategies for the Bridled Nailtail Wallaby *Onychogalea fraenata*, using combinations of different release numbers and strategies. In many cases the results of such analysis have returned the completely predictable result that larger release groups have a greater probability of surviving. There are cases of successful reintroductions involving both large and small group sizes, and as with so many other aspects of reintroduction, biology information in relation to the most appropriate number, demographic and genetic mix for a species and a site is best gained by an experimental approach to the problem.

Elements 6 & 8: *Selection & management of suitable release site*

The selection of a suitable release site, like many other elements of a reintroduction, requires the careful weighing up of a number of criteria, many of which are non-biological. Numerous documents have discussed the factors which must be considered in selecting a release site (ESAC 1995, Lindenmyer 1995, May 1991), and there is reasonable conformity in the set of factors each considered most important. The points below summarise the factors most often put forward in relation to selection of a release site. As is so often the case with conservation management, these are at best guidelines, and decisions will be influenced by the quality of background knowledge of the species by conservation and external priorities. In many cases, the appropriateness of sites will only ever be properly established through deliberately controlled and monitored releases as inferred by the design of the model:

- Species' former range: Except where there are unusual conservation reasons, it is preferable that species be reintroduced to locations either from which they have been recorded in historical times or where there is reasonable evidence to indicate that the species previously occurred.
- Ecological setting: The ecological setting into which a species is to be reintroduced will have a key influence over the success of efforts to re-establish a species at a site. Principal within this area is the need to identify and, if possible, remedy the causes which precipitated the decline or extinction of the species in the first instance. The level of background knowledge on a species and its resource requirements will have a major influence on the assessment of alternative sites. Suitable sites must be able to fulfil the nutritional and shelter requirements of the reintroduced species, and be resilient to the consequences of interactions between the reintroduced species, the environment and other resident species. Consideration must also be given to the potential for the population to expand, and hence must consider adjacent areas outside the immediate release site. The proximity of a proposed release site to existing remnant populations and the potential for transfer of genetic material and diseases between the two is an additional consideration. The survival of the wild population should not be jeopardised to reintroduce captives, unless the wild population's future existence depends entirely on the release (Kleiman 1989).
- Logistics: In addition to the biological factors, selection of a suitable site needs to consider such

things as land tenure, accessibility and other matters (eg costs, distances, travel times for management) and any potential land-use conflicts. For successful long-term conservation prospects for a reintroduced population, the tenure of the land will be important for security of the site from disturbance and ability to apply management regimes. Reintroductions to areas without specially protected tenure rely heavily on the good will of the leaseholders. For this reason they are fraught with the uncertainty of future changes in ownership. Similarly, the potential for conflicts between the reintroduction and existing land uses needs to be considered. Red Wolf *Canis rufus* reintroductions in the U.S.A. suffered substantial setbacks when releases occurred in prime sheep-raising areas, and in some instances landholders acted to control/kill the introduced wolves (Moore & Smith 1991).

As implied by the linkage between the selection and management elements (6-8), the concept of a Suitable Release Site is not constant in time but is modified on the basis of information gained before and during the reintroduction exercise. Thus the manager's initial impression of what is suitable habitat for a reintroduction may be modified by outcomes during the reintroduction. In some circumstances initially unsuitable habitat may be made suitable by management input. This aspect of the model is closely linked to the extrinsic factors which will act on the re-established population during later stages of the exercise. Management input such as predator control, implementation of a burning regime or manipulation of food or shelter resources may be required during the establishment phase of the program, or over longer time. The area of suitable habitat also needs to be sufficiently large to sustain the released population and allow for any projected expansion and dispersal.

Modern technologies including Geographic Information Systems (GIS) and satellite enhancement techniques will prove to be essential tools in site selection, as they provide a basis for overlaying the ecological, political, social and economic layers required for effective decision-making. The quality and quantity of the information from past studies of the target species will again be a key element in this selection process. As with other elements, refinement of the process comes from application of selection and management strategies within a structured model, and evaluation of project outcomes by rigorous monitoring. The release animals will obviously be the ultimate judges of habitat suitability, and hence a rigorous

approach to the reintroduction will provide information for future programs.

Element 7: *Development of release techniques*

As with most other phases of the program, techniques for the release of animals back into the wild are developed using information from previous ecological and technical research, but also from a process of experimentation. Reintroductions are a relatively new area in wildlife management, and hence in most cases there are no real tried and true techniques. In addition, what works for one species may not work for the species of interest. Despite this fact there is substantial scope to learn from other programs and species, which will remove the need to work everything out from scratch. For this reason there is a direct feedback loop to this area of the model, as trial reintroductions enable the managers to modify their techniques on the basis of observed responses by the animals.

An important consideration within this element of the program is whether animals are to be subjected to a "hard", or "soft" release strategy. Most reintroduction programs to date have adopted a "hard" release, involving little or no preparation of the animals before, or support after the release. Whilst some reintroductions have compared the survival of animals subjected to "hard" and "soft" releases (Carbyn *et al.* 1994, Stanley-Price 1991), the different behaviours and resource needs between species means that little can be extrapolated from these. An experimental approach provides a framework for testing the differences between the two approaches. Carbyn *et al.* (1994) adopted such an approach in their reintroduction program for the Swift Fox *Vulpes velox* in Canada.

2.8.7 The experimental or release phase: an experiment in small population biology

The release phase of a reintroduction program can be viewed essentially as an experiment in population dynamics, as it involves a detailed study of the processes which influence the establishment and persistence of a population. Hence the performance of a group of animals released in a reintroduction program can provide important information relating to both the species involved, and the environment at the release site.

In general during the early post-release phase of a reintroduction the population will

normally face the same challenges as other small populations, and hence monitoring should focus on the factors that can potentially cause the extinction of the population (Figure 2.3). The challenges to a small population can be categorised as either **Intrinsic** or **Extrinsic**. **Intrinsic** factors are those factors within the population which are relatively uninfluenced by environmental events, such as life history, inbreeding depression and demographic variation. **Extrinsic** factors are essentially the environmental factors such as habitat quality, human impacts and environmental variation which act on the population and hence affect the survival, fecundity and some genetic characteristics of the population. Whilst included as a separate factor, catastrophes are essentially extremes of environmental variation which can devastate a small population. Wildfire, extreme drought and invasion of a site by introduced predators could all be considered catastrophes likely to impact on small reintroduced populations.

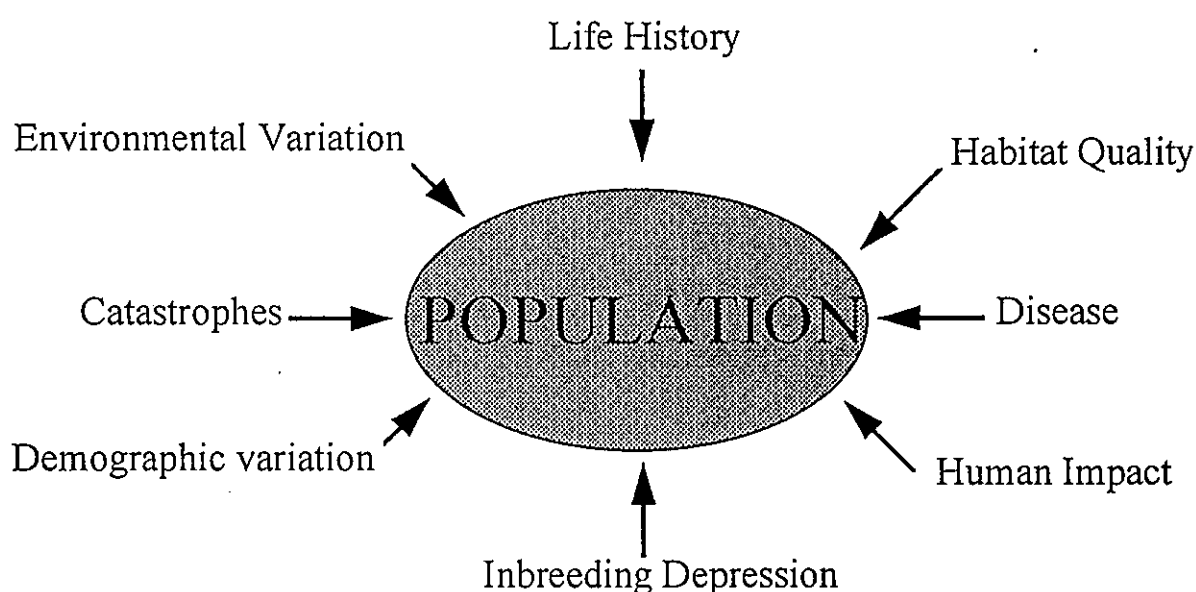


Figure 2.3. Representation of the interacting factors affecting a population's risk of extinction (modified from Ballou 1995)

Elements 9-10: *Successful translocation, establishment and short-term survival of the release group*

The initial stage of the release phase focuses on the survival of individual animals within the release group. Monitoring during this phase needs to be sufficiently intensive to distinguish mortalities due to:

- Movement and handling related to translocation of the animals, which could induce stress

or physical injuries.

- Extrinsic factors at the release site including climate, predators, food or shelter.
- Intrinsic factors including disease and behavioural/social interactions.

Short-term persistence and survival by the release group infers that release techniques are appropriate, and that resources at the release site are sufficient to support the group at the time of the release. The numerous connections between these elements of the model and the Intrinsic and Extrinsic factors, provide a basis for developing monitoring to detect factors influencing both short-term persistence, and longer-term survival by the released animals.

Elements 11-12: *Extrinsic and Intrinsic factors affecting the population*

Utilising available information derived from previous studies of the target species, or closely related species, it should be possible to derive a list of the Intrinsic and Extrinsic factors likely to affect the population at a selected release site. Production of such a list can form the basis for establishing testable hypotheses in relation to the persistence and survival of the release group. Having established hypotheses, an appropriate monitoring regime can be designed to evaluate the population's progress.

Table 2.3 illustrates the range of factors that could potentially influence the survival of a release group. Whilst it would be impossible to monitor all the aspects listed above, or to address the many questions they raise, it provides a checklist of things to consider when planning a specific reintroduction. In some instances, the effects of some of these factors can be discounted on the basis of either characteristics of the release site, or actual management that is being conducted at the site. In such cases these factors can act as controls to enable more targeted monitoring of other factors. The intention in linking the Intrinsic and Extrinsic factors back to portions of the planning stage is that, by adhering to a structured and rigorous protocol for reintroduction, all information derived from a program, whether ultimately successful or not, will improve the process. Without a rigorous approach where our understanding of the process is tested, reintroductions fall into the class of trial and error.

Table 2.3
Characterisation of intrinsic and extrinsic factors likely to influence successful establishment
of a reintroduced population (adapted from Clark 1996)

A. Intrinsic Factors			
(i) Genetic	(ii) Behavioural	(iii) Physiological	(iv) Demographic
• Mutation rate • Genetic fitness • Inbreeding • Heterozygosity • Phenotypes • Generation time	• Social Interactions • Mating system • Parental care • Predator avoidance • Foraging • Nesting/sheltering	• Water metabolism • Energy metabolism • Digestion • Thermo-regulation • Disease resistance/immunity	• Numbers • Density • Age structure • Sex ratio • Distribution • Mortality • Fecundity • Emigration • Immigration • Dispersal distances
B. Extrinsic Factors			
(i) Climatic	(ii) Food	(iii) Other animals & pathogens	(iv) Shelter
• Temperature • Light • Precipitation • Humidity	• Food abundance • Accessibility of food • Nutrient value • Seasonal availability	<i>Different Animals</i> • Competitors • Predators • Disease • Disturbances by humans <i>Same Animals</i> • Overdispersal • Crowding	• Habitat structure • Distribution & abundance of shelter • Nearness of shelter to food • Habitat-modifying agents including fire.

There is a further set of extrinsic factors, not graphically illustrated in the depiction of the model in Figure 2.2, whose occurrence and impact may ultimately override the influence of all other factors. **Catastrophic** factors such as Wildfires, Extreme Droughts, Earthquakes, Volcanoes and Epidemics act both unpredictably, and in a manner which can devastate small populations. Of course, not all sites and species are predisposed to the full range of **Catastrophic** factors, but the uncertainty of such events makes them difficult to consider in the context of conservation planning or experimental design. The most effective strategy for accounting for potential catastrophes is “risk-sharing”, whereby the risk of extinction is spread across many populations (Possingham 1996). Whilst such a strategy reduces the risk to the

species overall, it does not affect the extinction probabilities for individual populations either naturally occurring or reintroduced.

Elements 13-14: *Population growth and persistence*

Having established that animals can be successfully translocated and can persist at the release site in the short term, the next phase is to investigate the factors which will influence long-term survival, and successful breeding and rearing of further generations. During this stage the monitoring focus is more directed towards the population. At low population size the survival of individuals is obviously of paramount importance, but as the population increases the balance between births and deaths takes over. For the population to survive in the long term, births must at least equal deaths, but would preferably exceed them so as to allow the population to grow and disperse. Whilst the focus will be on population processes, the reintroduced population is still likely to be small and as a consequence individual monitoring of survival is still important.

For the purposes of this model the ultimate end point for a reintroduction will have been accomplished when a self-sustaining population of the species has been established at a release site. Self-sustaining in this sense does not mean an absence of management input, but refers to the population's ability to persist in the long term, without additional input of captive-bred stock over a full range of seasonal conditions. Some reviewers have sought to attribute success only to situations where populations can persist without further human intervention. Given the disturbance regimes that exist in most habitats worldwide, such expectations would seem unreasonable. Any management required to ensure the long-term persistence of the reintroduced population must also itself be sustainable. A management regime that requires high levels of human and financial input is likely to suffer the inevitable "death of a thousand cuts" as increasing demands are placed on those finite resources.

Element 1: *Body of background knowledge on species*

Consistent with the adaptive management approach which underpins the entire model, there are significant flows of information (indicated by broken lines) associated with all stages of the model. Hence the minimum outcome from any properly planned and executed reintroduction should be an increase in the body of background knowledge on species and the

system it exists in. Whilst this may seem a given, it is not supported well by some past reintroductions, which by their nature have added little to our understanding of the animals or the system, regardless of whether they were successful in re-establishing the species or not.

2.9 Hypothesis testing and the scientific method in reintroductions

Whilst from a practical standpoint it may be impossible to completely address the many elements identified by such a structured approach to reintroductions, the model provides a sound basis for formulating questions about the reintroduction process and designing experiments to test the responses of reintroduced animals. Armstrong *et al.* (1994) quite rightly reasoned that an experimental approach to reintroductions was needed because the fundamental factors affecting the outcomes of reintroductions are poorly understood. Although the word “experimental” has often been applied in the past with reference to reintroductions, in most cases these early attempts might more correctly have been termed “trials”, as little attention was paid to scientific methodology (Armstrong *et al.* 1994). To progress reintroduction as a scientifically-based wildlife management technique the results from reintroductions should, as far as practicable, be unambiguous (Caughley and Sinclair 1994).

Although an experimental approach does not automatically confer a program with a greater chance of success compared with a more intuitive approach, it at least ensures that we learn from our failures as well as our successes (Caughley and Sinclair 1994). In the absence of experimental design, managers are left to guess at the causes of failure, as reflected in the review conducted by Short *et al.* (1992) in which 32% of the reintroduction programs could only speculate on the possible factors which limited their success. Several recent studies have further highlighted the value of an experimental approach to reintroduction in identifying factors limiting population growth (Soderquist 1995, Southgate 1995), evaluating reintroduction techniques (Carbyn *et al.* 1994) and testing alternative management strategies (Friend and Thomas 1995).

The logic of the scientific method starts by observing patterns or events in nature and speculating on their underlying causes (Armstrong *et al.* 1995). In the model proposed in this

chapter such observations are represented in the past body of knowledge on a species and the system into which it is to be reintroduced. These data provide the basis for formulating testable hypotheses which are the essential element for adopting an experimental approach. Experimental design is then the process by which such hypotheses are tested, and its prime objective is to produce unequivocal results in the presence of confounding factors (Caughley and Gunn 1996). The principles involved in applying experimental design to wildlife management have been reviewed exhaustively (Caughley and Gunn 1996, Caughley and Sinclair 1994, Dickman 1996), and include consideration of such factors as replication, randomisation, factorial design, census methods and statistical techniques.

The essential elements to an experimental approach to reintroduction can therefore be summarised as (i) framing the right hypotheses, (ii) adopting an experimental design that will best answer these questions, and (iii) selecting appropriate census and statistical techniques (Armstrong *et al.* 1994, Jarman and Brock 1996). Given the ease of disproving rather than proving, hypotheses are most often inverted and become null hypotheses (Caughley and Gunn 1996). Experimental design is therefore based on the assertion of no difference, a null hypothesis (designated H_0), such as "there is no difference in the rates of survival of reintroduced animals of different ages". The alternative hypothesis, that the survival of animals differs with age (H_a), is accepted if the null hypothesis is rejected through experimentation. The null hypothesis is chosen for testing because it is unique - no difference is no difference (Caughley and Gunn 1996). Figure 2.4 provides examples of hypotheses which could be posed and tested in the transitional phases of the reintroduction model introduced in this chapter. Several of these hypotheses are investigated in detail in the analytical chapters which form the basis of the case study reported in this thesis.

One final action which is intrinsically linked to the scientific method, but has often been neglected in the past in relation to reintroductions, is adequate reporting of results (Caughley and Gunn 1996). Of the 28 separate reintroductions reviewed by Short *et al.* (1992) less than 25% were specifically reported in refereed publications. Of those which were published, many lacked basic information on the number of animals released or the factors influencing their successful establishment. In light of the urgency of problems facing many endangered species, sharing knowledge of failures is as important as successes.

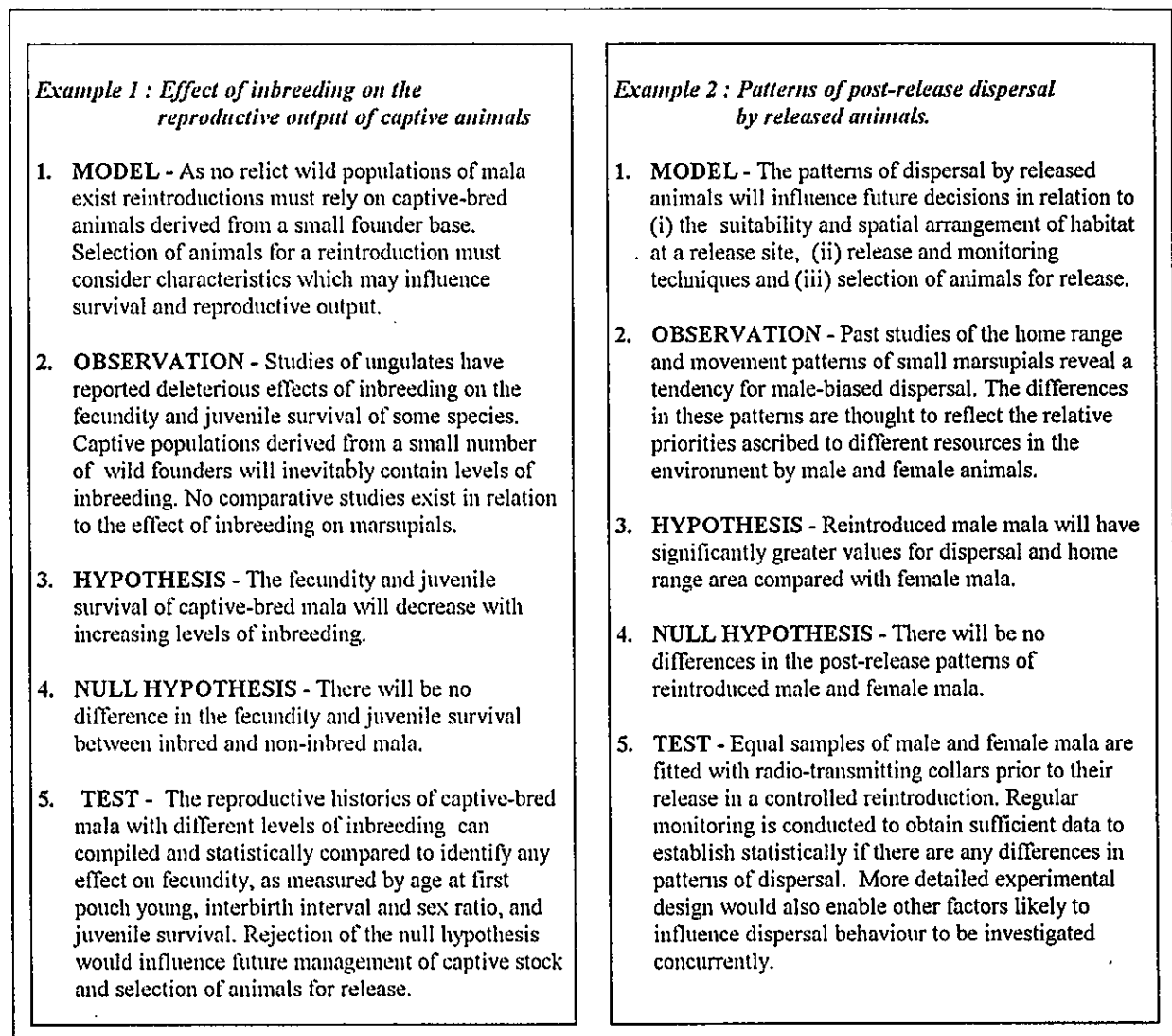


Figure 2.4 Examples of the application of hypothesis testing and experimentation within a reintroduction.

Whilst controlled reintroduction experiments are the ultimate goal they will inevitably be logistically difficult, whether they entail tests of alternative management or release techniques or behavioural responses of the study species (Armstrong *et al.* 1994). The feasibility of conducting definitive experiments will obviously be influenced by factors including the number of animals available, the number and proximity of alternate release sites and logistic constraints such as time and expense. Where such experimental design cannot be completely accommodated, compromises will need to be made which retain the experimental benefits at a minimal cost to scientific quality (Armstrong *et al.* 1994). The aim under these

circumstances should be to ensure, as far as practicable, that the results from the reintroduction are unambiguous.

2.10 The specifics of the mala program

The remaining sections of this thesis document a program of research aimed at evaluating both the forces that affect the success of a reintroduction of the Rufous Hare-wallaby or mala *Lagorchestes hirsutus* and the approach to reintroduction introduced in this chapter. The thesis is structured with reference to the various elements of the reintroduction model, and hence details the decision-making and experimental processes applied in a real reintroduction. Chapters 3 and 4 examine specific elements of the **cognitive** phase of a reintroduction program initiated for the mala. Chapters 5, 6, & 7 then summarise analytical information derived from the **experimental** phase of this reintroduction, implemented at a site in the Tanami Desert, by detailing the outcomes of intensive monitoring of the transition of the captive-bred source population following release. The final chapter attempts a synthesis of these results both in relation to their implications for future reintroduction/management of the mala, and evaluation of the model introduced in this chapter.

Chapter Three

Captive Breeding

3.1 Introduction

Captive rearing of endangered animals is becoming an essential adjunct to many conservation programs designed to re-establish or maintain populations in the wild. For species like the mala, where the animal is already extinct in the wild, captive rearing is the only option for their re-establishment. In such cases a viable, self-sustaining captive population (Pinder and Barkham 1978) will be a prerequisite for the success of such a program. To contribute effectively to the conservation of an endangered species, the captive population must be able to endure the loss of many animals over a long period while reintroduction techniques are developed and perfected. In addition to the size of a captive population, there are several important characteristics of captive-bred animals that will affect their capacity to survive translocation. These characteristics can be broadly categorised as genetic, behavioural and disease-related.

From the perspective of genetics the major concern in the maintenance of small, closed populations is loss of genetic diversity, through random gene frequency drift and inbreeding, and the impact that the resultant increasing homozygosity may have on the survival of these populations. Ralls and Ballou (1982) have linked a loss of vigour, decreased survivorship and decreased fertility in captive populations of large mammalian species to decreased heterozygosity. Numerous other authors have reported on the effects of captivity on a wide variety of species, and more particularly, the deleterious effect inbreeding has on the fecundity and juvenile survival of these species (Ralls *et al.* 1979, 1982, Laikre & Ryman 1991, Templeton & Read 1983).

Animals reared in captivity are most often raised in a relatively homogenous, depauperate environment that cannot mimic all aspects of the habitat into which they will eventually be reintroduced. There are two important potential consequences of rearing animals within such an environment. Firstly, it alters the natural selection pressures which act on animals within the wild, and may favour survival of individuals that, under more natural conditions, would be selected against. The second concern is that animals will lose behaviours or other traits essential for survival in the wild.

Whenever animals are maintained under captive conditions and/or moved from one place to another, there are inherent risks of transmission of diseases. There are many examples of the inadvertent introduction of diseases through the movements of both domestic and non-domestic stock, with consequences that were both expensive and potentially catastrophic to the wildlife population (Woodford & Kock 1991).

This chapter examines a number of aspects of the demography and genetics of captive-bred mala, in relation to a breeding program initiated in 1981. This examination is achieved through a combination of analysis of studbook records, and molecular DNA studies from the captive population. Behavioural considerations in relation to captive propagation and selection of animals for release were beyond the scope and time-frame of this study. A separate study by McLean *et al.* (1995; Appendix 1) investigated the potential of pre-release training in predator recognition for captive-bred mala. Likewise there was no attempt to thoroughly investigate the incidence or susceptibility to disease within the captive population.

3.2 The Rufous Hare-wallaby captive breeding program

3.2.1 Background

In recognition of the critical status of the mala, a captive population was established in 1980 when five animals (2M & 3F) were removed from the wild and taken to facilities in Alice Springs. Further additions of wild animals into the captive population took place over the next 6 years, until a total of 22 (10M & 12F) wild animals had been transferred to the captive breeding facilities. These animals were removed from two separate colonies located within a few kilometres of each other in the Tanami Desert (Bolton & Latz 1978). Animals from this captive colony were also used to establish populations at Western Plains Zoo (Dubbo), and Monarto Zoological Park (Adelaide), but these have been kept relatively small. Details of the housing and husbandry of the Alice Springs population are described in Lundie-Jenkins (1993). The colony serves the dual purposes of conserving the mainland form of the mala and providing stock for reintroduction of the species into parts of its former range.

3.3 Methods

3.3.1 SPARKS studbook analyses

Population records

An extensive record-keeping system was instituted when the colony was first established, to record census information, animal location and pen mates. This system was updated with the acquisition of the Single Population Analysis and Records Keeping System (SPARKS: ISIS 1989) program. This software was developed to assist in assembling, editing, analysing and producing reports on the status of captive populations. It also provides the capability to export appropriate parts of the captive data set to commonly used stand-alone demographic (DEMOG) and genetic analysis (GENES) programs.

A Mala studbook was assembled in SPARKS, with parentage, dates of birth, death or removal from the collection being recorded for each individual. Breeding within the captive population was intensively managed to ensure paternity could be unambiguously assigned. Founding individuals were assumed to be unrelated to each other, and individuals subsequently added to the collection were assumed to be unrelated to the existing population and to each other, unless the exact relationships of these individuals were known. This assumption was considered to best represent the genetic diversity detected in the founding stock, as the genetic goal for the captive population was to maintain the level of genetic diversity obtained from the wild. That is, to maintain in captivity a population that mimicked the actual genetic diversity in the wild. The assumption that every founder carries unique genetic material serves that goal. Therefore, even if the founding individuals were somewhat related, the frequency of different genes would most likely reflect their occurrence in the population.

Statistical analyses

Annual census data for the mala population, for the period 1980 to 1993, were compiled using the SPARKS studbook. The system was also used to calculate inbreeding coefficients, based on individual pedigrees, using the standard formula:

$$F = \{1/2 \sum (1/2)^n (1 + F_a)\}$$

where F is the inbreeding coefficient, n is the number of steps in a path from one parent of the individual through a common ancestor to the other parent, and F_a is the inbreeding coefficient of this common ancestor (Lasley 1978).

For the purposes of these analyses individuals were classified as non-inbred if the inbreeding coefficient was zero. Individuals with coefficients greater than zero were then assigned to three categories of inbreeding: 0.01 - 0.10, 0.11 - 0.20, and > 0.20

The log-likelihood ratio (G-test) and Fisher's exact test (FET), as applied by De Bois *et al.* (1990), were used to analyse differences between inbred and non-inbred individuals for juvenile mortality and sex of pouch young. One-way analysis of variance was used to test differences in age at production of the first pouch young and interbirth interval.

3.3.2 Genetic analyses

The genetic analyses reported here were conducted by Dr David Groth of the School of Biomedical Sciences, Curtin University (W.A.), on 12 samples collected by the author in relation to a recovery plan action clarifying the status of the 3 known mala sub-species (Lundie-Jenkins *et al.* in prep). The samples were obtained from 12 separate animals from within the captive colony at Alice Springs. The lineages of the sampled animals included 6 male and 5 female founders. DNA was extracted from blood by a proteinase K/SDS/phenol/chloroform extraction procedure. DNA was precipitated with isopropanol and resuspended in TE buffer. DNA was digested with the restriction endonucleases Hae III or HinfI and electrophoresed in a 0.7% agarose gel for 48hrs, Southern Blotted onto hybond N+ membrane and dried at 60°C. The blots were then subjected to hybridisation, at 60°C, with a radiolabelled hypervariable DNA probe, followed by stringency washes at 60°C in 2xSSC/0.1%SDS. Radioactive bands were visualised by autoradiography.

A trial genomic DNA sample was digested with the restriction endonucleases HaeIII or HinfI, electrophoresed and Southern Blotted. This blot was hybridised sequentially with the DNA

probes alpha HVR, M13 repeat and PER HVR. The PER HVR gave a suitable DNA fingerprint with both restriction endonucleases.

Genomic DNA extraction from the samples was digested with HaeIII, electrophoresed, Southern Blotted and hybridised with the DNA probe derived from *Drosophila* PER VNTR.

3.4 Results

3.4.1 SPARKS studbook analyses

Population size and growth

Annual census data for the captive mala population from 1980 to 1993 are shown graphically in Figure 3.1. The population grew steadily from 1980 up to the initial release of animals in 1984 (Lundie-Jenkins & Bellchambers 1995). The majority of this growth was from births in the captive population as importation of wild-caught animals peaked in 1981, and then steadily declined over the subsequent 12 years of census records.

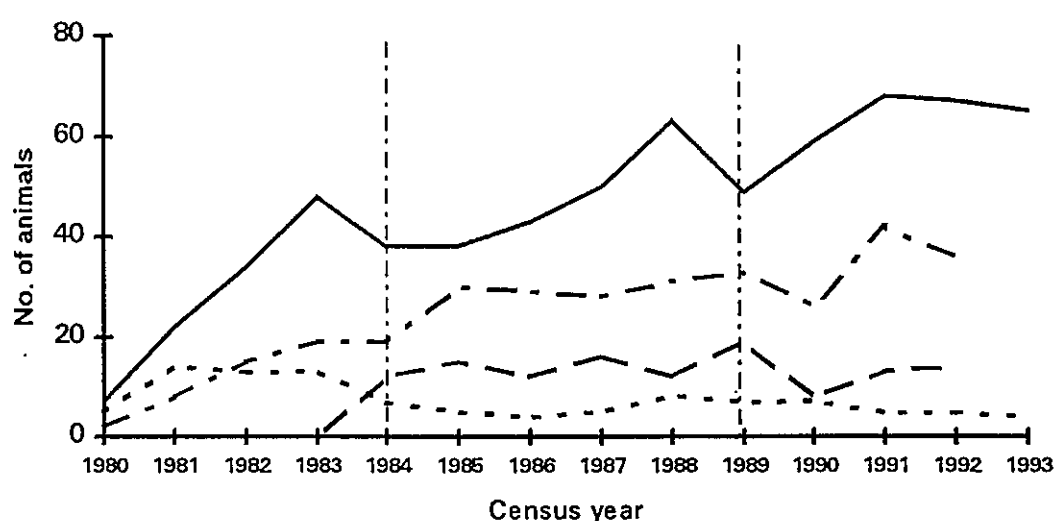


Figure 3.1 Graphical summary of annual census results from the captive mala population between 1980 and 1993. Indicated are: Total population numbers(—), annual captive births (---), the number of wild founders in the population (.....) and the number of animals released in experimental reintroductions (---). The vertical lines at 1984 and 1989 indicate the commencement dates for the two main reintroduction experiments.

The drain on the population due to the removal of animals for reintroduction experiments in 1984 is demonstrated by the corresponding decline in the total population. The capacity of the population, however, to sustain this removal of animals can be seen by the steady recovery of the population, even with the continuing removal of approximately 15 animals per year up to 1988. The removal of 20 animals associated with an increase in reintroduction efforts during 1989 did, however, have a negative impact on the overall population size. The subsequent recovery of the population was substantially faster when compared with that following the initial release during 1984. There was no detectable cause for this difference in relation to differences between the age and sex structures of the populations for these periods, and hence the difference may relate to improvements in the management and husbandry of the captive population, or in selection for breeding ability in captivity.

Inbreeding effects

The results of analyses of the mala breeding records, to detect any effects of inbreeding on several reproductive and demographic characters, are shown in Tables 3.1-3.4.

Between 1980 and 1993, 292 births were recorded whose details of survival over the first 12 months were known (Table 3.1). Of these births 197 or 67.5% resulted in non-inbred young. Survival was high for each of the 4 inbreeding classes, ranging from 93.3% for animals with an inbreeding coefficient > 0.2 to 72.1% for animals with an inbreeding coefficient in the 0.01 - 0.10 range. There were no significant differences in juvenile mortality between non-inbred mala and the 3 levels of inbreeding present in the population, using either the log-likelihood ratio or Fisher's exact test. The maximum survival rate for juveniles corresponds with the highest level of inbreeding, which is a counter-intuitive result. Whilst the difference is not significant, it suggests that continued monitoring should be conducted to establish if the effect is real.

The relative numbers of male and female pouch-young born to non-inbred and inbred mala over the census period are given in Table 3.2. The ratios of male to female births were near parity for all levels of inbreeding. No significant differences were found between the sex of pouch young produced by non-inbred mala and those resulting from the 3 levels of inbreeding.

Table 3.1

Juvenile mortality of non-inbred and inbred mala
born between 1980 and 1993. (Numbers in brackets are percentages).
Statistical tests compare each level of inbreeding with non-inbred mortality.

Inbreeding coefficient	Total No. of births	Deaths at < 1 year	Survived	Probability estimated by :	
				G-test	Fisher's exact test
0	197	37 (18.8)	160 (81.2)		
0.01 - 0.10	38	11 (28.9)	27 (71.1)	0.169	0.186
0.11 - 0.20	27	4 (14.8)	23 (85.2)	0.609	0.793
> 0.20	30	2 (6.7)	28 (93.3)	0.071	0.123
Total	292	54 (18.4)	238 (81.2)		

The apparent discrepancies between Tables 3.1 and 3.2 in the number of animals in each inbreeding class are due to incomplete records being kept in relation to some births. For example, records which did not provide details of the age at death for a young could not be included in Table 3.1.

Table 3.2

Sex of pouch young of non-inbred and inbred mala
born between 1980 and 1993. (Numbers in brackets are percentages)
Statistical tests compare each level of inbreeding with sex of non-inbred pouch young.

Inbreeding coefficient	Total No. of births	Male births	Female births	Unknown	Probability estimated by :	
					G-test	Fisher's exact test
0	200	83 (41.5)	85 (42.5)	32 (16.0)		
0.01 - 0.10	40	13 (32.5)	17 (42.5)	10 (25.0)	0.539	0.559
0.11 - 0.20	27	12 (44.4)	9 (33.3)	6 (22.0)	0.503	0.644
> 0.20	33	15 (44.4)	17 (51.5)	1 (3.0)	0.793	0.848
Total	300	123 (41.0)	128 (42.7)	49 (16.3)		

No significant differences were found between non-inbred and inbred mala for either age at

sexual maturity, as indicated by age at birth of first pouch young, or the time interval between consecutive births (Tables 3.3 & 3.4).

Table 3.3
Mean age at birth of first pouch young of non-inbred and inbred mala
born between 1980 and 1993.
(Statistical tests compare the mean ages of female mala at the birth of their first pouch young, for
non-inbred animals with each level of inbreeding)

Inbreeding coefficient	1st pouch young No. of births	Age at first pouch young in days (mean $\pm$ SE)	Probability from F-test
0	46	313 $\pm$ 21	
0.01 - 0.10	20	340 $\pm$ 25	0.4258
0.11 - 0.20	12	331 $\pm$ 29	0.6643
> 0.20	6	254 $\pm$ 29	0.2867
Total	84	318 $\pm$ 13	

Table 3.4
Mean interbirth intervals of non-inbred and inbred mala
born between 1980 and 1993
(Statistical tests compare the mean interbirth intervals of female mala for non-inbred
animals with each level of inbreeding)

Inbreeding coefficient	Interbirth interval No. of births	Interbirth interval in days (mean $\pm$ SE)	Probability from F-test
0	154	201 $\pm$ 09	
0.01 - 0.10	23	190 $\pm$ 20	0.6779
0.11 - 0.20	15	191 $\pm$ 18	0.7633
> 0.20	27	162 $\pm$ 17	0.1060
Total	219	194 $\pm$ 08	

Founder Representation

Representation of founder animals within the captive mala population is shown in Table 3.5. This indicates that while the founder population was 22 animals (10M & 12F), the majority of animals born in captivity descend from 4M and 4F with 1 founding male and 3 founding females

not represented by any descendants. A further two male founders and 1 female founder are each represented by 6 or fewer descendants throughout the history of the captive breeding program. The relative contributions of different founders to the genetic composition of the captive population are therefore quite disproportionate, and some genetic characters have presumably been lost.

Table 3.5

Relative contribution of founder animals to the captive mala population.
(Founders may appear more than once in a descendant's lineage)

mala ID	Total No. of descendants	No. of descendants of each sex			No. of generations
		Male	Female	Unknown	
Females:					
TF001	436	195	187	54	8
TF002	0	0	0	0	0
TF003	216	101	100	15	8
TF004	17	10	4	3	6
TF006	209	102	92	15	7
TF008	24	11	11	2	6
TF009	169	67	88	14	8
TF010	0	0	0	0	0
TF011	2	1	1	0	1
TF013	0	0	0	0	0
TF179	19	6	11	2	3
TF181	26	8	17	1	3
Males:					
TM001	455	197	213	45	8
TM002	0	0	0	0	0
TM003	270	119	129	22	7
TM005	16	8	7	1	5
TM008	269	125	119	25	6
TM009	17	6	10	1	3
TM010	185	71	98	16	7
TM059	14	8	6	0	2
TM077	6	4	2	0	2
TM089	1	0	1	0	1

3.4.2 Genetic Analyses

A total of 33 alleles were identified in the samples obtained from the captive mala population. The band-sharing between these 12 individual DNA samples, using the *Drosophila* HVR probe, was determined and is shown in Table 3.6. This table gives the number of bands

shared between any two individuals from within this sample of the population. The diagonal (in bold) is the number of bands scored for that individual. The mean band sharing value for the sample of the captive population was 0.47 ± 0.15 . Genetic variation, as measured by mean heterozygosity at 8 polymorphic loci, was 0.64.

Table 3.6

Band-sharing matrix for captive mala population derived from
Drosophila PER HVR DNA fingerprinting

50	13												
223	6	13											
314	4	2	11										
61	9	8	6	13									
422	8	5	4	6	11								
226	8	7	7	7	10	12							
416	8	6	6	7	6	8	11						
421	5	2	4	5	6	5	2	9					
419	4	3	9	5	6	8	4	4	10				
316	8	6	6	6	3	7	6	3	3	10			
420	6	5	6	7	4	7	5	4	5	5	8		
324	6	3	6	5	6	7	4	5	5	3	4	10	
Animal	50	223	314	61	422	226	416	421	419	316	420	324	

3.5 Discussion

Whilst the original motive for establishing a viable captive population of mala in 1981 was to provide stock for future reintroductions of the species, its prime significance now lies in the fact that no free-ranging wild populations of mala remain on the Australian mainland. Catastrophic events in 1987 and 1991 pushed known wild populations in the Tanami Desert to extinction (Lundie-Jenkins 1993, Gibson *et al.* 1995). Without the establishment of this captive population it is probable that the mainland form of the mala would now be extinct. Over 15 years after its establishment, captive-bred offspring from this population have been reintroduced at two sites in the Tanami. This fact is testimony to both the foresight of those original managers and to the subsequent management of the population. It also serves to demonstrate the potential multiple roles played by captive breeding programs in the recovery of endangered species. These other roles, including : serving as an “ark” for species facing extinction in the wild, providing animals for practical research that will improve management and as a resource in public education, are often

overlooked compared with the glamorous notion of reintroducing species to the wild.

Despite the successes of the mala captive breeding program, there is much that can be learned from a critical analysis of the data collected from a program which has spanned over 15 years. The remainder of this chapter will examine the results presented in section 3.4 in relation to previous studies and their impact on future management of captive mala.

Population size and growth

Pinder and Barkham (1978) conducted an assessment of the contribution that captive breeding had made to the conservation programs for 61 different species. Based on this investigation, they generated a theoretical model that lists five consecutive stages in the development of a captive population. They used the model to assess the success of each program in terms of its progress towards developing a self-sustaining captive population. Table 3.7 defines the population characteristics of these five stages of a hypothetical population, and includes values calculated for the mala population. For the period 1986-1988, the captive mala population met the tabled criteria for classification as a self-sustaining population. The increased removal of animals for reintroduction experiments from 1989 drove the population's rate of increase into the negative and hence removed its ability to match the final two criteria. Of the 61 species included by Pinder and Barkham (1978), only 26 met their criteria for being regarded as self-sustaining. It is apparent that the major factor influencing the mala captive population's ability to meet these criteria is deliberate management decisions, both with respect to total capacity and numbers removed for reintroductions. Despite this intervention it is evident that the captive mala population is sufficiently robust to sustain itself despite the ongoing removal of a significant number of animals for reintroduction.

In a separate analysis, Perry *et al.* (1973) proposed two requirements that a zoo species should fulfil before being considered self-sustaining: the captive population should exceed 100 individuals and at least 50% of the population should have been bred in captivity. The captive mala population meets the second of these criteria, but space limitations have prevented it meeting the first. Consequently, as with the criteria introduced by Pinder and Barkham (1978) there has been a management restriction, rather than a biological restriction, on the population. Having established that the population can sustain a level of population growth sufficient to supply animals for

reintroduction, it is of interest to examine the quality of these animals and the possible consequences of inbreeding and founder effects on the population.

Table 3.7
Population characteristics of the five stages of hypothetical captive populations
proposed by Pinder and Barkham (1978)

Values for the captive mala population are appended to the base of the table.

Population characteristics of the five stages of hypothetical captive populations	Average population numbers	Percent wild-caught	Percent increase	No. surviving births increase in population No.s	
Stage 1: Low numbers on exhibit in few zoos, with very few births and little overall increase in numbers, total and wild population plots (Fig 3.1) are not significantly different.	Low	≥ 85	Low	Very low < 1	
Stage 2: Great increase in numbers of both total and wild-caught populations; births, while increasing, contribute little to population increase. The plots (Fig 3.1) thus follow similar paths.	Medium	60 - 85	Medium	Low < 1	
Stage 3: Births have now increased, so that the two plots, while still increasing, separate from one another. Well managed zoo populations could now be self-sufficient, but imports still take place.	Medium	40 - 60	Medium	≥ 1	
Stage 4: Imports of wild-caught animals no longer account for any increase in total numbers, thus the wild-caught populations reach a maximum value.	Medium - High	15 - 40	Medium	> 1	
Stage 5: Numbers of wild-caught animals decline, eventually to zero, while the total population continues to increase until space limits numbers.	High	≤ 15	Medium - Low	> 1	
Actual values calculated from annual census data of captive mala population for years	1980	7	71	100	0.14
	1981	22	64	68	0.33
	1982	34	38	35	1.00
	1983	48	27	29	0.93
	1984	38	18	-26	-0.90
	1985	38	13	0	*
	1986	43	9	12	2.80
	1987	50	10	14	2.43
	1988	63	13	21	1.00
	1989	49	14	-29	-0.50
	1990	59	12	17	1.30
	1991	68	7	13	0.33
	1992	67	7	-2	0.00
	1993	65	6	-3	*

Inbreeding effects

The analyses indicate no significant difference between non-inbred mala and 3 levels of inbreeding for juvenile mortality, sex of off-spring, age at first pouch young and interbirth interval. There are no previously published accounts of similar analyses for any other Australian marsupials, and the results are contrary to similar studies of other species including ungulates, rodents and primates (Ballou & Ralls 1982, Ralls & Ballou 1982), although the levels of inbreeding recorded for mala to date are reasonably low. Similar studies of eutherian mammals have revealed significant negative effects of inbreeding. Investigations by Laikre and Ryman (1991) into inbreeding in captive wolves revealed that inbreeding negatively affected all characters included in their analysis (reproductivity, longevity, juvenile weight & occurrence of blind animals.) Caughley (1994) has suggested that high levels of inbreeding in localised wild populations may purge these systems of deleterious alleles.

Founder representation

The data indicate that despite founding the captive population on a small number of individuals, a reasonably high level of genetic variance has been retained. The fact that a proportion of these founders made only minor contributions to the populations breeding output makes this even more remarkable. Genetic investigations indicate a reasonably high level of variance remaining in the population, as indicated by DNA variability. As no base line is available, it can only be said that the degree of band-sharing in the population was relatively low. The mean band-sharing value of 0.47 ± 0.15 is comparable to levels recorded for several domestic animals including sheep, cattle and horses, but does not approach that seen in an outbred population or a population not subjected to any population bottlenecks. The value of 0.62 for mean heterozygosity determined for the captive mala is similar to values observed in several other species of marsupials (Table 3.8). This is particularly encouraging, as it has been suggested by Bolton and Latz (1978) that the Tanami Desert populations were reduced to critically low levels (as few as 6 individuals in each of the 2 populations they surveyed). Comparable genetics analyses completed for mala populations on both Bernier and Dorre islands showed high band-sharing and low heterozygosity (Table 3.8) suggestive of high inbreeding (Spencer & Eldridge 1998). Additional analyses currently underway may provide information to test the validity of the assumption that founder stock are not closely related.

Table 3.8
Levels of heterozygosity observed at microsatellite loci in several Australian marsupials

Species	Sample size	Number of loci	Mean heterozygosity	Reference
Mala (Captive)	12	8	0.62	1
Mala (Bernier Island)	8	8	0.22	5
Mala (Dorre Island)	14	8	0.29	5
Yellow-footed Rock-wallaby	50	4	0.73	2,3
Bridled Nailtail Wallaby	73	7	0.83	2
Northern Heiry-nosed Wombat	28	16	0.27	2,4
Southern Hairy-nosed Wombat	16	16	0.65	4

References: 1. This study, 2. Moritz *et al.* 1996., 3. Pope *et al.* 1997., 4. Taylor *et al.* 1994., 5. Spencer and Eldridge 1998

Frankel and Soulé (1981) estimate that for a founding population of 22 animals the expected retention of the original genetic variance would be approximately 97.7%. Even using the scenario whereby the majority of the mala population is derived from only 8 animals, we could expect to retain 93.8% of the original variance. Maintenance of the colony at present (or slightly higher) numbers would see this level of genetic variance retained for many generations. Estimates indicate a potential loss of between 20 to 30 percent of this variance over ten generations of the captive population (Frankel & Soulé 1981).

After the bottleneck created when animals were brought into captivity, there was no early analysis of inbreeding, nor any attempt at founder equalisation. Initial management of the population was directed towards quickly increasing the size of the population. The implications and benefits of a captive colony rapidly expanding away from its founding numbers, compared with being maintained at low numbers over a long period of time, have been discussed by a number of authors (Frankham *et al.* 1986, Foose *et al.* 1983). The observed heterozygosity measured from a sample of the captive mala population may be a consequence of this quick expansion of the population.

Even if a captive population starts with a sufficient number of founders to keep most of the natural gene pool intact, and even if those founders are kept under conditions where unusual selection pressures do not cause changes, loss of the wild genetic variation (that is, domestication) is inevitable if the animals are kept long enough (Frankham *et al.* 1986). It is therefore desirable to keep the number of generations between capture from the wild and reintroduction as low as possible (May 1991).

Future management for conservation and reintroduction

It is apparent that in relation to the characteristics examined in this chapter, the captive mala population is well managed, as evidenced by the fact that none of the demographic or genetic characteristics which have resulted from current management of the population appear to have had a detrimental effect on the survival, reproductive output or environment adaptiveness. The adaptiveness of some genetic traits resulting from the selection pressure of captivity may not be ultimately tested without significant environmental change. The best means for ensuring that such selection is not detrimental to the species in the long term will be to maintain, as far as possible, the genetic diversity that is currently present in the population, and equalise the contributions by breeding animals to subsequent generations. Current strategies used within the captive mala population, such as minimising inbreeding coefficients of pairings, and using mean kinship and founder representation to prioritise preferred mating within the population, will facilitate this process.

During the initial stages of development for the captive mala population, management of the breeding program to reduce inbreeding and equalise the contributions of founders was reasonably straight forward, as there were few generations beyond the original founding stock. As the number of generations has grown and matings within the second and third generations of the captive population have increased, so has the task of managing the population. During the past 6 years, this management has been greatly facilitated by studbook management systems such as SPARKS, that enable managers to model different breeding plans in relation to their impact on the level of inbreeding, genetic diversity and founder representation. Tools such as this will continue to be critical to management of the population, particularly with animal holdings spread between 3 major institutions.

Whilst it appears that with respect to genetics and demographics the captive mala population is producing stock suitable for reintroduction, additional work is required to determine whether a similar scenario exists for behavioural and disease susceptibility. Observations by McLean *et al.* (1996; Appendix 1) imply that captive-bred mala may have a reduced capacity to identify and respond to predators. In that study, mala were found to be more wary (expressed by

the use of more alert postures) of model predators introduced to their environment following training events designed to associate the predators with a flight response. Whilst such training was not tested in the ultimate sense by comparing survival in the wild of trained and untrained animals, there was sufficient data from captive observations to support such a trial in the future. Unfortunately, such trials will be the only means of determining what are preferred behavioural traits for captive-bred mala destined for reintroduction. Without "wild" animals to compare with captive-bred animals there is no benchmark to determine what are appropriate behavioural traits, compared with behaviours which have arisen due to extended captivity. One strategy that could be adopted to reduce the likelihood of captive animals developing peculiar habits associated with captivity is to make, as far as practical, the captive environment as similar as possible to their natural environment. This approach, referred to as "environmental enrichment" (Shepherdson 1994), could include: providing the substrate or vegetation structure for sheltering, but not providing artificial shelters; shifting the timing, location and type of food supplementation provided, thus requiring the animals to search and identify food; and minimising handling to reduce any tendency towards domestication. Such techniques would presumably better ensure that the natural behavioural diversity of captive animals is maintained, and that they are provided with opportunities to learn skills necessary for life in the wild. The true value of such an approach will, however, only be revealed by comparing the survival and establishment in the wild of animals from both an enriched, and a more traditional captive environment. The increased expense of adopting an environmental enrichment approach would require a significant demonstration of improved survival to support its implementation.

There are essentially two significant areas of concern relating to diseases and the use of captive-bred stock in a reintroduction program. Firstly, there is the risk that captive-bred stock may be exposed to exotic pathogens which could then be introduced to an environment by the act of reintroduction. A Canadian program to reintroduce captive-bred Plains Bison *Bison b. bison* led to the introduction of tuberculosis to the area, which affected populations of Wood Bison *Bison b. athabasca* (EPA 1990). In a similar case in Arabia, captive-bred Arabian Oryx introduced tuberculosis into an existing translocated population of Oryx (Kock and Woodford 1988). The second type of disease concern relates to the resistance of captive-bred stock to natural pathogens that they may encounter at a release site. Having been raised in a reasonably protected epidemiological environment, captive animals may lack acquired immunity or resistance to

particular natural infections. An example of this type of effect is the translocation of 50 koalas *Phascolartos cinereus* from a tick-free area in Victoria to a nearby range infested with the Ixodid vector of tick paralysis. Over half the translocated animals succumbed to tick-borne paralysis (Woodford & Rossiter 1994). Both types of disease risk could clearly be reduced by the inclusion of a process of screening both the captive animals and the release site for diseases.

Whilst a number of diseases of concern (Avian tuberculosis, ring-worm) have periodically been detected within the captive mala population, their persistence and spread within the population has generally been controlled by modifying husbandry practices. These modifications have generally incorporated quarantining infected animals and enclosures, screening animals exposed to infected animals and enclosures, and the implementation of control measures to reduce or remove the environmental conditions which favoured the particular pathogen. To date no routine screening of captive mala for diseases prior to their use in a reintroduction program has been undertaken. The condition of all captive mala has been monitored on a monthly basis during routine recaptures, and animals that show any signs of failing condition (i.e., loss of body weight) or external evidence of infection (i.e., lumps, lesions, hair-loss etc.) are not selected for reintroduction. The expense of total disease screening was an obvious limiting factor in its application in the mala program, as well as the lack of unambiguous testing procedures for pathogens such as Avian tuberculosis in small marsupials.

Chapter Four

Experimental Reintroduction of the Mala

4.1 Introduction

The major factor influencing the initial decision to commence a reintroduction program for the mala was the realisation that the species had suffered a dramatic decline, to the point where it was known only from a small region of the Tanami Desert (Bolton & Latz 1978). Subsequent catastrophes during the late 1980s (detailed in Chapter 1) led to the extinction of these Tanami populations, and created a situation where there were no known extant populations of the species remaining on the Australian mainland (Lundie-Jenkins 1996). This deterioration in the species' already tenuous status provided the impetus for the reintroduction experiment that acts as the case study for this thesis. The recognition that our understanding of the ecology and management of the mala was essentially crude led to the decision to adopt a rigorous experimental approach, and hence examine the reintroduction process itself.

The subsequent sections of this chapter detail not only the methods applied to this experimental reintroduction, but examine them in relation to specific elements of the model introduced in Chapter 2. The intention in adopting such an approach is to highlight the processes involved in the "Cognitive", or planning, phase of a reintroduction. Much of the general background for decisions made during this phase of the program is reviewed in Chapter 2. To avoid repetition, the discussion in this chapter will be limited to the specifics of this reintroduction program.

4.2 Body of past knowledge on species

As depicted in the model introduced in Chapter 2, there is a significant flow of information into the design and implementation of a reintroduction, which emanates from an entity defined in the model as the body of knowledge on a species. In the case of the mala our knowledge derives from several diverse sources, ranging from the accounts of traditional Aborigines and early European explorers to the results of modern scientific investigations.

The earliest documented accounts of mala relate to encounters by early European explorers with creatures they variously described as “spinifex rats” and “kangaroo rats”. Whilst such terms were applied liberally to a range of species, some of the characteristics described for such creatures clearly indicate early encounters with mala. These accounts (Spencer 1896), and information obtained from older Aborigines (Burbidge *et al.* 1988), provided valuable insights into such aspects of the mala’s biology as diet, responses to fire (Finlayson 1963), impacts of predators and preferred habitats.

Since the rediscovery of mala in the Tanami Desert in 1973 (Parker 1973), the species has been the subject of a series of studies which have investigated: the status and associations of the extant population (Bolton & Latz 1978), patterns of habitat use (Lundie-Jenkins 1993), interactions with introduced mammal species (Lundie-Jenkins *et al.* 1993a), diet (Pearson 1989, Lundie-Jenkins *et al.* 1993b, Jarman 1994), digestive tract function (Bridie *et al.* 1994), blood metabolism (Agar and Godwin 1991), capture-myopathy (Cole and Langford 1994), behaviour (Lundie-Jenkins 1993, McLean *et al.* 1993, McLean *et al.* 1995 & 1996) and reproduction (Lundie-Jenkins 1993).

As indicated in the introductory chapter, the reintroduction experiment which forms the case study for this thesis is far from the first such effort undertaken with the mala. Included within these past actions are two other attempts to reintroduce the species to areas of the Tanami Desert (Gibson *et al.* 1995, Johnson *et al.* 1996, Lundie-Jenkins & Bellchambers 1995). These previous reintroduction programs have provided technical and biological information that has been important in the planning and implementation of this reintroduction. The paragraphs below summarise more detailed accounts of both previous projects gleaned from Gibson *et al.* (1995), Johnson *et al.* (1996) and Lundie-Jenkins & Bellchambers (1995).

4.2.1 Previous attempts to reintroduce the mala

A first attempt at reintroduction - the Mala Yard (1984-1986)

In May 1984, staff from the Conservation Commission of the Northern Territory and Warlpiri Aborigines from Willowra, in the Tanami Desert, visited an area near the ephemeral fresh

water lake known as Lake Surprise (Yinapaka), to ascertain its suitability for the reintroduction of mala. The area had previously been identified during extensive surveys conducted in the Tanami Desert by Gibson (1986). After consultation with those Aborigines having authority for the area, a site was chosen on the floodout of the Lander River, 500 kilometres NNW of Alice Springs and about 15 kilometres from Lake Surprise.

At this locality, a small 50 m x 50 m enclosure was constructed from chicken wire. A total of 27 mala were released into the pen, in 2 separate releases, 12 months apart. The first group of 12 animals were released in October 1984, and the second of 15 animals in July 1985. Each group of animals was held in the pen for ten days to enable the animals to develop an affinity with the area, and reduce the likelihood of over-dispersal after release. Despite 1080 poison baits being laid to kill predators in the release area, two animals were killed soon after release, one by a dingo and another by a feral cat. The paragraphs below summarise the fate of these released animals.

The dispersal and survival of the first group of 12 mala released was monitored with tracking by Warlpiri Aboriginal people and radio-tracking of 3 males that had been fitted with radio-transmitters. Over the following 5 months animal movements were tracked up to 1.5km from the release pen, and the remains of one release and one *in-situ* bred animal were found. Both deaths were attributed to predators (dingo and feral cat). Surveys of track and faecal pellet densities in the release area in March indicated that potentially half the original 12 mala were inhabiting an area of about 2 km² around the enclosure.

The second group of 15 mala were monitored for 7 months using a combination of traditional Aboriginal tracking and radio-telemetry. Over the initial 3 months the population appeared to do well despite the discovery of remains from 2 animals inside the release pen. The available evidence suggested that fighting associated with overcrowding may have caused these deaths. In February contact was lost with the collared animals, and despite an extensive search of the area from the ground and from the air, the colony could not be located. Aboriginal assistants speculated that the mala may have scattered after recent rain, but no evidence was discovered to support this theory. The disappearance of these animals did, however, follow a prolonged dry period, and favoured mala food resources were visually assessed as being scarce.

Despite the failure of this initial program to establish a new population of mala there remained significant reasons to attempt further reintroductions, not the least of which was the critically endangered status of the species.

A second attempt at reintroduction - The Mala Paddock (1986-1994)

Based on knowledge gained of the mala's behaviour on release from the small enclosure, it was decided to enclose a large area of suitable habitat with a more substantial fence. It was reasoned that the confinement would allow captive-bred mala time to adapt to their new environment and develop site fidelity. The fence would also exclude predators during this initial adjustment period. It was presumed that the enclosure would improve the likelihood of individual mala finding a mate, thereby enhancing the breeding prospects, and making more animals available for release and long-term establishment of a population outside the protection of the paddock.

A new site on the Lander River floodout was chosen, again with the assistance of traditional owners, at a location about nine kilometres from the previous site. The river at this locality is highly braided, dissecting the floodplain into a patchwork of spinifex and Acacia clad dune ridges, and surrounded by alluvial deposits supporting trees and shrubs. The site contained sizeable areas of mature, clump-forming spinifex, in addition to recently burnt areas in various stages of regrowth. An electric fence enclosure containing an area of approximately 81 ha. was constructed at the site in 1986, and through a series of development phases successfully contained mala and excluded predators. The survival and breeding of the enclosed population was comparable to captivity, and the population quickly grew.

A total of 81 mala were released sequentially, in groups of approximately 12 animals, into the area surrounding the large electrified enclosure. There were a large number of known mortalities attributable to predation by feral cats. Despite extensive ongoing efforts to control feral cats in the release area, further releases at the site were curtailed pending the development of more effective means of controlling cats.

Where relevant, information derived from both these reintroductions will be included in the justification for adopting a particular approach to this reintroduction experiment. Significant aspects

of both will also be incorporated in the discussion of the results from this program.

4.3 Selection of animals for release

The process of selecting animals for release incorporates two basic questions: How many animals? and, Which individuals? In the present reintroduction program, the following approaches were adopted in relation to these questions.

All animals used in this reintroduction experiment were sourced from a captive population maintained in Alice Springs (Chapter 3). During the period over which this study was conducted (1989 - 1993), the captive population ranged in size from 49 to 68 individuals. Experience from previous reintroductions had shown that this captive population was capable of providing between 15 and 20 individuals on an annual basis without threatening the population's viability.

During the initial releases conducted in October 1989 and March 1990 groups of 3-4 animals were released into each of two temporary pens (refer to 4.5.2). This number was chosen to ensure that each release event could be adequately monitored by an individual operator, since no field assistance was available during the initial stages of the project. Observations following these initial releases indicated a high degree of aggression between individual animals whilst housed in the temporary pens. Based on these observations, and the likely effects of this aggression on animal survival and dispersal from the release site, all subsequent releases involved only a single pair of animals in each pen.

To avoid any detrimental effect on genetic diversity within the captive source population, no founder animals, nor animals with few living siblings within the captive population, were selected for this reintroduction. Pairs of animals for simultaneous release were selected on the basis of calculated low values for inbreeding coefficients for such pairings. Only animals that had reached sexual maturity, as determined from testicular growth and pouch development (Lundie-Jenkins 1993a), were selected for release. No animals were selected on the basis of size, body weight, behaviour or breeding success, since there was no data from previous reintroductions to suggest that any such factors influenced the success of reestablishment. In addition, any selection based solely on a theoretical consideration of the factors likely to influence survival would have

biased the sample, and created the potential for ambiguous results from monitoring.

4.4 Selection of a suitable release site

As discussed in section 2.4.4, the process of selecting a suitable site for reintroduction of an endangered species, like the initial decision to reintroduce or not, is a complex balancing act between biological and non-biological considerations. Adding to this complexity is the necessity for the selection process to be undertaken at several geographical scales (regional, habitat, micro-habitat).

Extensive surveys of the Tanami Desert were conducted in the 1980s by Gibson (1986), in order to assess the vertebrate fauna in the region, locate remnant populations of endangered species, and identify potential reintroduction sites for the mala. Based on these surveys, Gibson identified 2 sites which he considered had the most potential for future reintroduction of the mala. These sites were both associated with saline drainage systems (Spider Lake and Lake Surprise (Figure 4.1)), and were similar in character to the Sangster's Bore site which at that time still supported a population of mala. As summarised earlier in this chapter (4.2.1), Lake Surprise was selected as the site for implementing the initial reintroduction effort for the mala, commencing in 1984. The subsequent extinction of mala from the Sangster's Bore site provided the additional impetus for a reintroduction to be initiated at that site.

4.4.1 Justification for site selection in this study

The Sangster's Bore site, in a portion of the Tanami Desert in the Northern Territory 560 km north-west of Alice Springs (20°50'S., 130°20'30"E.) (Figure 4.1), was chosen for this experimental reintroduction based on the following information:

- The site is well within the species' former distribution area, and it is known to have been recently occupied by mala (Bolton and Latz 1978, Lundie-Jenkins 1989, 1993)
- The general environment has recently shown that it was capable of sustaining populations of mala. The key characteristics in this respect were: the presence of the hummock growth form of Soft Spinifex *Triodia pungens* that provides the principal shelter for mala (Lundie-Jenkins

1993), and a diverse range of important food plants, from perennial grasses to saline-tolerant sub-shrubs (Pearson 1989, Lundie-Jenkins *et al.* 1993a).

- The factor which contributed to the local extinction of mala from that site, predation by foxes, was known and considered to be manageable at the site (Lundie-Jenkins *et al.* 1994b).
- A substantial bank of background biological data for the area existed from previous mala studies, and also from related work by officers of CCNT (Bolton and Latz 1978, Gibson 1989, Lundie-Jenkins 1993, Lundie-Jenkins *et al.* 1993a & b) and CSIRO (Griffin, 1990, Masters 1993, Morton 1984) in relation to fire and habitat management. Much of the CCNT data relates specifically to studies of the mala, and hence has direct relevance to the reintroduction.
- The land tenure, whilst not national park, was Aboriginal free-hold land, and there was a well developed relationship and process for consultation and cooperation with local traditional Aboriginal land owners. The Warlpiri people have a strong totemic attachment to the mala and were enthusiastic about efforts to return it to the Tanami (Loorham 1985).
- Some established infrastructure to support field based research programs existed at the site in the form of fire-breaks, tracks, transportable accommodation and vegetation monitoring sites.
- The suitability of the site would facilitate better evaluation of the forces that affect the success of a reintroduction program, and provide further insights into the reasons behind the local demise of the hare-wallabies.
- Extensive ground surveys carried out by the Conservation Commission in the Sangster's Bore region during December 1987 also identified a number of other potential sites for reintroduction, based on similarities in vegetation dominance and structure (Lundie-Jenkins 1989). These areas were considered as potential sites for a second series of releases, dependent upon the outcomes of the initial release program.
- Of the two reintroduction sites identified by past extensive surveys of the Tanami Desert, Spider Lake was the only one at which reintroduction work had not already commenced, and there were significant logistic problems associated with that site. The Spider Lake site was extremely remote, there was no road/track access, no fire management had been undertaken at the site and there was no direct evidence of past occupation by mala.

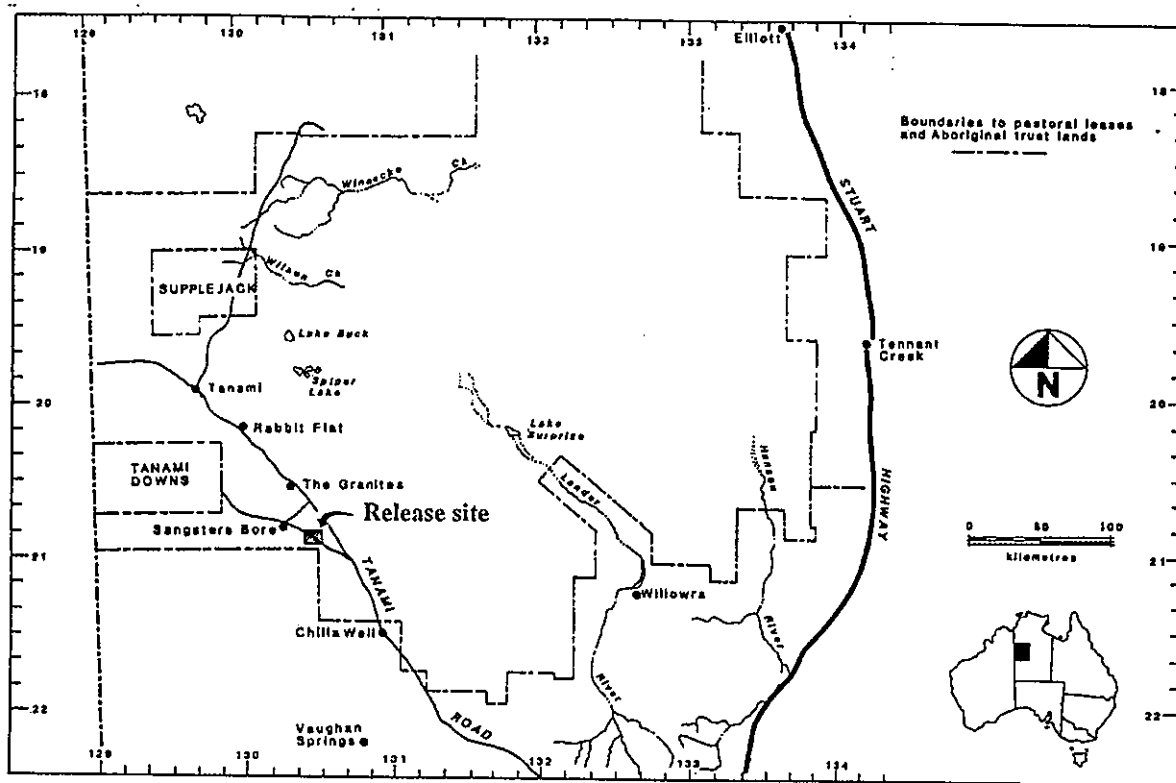


Figure 4.1 Map of the Tanami Desert showing the location of the Sangster's Bore release site and alternative sites.

4.4.2 Ecological setting of release site

Location

The release site is located in the Tanami Desert, which covers an area of about 160 000 km², and incorporates an extensive area of the true arid zone and southern extent of the wet/dry tropics, in the central western portion of the Northern Territory. As a distinctive phytogeographic region it extends from eastern Western Australia to the eastern Northern Territory (Burbidge and McKenzie 1983). The area is largely unoccupied. Scattered homesteads and Aboriginal communities, together with the semipermanent mining settlements of The Granites and Tanami, account for the only forms of settlement within the region. There are few roads or tracks, except in the northwest, and vehicular access to large parts of the area is limited. The main access route in the region is the unsealed road from Alice Springs to Halls Creek which passes southeast-northwest, through The Granites, Rabbit Flat and Tanami.

Climate

The region has a warm dry monsoonal climate and is mostly semi-desert. Long-term weather records from Rabbit Flat, the nearest meteorological station (approx. 120 km to the north-west) indicate the general weather patterns for the area.

Mean annual rainfall (1970-1993) is 479 mm, with a range from 159mm (1992) to 847mm (1974). Monthly rainfall generally increases from September to February, and decreases to a minimum in July. December to March receives 58% of the annual average rainfall while May to September receives only 8%. The climate is hence dominated by summer rainfall. Reliability of rainfall is typically low, but is most reliable from November through to February. Drought is a common feature of the Tanami, and as a consequence rainfall is the major factor influencing primary production in the region.

Monthly mean daily maximum temperatures are highest in December (39°C) and lowest (25°C) in June and July. Daily maxima in January and February are lower than in December because of cloud cover associated with the northern monsoon. During 8 months of the year the mean daily maxima exceed 30°C.

Soils, geology and geomorphology

The dominating feature throughout the Tanami Desert and much of the study area is a very gently undulating desert sandplain, made up of red earthy sands and supporting shrub and spinifex communities (Gibson 1986). These areas are broken by longitudinal sand dunes and low rises of laterite outcropping (Blake *et al.* 1979). Small termitaria in the form of pinnacles are common at the site and throughout the sandplain country.

Vegetation

The study area occurs within a landsystem characterised by spinifex sandplain interspersed with low caliche areas, distinguished by sandy clay soils heavily impregnated with salt and dominated by halophytic grasses and subshrubs. The entire system has developed from a chain of ancient lake beds now covered by encroaching sand dunes (Bolton and Latz 1978). Vegetation

dominance in the area is influenced by local variations in the depth of sand overlying saline sediments (Mazzer 1988). The vast sandplains support mainly soft spinifex communities dominated by *Plectrachne schinzii* and *Triodia pungens*, with scattered shrub cover of *Melaleuca* and *Acacia* species. In contrast the lower saline depression areas, referred to throughout the remainder of the text as caliche areas, are dominated by a number of salt-tolerant sub-shrub and grass species. Within the study area these vegetation systems formed roughly parallel bands, determined by local topography (Mazzer 1988, Thomas 1988).

4.5 Development of release techniques

4.5.1 Soft release vs hard release

Both of the original reintroduction programs initiated for the mala utilised a "soft release" strategy. Using this approach, animals were initially introduced to a temporary holding/release pen in order to acclimate to the conditions prior to being allowed to free-range. Based on the apparent success of this approach in previous programs, a similar one was adopted for this program. The advantages of such an approach were that it:

- enabled animals to be monitored both for any adverse effects or injuries associated with the transfer from the captive population to the remote release site, and for proper functioning of their individual telemetry collars.
- ensured that transferred animals had immediate access to easily located food and water, both of which were provided in the holding/release pens. Thus captive animals were not required to locate and utilise natural food resources immediately.
- forced animals to locate and establish shelters within the enclosure. This was considered likely to increase their fidelity to the release site, thereby reducing the likelihood of animals dispersing large distances (possibly into inhospitable habitat) following free-release.
- enabled the timing of the free-release to be varied to avoid situations, such as major thunderstorms or windy nights, which might have influenced the behaviour of animals upon release.

Observations during this program showed that the temporary holding/release pens also provided a means for newly transferred animals to interact, through the fence, with animals already established

at the site, without the potential for injury or forced dispersal that might have resulted from an initial direct confrontation.

4.5.2 Release site infrastructure

Roads, firebreaks and layout

The release site was established in an area extending from the eastern shore line of a large salt-lake (Fiddler's Lake), approximately 10 km south of Sangster's Bore. The site consists of two east-west parallel sandy rises, supporting soft-spinifex *Triodia pungens* communities, separated by interdunes. These interdunes are dominated by saline tolerant grasses and sub-shrubs. The site is adjacent to areas utilised in previous studies of mala (Pearson 1989, Lundie-Jenkins 1993, Lundie-Jenkins *et al.* 1993a & b) and the effects of fire on desert fauna (Gibson and Cole unpublished). As such there is a well established track through the site, a managed mosaic of fire recovery states, and some existing vegetation monitoring sites. The layout of this existing infrastructure, and other elements established in relation to this reintroduction, is shown in Figure 4.2.

Design and construction of release enclosures

Two 50mx 50m temporary enclosures were constructed at the release site within *Triodia pungens* habitat approximately 1.5 km apart. Previous studies of habitat use by a now extinct population of mala at this site (Lundie-Jenkins 1993) had revealed a strong preference for the shelter provided by this spinifex habitat. The yards consisted of 2m high chicken mesh supported by star pickets and tensioned between pine strainer posts. The mesh was buried to approximately 40 cm on 3 sides, whilst the fourth side was modified to act as a gateway allowing free release of the translocated animals. This approach to releasing translocated animals was preferred to retrapping and release outside the pens, as it would reduce the likelihood of the flight response of animals influencing the extent and direction of post-release dispersal.

Elevated observation seats were erected adjacent to one fence-line on each of the enclosures to permit nocturnal observations of the enclosed animals. Observations were used to monitor survival and social interactions within the enclosure.



Figure 4.2 Map of Sangster's Bore release site showing the location of the temporary enclosures (□), radio-telemetry towers (•), supplementary feed and water points (•), tracks (---) and fire history.

4.5.3 Transportation of animals to release site

Animals selected for release were initially captured between 2-5 days prior to transfer to the release site to allow their condition to be assessed and radio-collars to be fitted. At this stage proposed release pairs were placed together in the same enclosure in Alice Springs. This facilitated the process of recapture for transfer, and also enabled the pair to be monitored for any aggressive behaviour that might have suggested an incompatible pairing.

On the day of transfer to the release site, animals were captured during the cool of the morning (7-9 am), weighed and placed into individual hessian sacks. The sacks of release pairs were placed into plastic laundry baskets, and the animals were then transported to the release site in airconditioned 4WD vehicles. Regular checks were made during the course of the journey to minimise any likelihood of the animals overheating. Past movements of animals (both wild to captive, and captive to reintroduction site) had been undertaken successfully using this procedure.

4.5.4 Provision of feed and water supplements

A total of 5 feed and water stations were established in conjunction with each of the release pens. One station was erected inside each pen and the remaining 4 at each site were distributed in lines away from the enclosure. The external stations were aligned in an essentially linear fashion at 100m intervals from the pen. Each station consisted of a galvanised tin feed hopper (dimensions 45cm x 60cm x 12cm), and a commercial pig drinking-nipple connected to a 10 litre plastic drum. The intention in establishing these food and water points was to encourage animals to remain in the general vicinity of the release area, and to reduce the need for free-released animals to immediately locate and use natural food resources. The use of food supplements by both captive-bred and subsequent *in-situ* bred animals was monitored by way of microscopic analysis of faecal samples collected from trapped individual animals. Details of the methods employed in this analysis are presented in chapter 7.

4.5.5 Release from enclosures

Following transportation to the release site, pairs of animals were released into each of the

holding/release pens after dusk. Animals were maintained in these pens for an average of approximately 1 month, after which the modified section of fencing was raised to enable the animals to freely move in and out of the enclosure. Whilst within the enclosure the animals were monitored remotely to check survival and continued functioning of radio transmitters. The 1-month period of acclimation was based on the frequency of management visits to the release site, rather than any attempt to assume a rate of acclimation by the captive animals.

4.6 Post-release monitoring procedures

In order to examine both the process involved in captive-bred mala adapting to conditions following free-release at the site, and the factors influencing this adaptation, a rigorous program of monitoring was implemented at the release site. Monitoring targeted both the individual animals released at the site and elements of the environment.

4.6.1 Environmental monitoring

Meteorological data

Meteorological data was obtained from the Rabbit Flat Meteorologic Station. Rainfall recordings from this station were compared with limited data sets obtained from the Granites Gold Mine (approximately 60km west of the release site), and found to be closely correlated with respect to timing and magnitude of rainfall events.

Vegetation transects

Vegetation cover and diversity were measured quarterly at five sites, by wheelpoint along fixed transects. This procedure proved to be extremely time-efficient, and was considered preferable to more exact, time-consuming methods that might not have truly reflected the availability of less common species (Winkworth *et al.* 1962). Transects were established in *Triodia pungens* and *Plectrachne* / caliche habitats adjacent to each of the release enclosures, and a single transect was established in recently burnt *Triodia pungens* habitat between the two release sites. Wheelpoint data was collected onto a Sharp 1200 pocket computer and subsequently downloaded to a Toshiba 2400 laptop computer. Programs developed by Griffin (1985) were utilised in data collection and analysis.

Plant water status

Clipped samples of vegetation were obtained quarterly, from 12 species previously recorded as important food species for the mala (Lundie-Jenkins *et al.* 1994). These samples were weighed immediately upon collection, before being oven dried at 75°C for 3 days and reweighed to determine moisture content. These measurements were required in relation to changes in the water content of the mala's diet and its relationship with other aspects including survival, dietary composition and water and energy expenditure.

4.6.2 Radio-telemetry

Radio-tracking was used as the principal means of monitoring the survival and dispersal of mala, released into and outside the enclosure. All released animals were fitted with individually tuned (150 Mhz) radio-transmitting collars (Sirtrack- NZ). Despite some initial problems with collar reliability, this technique had been successfully applied in relation to the reintroduction of mala at the Lake Surprise site (Johnson 1996, Lundie-Jenkins and Bellchambers 1995). Locational information was obtained using the following means:

i. Triangulation from fixed towers

Four fixed radio-towers were established at the release site to monitor the movements and dispersal of released animals. All towers utilised single high gain yagi antennae and operated a peak system. Telonics TR-2 receivers fitted with TS-1 scanner units were used to monitor the radio signals. The direction to a collared animal was determined by locating the point in a 360° rotation of the antenna where signal strength was greatest. In most cases this involved recording null points either side of a broad area of strong signal, and calculating the midpoint. Bearings to the collared animal were recorded from compass roses fitted to the antennae bases. Locational fixes were determined by triangulation of bearings recorded simultaneously from a minimum of two of the fixed stations. The typical tracking protocol was to monitor released animals intensively for the first night following release by tracking their movements over the entire night. After this initial period, tracking was carried out intermittently.

During most field trips to the release site, all animals carrying active radio-collars were also

located daily by triangulation of signals received from fixed radio towers. Fixed point tracking and location by triangulation were selected as the primary means of locating mala following free-release, as they provided the opportunity to monitor the movements of un-disturbed animals. Transverse studies were trialed in order to closely observe the movement patterns of individual animals at night. However, the combined effect of the small size of the mala relative to the spinifex and the animals' flighty nature meant that animals were frequently flushed, and hence movements were unduly influenced by the observer.

ii. Physical location using hand-held antennae

Daytime locations and survival of animals were also routinely checked by tracking down individuals using hand-held antennae and flushing them from their squats. This method was generally used at the end of a period of fixed-point triangulation, in order to ensure that the monitored animals were alive and that triangulated locations were reasonably accurately reflecting the animals' locations. The locations of individual animals were determined using compass bearings and GPS (Global Positioning System). The "walk-down" method was also used to locate animals for recapture using techniques described in section 4.6.3.

4.6.3 Trapping and netting

Regular trapping of the release population was conducted, to monitor the survival and condition of released mala, and to detect the recruitment of *in situ* bred animals to the population. Two methods were principally employed in the capture of mala, those being:

i Bromilow traps

Modified Soft-meshed Bromilow traps (Kinnear *et al.* 1988) baited with fresh lucerne were placed in areas showing high evidence of mala activity in the form of tracks and faecal pellets. The soft mesh netting which lines the Bromilow traps was preferred to traditional wire cage traps, on the basis of observations of trapping behaviour within the captive animals. Some animals were found to react convulsively when initially confined in the trap and the soft mesh was expected to reduce the likelihood of capture injuries, compared with the wire cage traps. During any trapping period, traps were checked at 1-2 hourly intervals throughout the night, both to minimise the risk of animals sustaining injuries and to ensure that trap availability was maximised over each night.

ii Capture by encirclement with a modified fishing net

Animals fitted with radio-collars were located during daylight hours (as described in 4.3.2) and carefully encircled by a modified fishing net supported by light weight fibreglass poles. When flushed, the animals became entrapped in the net and could then be extricated and placed in a hessian sack. This technique was most frequently applied in order to recapture specific animals, for changing collars or in relation to water and energy turnover studies (Chapter 7).

The condition and reproductive status of all animals was recorded on standard data sheets at each capture. The reproductive status of females was recorded and new pouch young were sexed. When sufficiently large, they were marked with finling ear tags. Any independent second and third generation animals were marked with either reflective or radio-collars, and details of their size and sex were recorded. The progress of these animals was then monitored together with that of the original release animals. If necessary, previously radio-collared animals were refitted with new radio-collars.

4.7 Management of extrinsic/habitat factors

Previous ecological studies and reintroduction attempts had highlighted the need for management of a number of extrinsic/habitat factors, in order to protect naturally occurring and re-establishing mala populations. Consistent with the feed-back mechanisms identified in the model introduced in Chapter 2, some of these management approaches were adapted and changed with the program.

4.7.1 Predator control

Based on observations derived from previous ecological studies of the interactions between mala and introduced mammals (Lundie-Jenkins *et al.* 1993), no broadscale baiting was undertaken to control dingoes or foxes around the release site. These studies had implied that baiting might have selectively removed dingoes and hence led to an increased abundance of both foxes and feral cats. Observations from reintroductions of other small macropods such as that attempted by Christensen and Burrows (1996) in the Gibson Desert, provide additional support for this belief.

Following initial losses of release animals to both foxes and feral cats, a program targeting these predators was initiated using trapping and shooting. Trapping employed the use of Lanes Leghold traps, which were placed along fire trails where predator activity had previously been detected. A barrier of spinifex was erected across the trail, and single traps were set either side of a narrow opening in the centre of this barrier. Any predators trapped in this manner were humanely disposed of by shooting at point blank range. Shooting was conducted both at night by spotlight and during daylight, with the assistance of Aboriginal trackers. During the course of the study a total of 3 foxes and 6 feral cats were destroyed by trapping and shooting.

No quantitative monitoring of predator activity was undertaken during the course of the reintroduction program, as monitoring undertaken in relation to previous reintroductions at the Lander River site (Lundie-Jenkins & Bellchambers 1995) had failed to identify a reliable (accurate or precise) method for monitoring predator abundance. This previous work had incorporated both direct (spotlight counts) and indirect (track counts) techniques. Neither approach had been found to provide a reliable index of predator abundance, due to significant spatial and temporal variation in daily counts obtained from each method.

4.7.2 Fire management

Since the recovery program's inception in 1979, numerous small-scale controlled burns have been carried out on an annual basis, by staff of the Conservation Commission, in the Sangster's Bore area. In using fire as a management technique, the Conservation Commission has tried to reproduce the "patchwork" or mosaic patterns of vegetation that were created by the traditional burning practices of Aborigines (Bolton and Latz 1978, Johnson 1988). This has been achieved by a program of consultation and co-operation with Warlpiri Aborigines (Johnson 1988). The older people, in particular, with their knowledge and traditional responsibilities, have been important in helping formulate and implement fire-management plans for enhancing hare-wallaby habitat (Bolton and Latz 1978, Lundie-Jenkins 1993). The aim of this type of burning strategy has been not only to increase the diversity of feeding and shelter sites for *L. hirsutus*, but also to provide the area with some protection from summer wildfires caused by lightning strikes. Summer

wildfires can be extremely large and lead to homogenisation of the vegetation. The ultimate result of the management activity undertaken at the study area has been to create a well-defined mosaic of vegetation in different fire recovery states. This mosaic was one of the factors which influenced the selection of the Sangster's Bore site.

During the course of this reintroduction experiment, controlled burning operations were principally conducted to provide protection for the enclosures and the released mala population. Burning was concentrated on the periphery of the release area, and utilised existing roads as firebreaks. Assistance from Aboriginal people from the Yuendumu community was generally sought when burning was to be conducted. Most burning was conducted during the cooler winter months and fires were usually ignited in the late afternoon or early evening. Aerial photography and satellite imagery were used to plan burning operations.

4.8 Aboriginal involvement

The release program was conducted on Warlpiri Aboriginal land in a region of the Tanami Desert. Permission to access the site and conduct the research was granted through the Central Land Council.

The mala is particularly important to the Warlpiri Aborigines, being both a component of living memory for the old people, and, perhaps more importantly, a creature of myth and legend manifested in the songs, stories and ceremonies of their culture. The Warlpiri have been saddened by the loss of the species from their lands, and therefore the re-introduction program has particular relevance to them (Gibson pers. comm.). From its inception, Warlpiri people have enthusiastically cooperated in this project.

The work could not have been carried out without the assent and co-operation of the Warlpiri people, which they have given unhesitatingly. During the course of the program, considerable assistance was received from traditional Warlpiri people from the Yuendumu community. This took the form of assistance in selection of sites, construction of enclosures, control of predators, tracking/monitoring of release animals and controlled burning operations. The older Warlpiri men in particular were happy to share their knowledge, and many rare insights into

the ecology and behaviour of the hare-wallabies (mala) were obtained from these discussions. Throughout the program they have shown great enthusiasm for the reintroduction and indeed have been instrumental in its implementation.

Chapter Five

Survival and Fecundity of the Reintroduced Population

5.1 Introduction

The ultimate success of a reintroduction is concerned more with the persistence and dynamics of the population than that of individual animals (Stanley Price 1991). Very small populations, such as might be encountered during the initial stages of a reintroduction, face an increased risk of extinction simply as a consequence of their size. The very probabilistic nature of extinction is such that some small populations will survive, but many will lose out when faced with the risks characteristic of small numbers (Caughley and Gunn 1996). These risks are most often characterised as either 'demographic stochasticity', 'environmental stochasticity' or 'loss of genetic variability'.

'Demographic stochasticity' is described as the effect of random differences among individuals in a population on whether a population of a few animals increases or decreases over a time period (Ballou 1995). A population can experience 'good' or 'bad' years in terms of population growth simply due to random variation at the individual level. Year-to-year variation in environmental conditions, termed 'environmental stochasticity', is the second category of risk facing a small population (Caughley and Gunn 1996). This variation in environmental conditions clearly impacts upon the ability of a population to reproduce and survive (Ballou 1995). However, unlike demographic stochasticity, the effect of environmental stochasticity is largely independent of the size of the population. The third category of risk is a reduction in genetic variability. A loss of variability will arise as a consequence of random sampling of genes (genetic drift) and the increased likelihood of inbreeding associated with a small population (Caughley and Gunn 1996).

In order to understand the factors influencing the persistence and dynamics within the reintroduced mala population at Sangster's Bore, a detailed analysis of a number of measurable parameters of survival and fecundity was undertaken. This analysis investigated parameters such as age and sex related survival and recruitment rates, causes of mortality, seasonality of births, and population growth. The results are discussed in relation to both the process of transition by

translocated captive animals towards a self-sustaining reintroduced population, and the factors likely to limit the successful re-establishment of a viable population.

5.2 Methods

The survival and reproductive status of reintroduced hare-wallabies were monitored by a combination of recapture and regular physical location using radio-telemetry. All captured hare-wallabies were sexed and weighed to the nearest gram. The pouches of females were examined for lactating, non-lactating and regressed teats. All pouch young were sexed, and the month of birth estimated by means of body measurements and external appearance using growth functions derived from captive studies (Lundie-Jenkins 1993a). Radio-telemetry was used to confirm continued survival and, in instances where close approach was possible, could be used to detect the presence of large pouch young in females. Ages for all released animals were known from studbook records maintained on the captive population.

Field evidence, including necropsy, was used to determine the apparent causes of death for hare-wallaby carcasses recovered during the program. Survival was calculated as **Minimum survival** by including both confirmed mortalities and radio-collared hare-wallabies whose signals were lost, and which were not subsequently detected by trapping.

Survival time-lines were generated for all animals released between October 1989 and October 1993. Survival distributions were then calculated for the released population for consecutive 3-month intervals. This division was chosen rather than the more conventionally used 12-month interval because of the small sample sizes. Thus the calculated values represent the probability that an individual alive at time t_0 will survive to the start of the next 3-month period. Whilst it has certain limitations in terms of its usefulness in comparisons with other studies, it provides useful information on the sex and age-related survivorship of the released animals. As no values for survivorship in field populations of mala have previously been collected, survival distributions derived from the released animals were compared with distributions calculated from the captive mala colony in Alice Springs. Age-related survival distributions were compared using Fisher's exact test

statistic (Zar 1989). The Kaplan-Meier or product limit estimator procedure (Pollock *et al.* 1989) was used to construct survival estimates based on time-since-release, as it permitted staggered entry of additional animals. The log rank test was used to compare survival estimates (Pollock *et al.* 1989, Wilson *et al.* 1992). Statistical significance at the 5% level was used as the basis for establishing if samples were significantly different. Minimum known-to-be-alive estimates of the population were derived from survival time-lines for captive and *in situ* bred animals.

The distribution of births was derived from estimated birth dates calculated from measurements of pouch young. Where possible the survivorship of individual pouch young was determined by assessment of the mother's reproductive status at subsequent recaptures. Data on survival of *in situ* bred animals was derived from pouch-young counts conducted on trapped females, and recaptures of independent *in situ* bred animals. Few pouch young could be followed from birth through to weaning, and hence most information relates to post-weaning survivorship.

5.3 Results

5.3.1 Survival and mortality of reintroduced animals

Between October 1989 and September 1993 a total of 51 captive-bred mala, consisting of 26 males and 25 females, were transported to and sequentially released at the Sangster's Bore study area. Only two mortalities were recorded in relation to transportation of animals to the release site, both as a result of heat stress. Figure 5.1 depicts the scheduling of the releases and indicates the survival patterns for all individuals released. The lines represent the range of dates over which each animal was known to be alive, and hence will underestimate actual survival time in most cases.

It can be seen that there was considerable variation between individual animals and release periods in terms of survival. Known survival times range from two days post-release recorded for one male, to 37 months for one female. The apparent low survival of the initial release group of 8 animals is also related to difficulties with telemetry equipment which limited the period of contact with this group. The large mortality of animals indicated between 24 and 28 months after the first release reflects predation by feral cats in the last quarter of 1991, as

reported in Gibson *et al.* (1994). Clearly this predation had a devastating impact on this small establishing population. Releases following this predator impact showed encouraging signs of establishment by released animals.

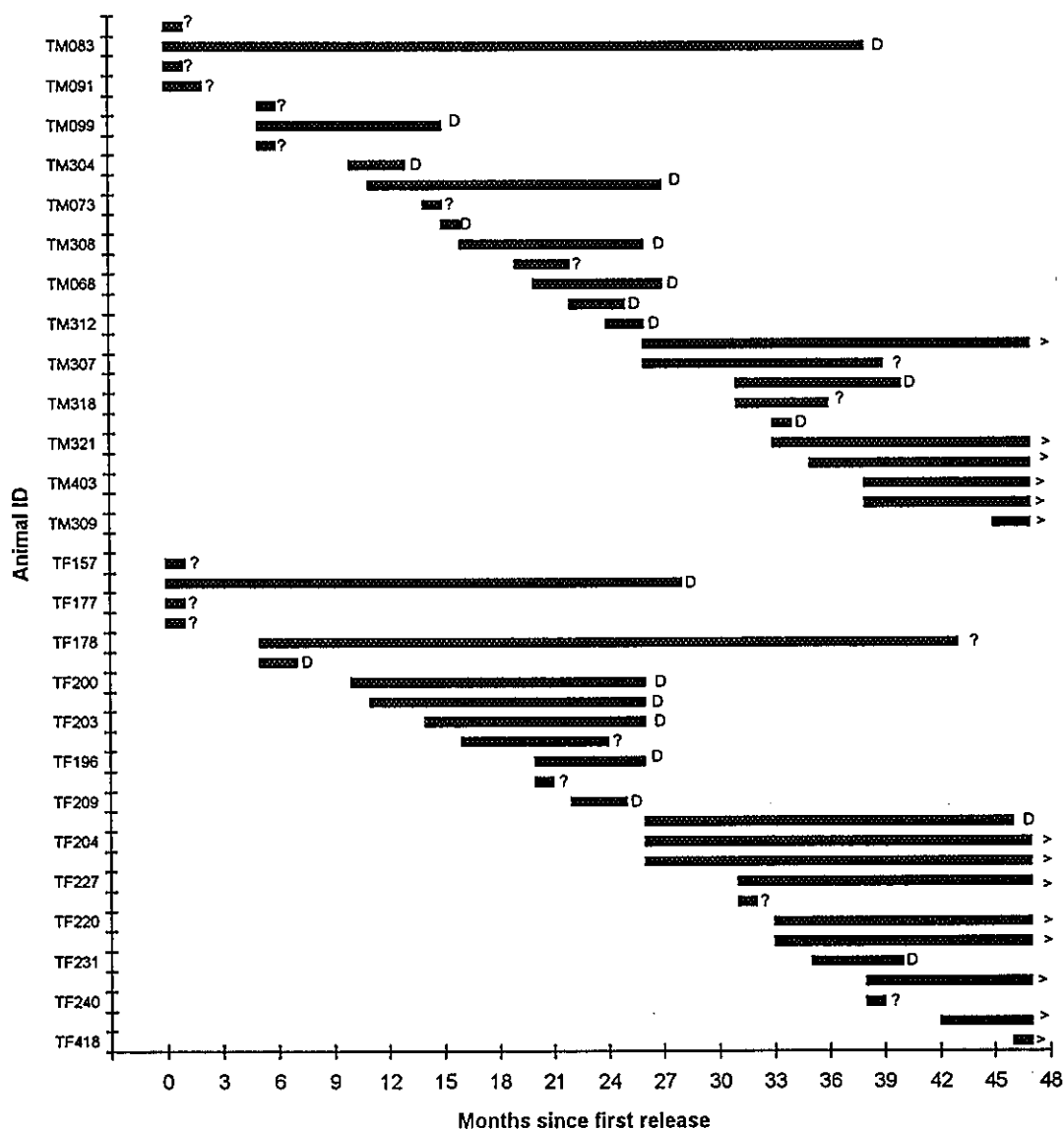


Figure 5.1 Survivorship timelines for captive-bred mala released at the Sangster's Bore site between October 1989 and August 1993. Lines commence on the date of release at the site, and end on the last date each animal was known to be alive.

Figure 5.2 shows the estimated comparative survivorship for male and female mala for each consecutive 3-month sample period over the course of the study. Some of the dramatic shifts in the values for survivorship are a function of the low numbers of animals at risk during some sample periods. In October 1989, for example, only one of the four male animals released survived that initial 3-month period, thus corresponding to a survival rate of 0.25.

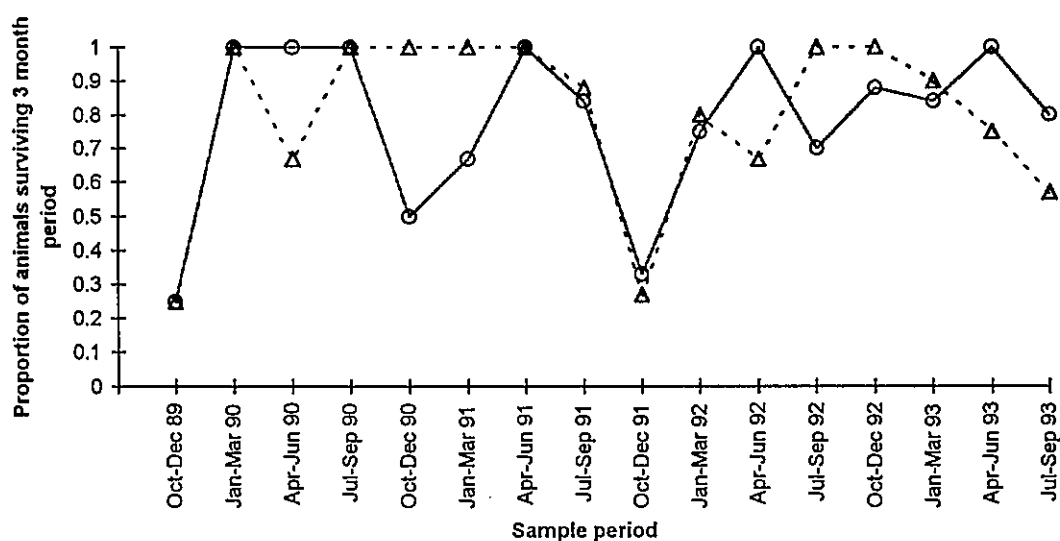


Figure 5.2 Changes in the 3-monthly survivorship for male (circles) and female (triangles) captive-bred animals within the released population between October 1989 and September 1993. (Survivorship expressed as probability that an individual alive at time t_0 will survive to the start of the next 3-month period)

Despite heavy mortalities during some sample periods, the mean 3-month survivorship pooled for males and females over the course of the study was 0.77, which is equivalent to an annual survivorship of 0.35.

5.3.2 Variation in survivorship with age, sex and time-since-release

The recapture data were further analysed to investigate any effects of sex, age and time-since-release on the survival of individual captive-bred mala. The results of these analyses are shown in Tables 5.1-5.3. As in previous sections, survivorship is expressed as probability that an individual alive at time t_0 will survive to the start of the next 3-month period.

There was a significant and expected difference in 3-month survivorship between animals

released at Sangster's Bore and those maintained in the captive colony (Tables 5.1-5.2). Survivorship in all age classes was, on average, 24% higher for captive males and 14% higher for captive females than for released males and females. No comparable data from wild hare-wallaby populations exists with which to make the more realistic comparison of survivorship under natural conditions, including such effects as food and moisture limitations, and predation.

Table 5.1

Comparison of survival distributions for captive-bred mala released at the Sangster's Bore site and those maintained at Alice Springs between October 1989 and July 1993. (Fisher's exact test for proportions (Zar 1989) was used to test differences between survivorship values for males and females in each age class)

Sex	Age (years)	Comparative survival for released and captive maintained mala						Prob. Fisher's exact test
		Release			Captive			
		No. at risk	No. deaths	Percent Surviving %	No. at risk	No. deaths	Percent Surviving %	
Males								
	<1	20	6	70.0	101	1	99.0	0.0002
	1-2	26	7	73.1	48	2	95.8	0.0012
	2-3	10	2	80.0	33	1	97.0	0.0108
	3-4	11	2	81.8	24	1	95.8	0.0434
	4+	2	1	50.0	82	1	98.8	0.0002
	Total		18			6		
Females								
	<1	17	2	88.2	103	5	95.1	0.0930
	1-2	37	9	75.7	29	1	96.6	0.0072
	2-3	20	3	85.0	14	2	85.7	0.5824
	3-4	10	2	80.0	20	0	100	0.0044
	4+	7	2	71.4	116	8	93.1	0.0060
	Total		18			16		

The probabilities of survivorship were lower for males than for females in all age classes except 3 - 4 years. These differences were not, however, significant for the sample of animals involved in the release program at Sangster's Bore (Table 5.2). Therefore, for analysis to investigate any differences in survival between age classes, data for males and females was pooled. A matrix indicating the significance of differences between the various age classes is presented as Table 5.3. There were no significant effects of age on survivorship found in paired comparisons of survivorship for each age class against all other age classes. Whilst survivorship for the 4+ years age class was much lower than survivorship for all other age classes, the small size of the samples rendered the statistic non-significant.

Table 5.2

Comparison of values of survivorship for male and female captive-bred mala released at the Sangster's Bore site between October 1989 and July 1993.

(Fisher's exact test for proportions (Zar 1989) was used to test differences between survivorship values for males and females in each age class)

Age (years)	Males			Females			Total Population			Prob. Fisher's exact test
	No. at risk	No. deaths	Percent Surviving %	No. at risk	No. deaths	Percent Surviving %	No. at risk	No. deaths	Percent Surviving %	
<1 [@]	20	6	70.0	17	2	88.2	37	8	78.4	0.0818
1-2	26	7	73.1	37	9	75.7	63	16	74.6	0.5962
2-3	10	2	80.0	20	3	85.0	30	5	83.3	0.3844
3-4	11	2	81.8	10	2	80.0	21	4	81.0	0.6528
4+	2	1	50.0	7	2	71.4	9	3	66.7	0.1556
Total		18			18			36		

[@] Only includes post-weaning/independent young

Table 5.3

Matrix of probabilities calculated from Fisher's exact tests comparing survivorship between age classes for captive-bred mala released at the Sangster's Bore site.

(Data for males and females has been pooled)

Age Classes	< 1	1-2	2-3	3-4
1-2	0.8966			
2-3	0.4296	0.3422		
3-4	0.5754	0.4902	0.8572	
4+	0.2846	0.3078	0.1142	0.1646

On the basis of the non-significance of age as an influence on 3-monthly survivorship for released mala, the data were recollated to derive survivorship tables based on time-since-release for male and female animals (Table 5.4). Using the Kaplan-Meier procedure, estimates of survivorship were derived that calculate the relative probability of released male and female animals surviving for a particular time following release, based on 3-monthly survival estimates. As survivorship calculations are based on 3-month periods, the value for the total number of animals at risk will necessarily exceed the total number of individual animals known to survive to that time-since-release. This may create some bias in the higher classes, as long-lived individuals contribute several of the entries identified in the number of animals at risk. Testing of this effect by elimination of multiple entries from one animal did not affect the overall trends in survivorship, but did effect statistical significance as it dramatically reduced the sample size. Multiple entries were therefore retained for all subsequent analysis. In light of the potential problems associated with this 'pseudoreplication', any trends towards significance were interpreted conservatively.

There was no significant effect of sex on survival relative to time-since-release for the first four classes of time-since-release, from < 2-months to 6-8months. However, from the 8-10month time-since-release class upwards there was an increasingly significant tendency for the 3-monthly survivorship for females to be higher than males. In the time-since-release classes of 8-10months, 10-12months and >12months, female survivorship was approximately 50% higher than that recorded for males (Table 5.4). This can be restated that females having survived 10 months post release had a 50% higher probability of surviving subsequent 3-month periods than did males with a similar time-since-release.

Table 5.4

Comparison of values of survivorship based on time-since-release of male and female captive-bred mala released at the Sangster's Bore site between October 1989 and July 1993. (Survival distribution calculated using the Kaplan-Meier or product limit estimator procedure) (Approximate normal (Z) statistic calculation based on log-rank test (Pollock *et al.* 1989))

Time since release (months)	Males			Females			Total Population			Prob. Approx. normal Z
	No. at risk	No. deaths	Survival S(t)	No. at risk	No. deaths	Survival S(t)	No. at risk	No. deaths	Survival S(t)	
<2@	21	7	0.6667	20	6	0.7000	41	13	0.6829	0.3897
2-4	10	3	0.4667	11	2	0.5727	21	5	0.5203	0.2483
4-6	7	1	0.4000	12	2	0.4773	19	3	0.4382	0.1587
6-8	9	3	0.2667	7	1	0.4091	16	4	0.3286	0.3085
8-10	5	1	0.2133	7	0	0.4091	12	1	0.3012	0.0901
10-12	3	1	0.1422	9	1	0.3636	12	2	0.2510	0.0367
>12	14	2	0.1219	25	6	0.2764	39	8	0.1995	0.0030
Total		18			18			36		

@ Only includes post-weaning/independent young

A matrix indicating the significance of differences in survivorship, pooled for male and female captive-bred mala, between the time-since-release classes, is presented as Table 5.5. There were no significant effects of time-since-release on survivorship found in paired comparisons of survivorship for each time-since-release class against all other time-since-release classes.

5.3.3 Causes of mortality

Table 5.6 summarises the causes of mortalities for 28 mala recovered during the course of the release program; this total includes both captive-bred and *in situ* bred animals. For simplicity of interpretation mortalities have been defined as either natural or unnatural causes. So-called natural causes, including predators, dispersal into unfavourable habitat

and accidents, contributed to 89.3% of the known mortalities. Only 3 mortalities could be related to human handling, two from heat stress associated with transportation and one from myopathy related to capture.

Table 5.5

Matrix of probabilities calculated from Fisher's exact tests comparing survivorship between time-since-released classes for captive-bred mala released at the Sangster's Bore site.

(Data for males and females has been pooled)

Time since released	< 2 months	2-4 months	4-6 months	6-8 months	8-10 months	10-12 months
2-4 months	0.584					
4-6 months	0.248	0.538				
6-8 months	0.722	0.892	0.483			
8-10 months	0.169	0.335	0.631	0.298		
10-12 months	0.418	0.720	0.858	0.648	0.535	
> 12 months	0.269	0.694	0.755	0.608	0.466	0.933

Exotic predators, chiefly the feral cat and fox, were the major cause of known mortalities within the reintroduced population. There were no discernible patterns in this mortality in relation to the age, size, sex or time-since-release of the animals killed by predators. Specific details in relation to the incidence of feral cat predation in this reintroduction program, and that at Lake Surprise (see Chapter 4, 4.2.1) are described in Gibson *et al.* (1994).

The mortalities ascribed to the category of "dispersal into unfavourable habitats" relate to two incidents in which animals dispersed large distances during the first days following release from the pens. Both animals were males and both dispersed to, and were found dead in, areas with limited cover, and are thought to have died from the combined effects of stress, heat and dehydration. The single death listed against the heading "accident" involves a female whose carcass was located in a collapsed burrow with no other signs to associate with death aside from her entrapment. The remaining deaths clumped under the title of "unknown" involve carcasses which were recovered that showed no outward signs to suggest cause of death. Animals within this category ranged from 30 days post-release up to 462 days post-release. There was no evidence of predation or disturbance by predators

on the carcasses of animals allocated to the "unknown" category.

Table 5.6
Summary of causes of death for 28 mala
recovered during the reintroduction between October 1989 and October 1993.
(Includes both captive and *in situ* bred animals)

Cause of death		No. of deaths	Proportion of known deaths
<i>Natural Causes:</i>			
Predators	- Fox	2	7.1
	- Feral Cat	11	39.3
	- Raptor	1	3.6
	Subtotal	14	50.0
Non-predator	- Dispersal into unfavourable habitat	2	7.1
	- Accident	1	3.6
	- Unknown	8	28.6
	Subtotal	8	39.3
<i>Unnatural causes:</i>			
	- Heat Stress	2	7.1
	- Myopathy	1	3.6
	Subtotal	3	10.7
Total		28	

5.3.4 Changes in body weight

As hare-wallabies are by nature nocturnal and secretive, there was little chance to monitor changes in the post-release condition except by recapture. For the purposes of this study the body weight of adult animals was used as the primary indicator of condition. Table 5.7 summarises the changes in body weight between release and first capture for all animals recaptured during the program. Whilst there was considerable variation between the length of the period between release and first capture for individual animals, it was considered a reasonable indication of initial response to release.

The overall mean change in body weight between release and first capture was essentially trivial in both sexes, -1.9% in males and +0.44% in females, for animals with a body weight at release greater than 1200g. In contrast, substantial positive weight gains were recorded for both males and females with a body weight at release less than 1200g. Animals below 1200g on average would be classed as sub-adults, and this gain is likely to reflect continuing growth to adult size following release. There was no significant effect of

sex on weight change after release for either of the weight categories.

Table 5.7
Changes in body weight between release at Sangster's Bore and first subsequent recapture for captive-bred mala released between October 1989 and August 1993.

Change in body weight between release and first recapture measured for:							
	Males			Females			Prob. F. Statistic
	Animal No.	BW change (grams)	Percent BW change	Animal No.	BW change (grams)	Percent BW change	
Release weight							
< 1200g	TM93	33	2.79	TF198	40	3.81	
	TM309	54	4.55	TF200	218	18.29	
	TM321	11	1.11	TF203	-10	-0.90	
	TM403	292	28.40	TF205	84	8.35	
	TM406	74	6.40	TF231	-1	-0.09	
				TF233	314	29.18	
				TF242	350	44.87	
	Mean	92.8	8.65	Mean	142.1	14.79	0.5591
Release weight							
1200 g +	TM73	41	2.99	TF176	-28	-1.96	
	TM83	-17	-1.27	TF178	-100	-7.14	
	TM98	-111	-7.59	TF196	14	1.07	
	TM99	-162	-12.16	TF204	66	4.77	
	TM303	-83	-5.71	TF208	2	0.14	
	TM307	-80	-5.59	TF215	6	0.48	
	TM308	54	4.55	TF220	-171	-12.47	
	TM319	123	9.71	TF229	236	18.67	
	Mean	-29.4	-1.88	Mean	3.12	0.44	0.5523
Prob. F. Statistic		0.0619			0.0592		

Table 5.8 summarises the weight changes recorded for 9 males and 11 females, recaptured 31 and 33 times respectively, during the study. The weight changes averaged across all individuals indicate continued maintenance or increases of release weights with mean weights not significantly different to those of captive animals. There was a significant difference between the weight changes recorded for males and females, with females tending towards greater weight gain. This tendency most probably reflects increases in body weight associated with female reproductive activity, as a high proportion of the females recaptured during all trapping periods were either carrying young or lactating. Whilst pouch young weights were routinely subtracted from female weights, females carrying early to mid-stage pouch young were generally scored in better condition than males trapped during the same period, based on visual assessments and rankings of good, fair or poor condition.

Table 5.8

Changes in body weight between subsequent recapture events for captive-bred mala with initial body weight >1200 grams, released between October 1989 and August 1993.
(Does not include change between release and first capture)

Mean change in body weight between recaptures measured for:						
Males			Females			Prob. F. [#] Statistic
Animal No.	No. of recaptures after first	Percent BW change [@]	Animal No.	No. of recaptures after first	Percent BW change [@]	
TM083	10	1.61	TF176	6	1.34	
TM093	2	-0.49	TF178	9	1.86	
TM098	5	-1.39	TF196	2	6.61	
TM099	2	0.07	TF198	2	13.07	
TM307	4	-0.29	TF200	1	8.76	
TM308	2	4.36	TF203	3	4.44	
TM318	1	4.80	TF204	2	2.38	
TM319	2	-1.17	TF208	3	1.42	
TM321	1	-1.07	TF215	2	4.24	
			TF220	1	18.33	
			TF227	2	8.51	
Mean		0.71	Mean		6.45	0.0086

[@] Percentage body weight change for each individual calculated as mean percentage from values for percentage change between all subsequent recapture events.

[#] Value of F = 8.70

5.3.5 Seasonality of births

There was no apparent seasonality of births within either the captive colony or the released population of mala, with pouch young in various stages of development recorded throughout each year of the program. Figure 5.3 clearly shows this pattern of births within the release population between October 1989 and September 1993. The gap in birth records during the early part of the program relates to low recapture rates rather than a lack of actual births in the population. The appearance of non-seasonality of births within the released population is further reinforced by the consistently high proportion of females in reproductive condition, as indicated by the presence of pouch young or lactating teats, recorded during routine trapping (Table 5.9).

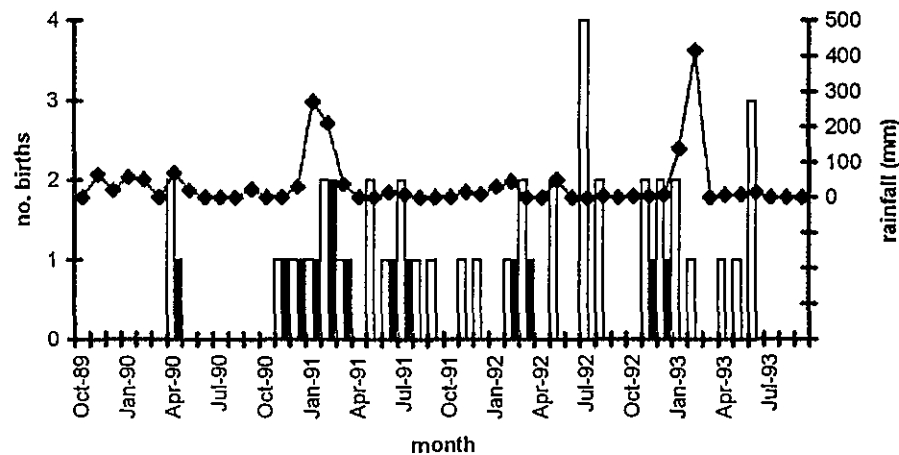


Figure 5.3 Distribution of births within the released mala population at Sangster's Bore between October 1989 and September 1993 in relation to recorded rainfall in the release area. (Rainfall over the period is indicated by the plotted line with reference to the right-hand axis. The open bars indicate the distribution of births for all births recorded within the released population, and the closed bars indicate only those births where individuals were subsequently detected as independent young).

Table 5.9
Proportion of females in reproductive condition
during 3-month periods between October 1989 and October 1993

Sample Period	No. of adult females known to be alive	No. of females recaptured during period	No. of recaptured females with pouch young	No. of recaptured females without PY but lactating	Proportion of recaptured females either with PY or lactating
Oct 89 - Jan 90	4	0	-	-	-
Jan 90 - Apr 90	2	0	-	-	-
Apr 90 - Jul 90	3	2	2	0	1.00
Jul 90 - Oct 90	4	2	0	0	0.00
Oct 90 - Jan 91	5	3	2	0	0.67
Jan 91 - Apr 91	6	6	4	0	0.67
Apr 91 - Jul 91	7	2	0	0	0.00
Jul 91 - Oct 91	8	7	6	0	0.86
Oct 91 - Jan 92	11	5	2	1	0.60
Jan 92 - Apr 92	8	4	3	0	0.75
Apr 92 - Jul 92	9	6	4	0	0.67
Jul 92 - Oct 92	11	8	5	1	0.75
Oct 92 - Jan 93	14	3	3	0	1.00
Jan 93 - Apr 93	13	5	5	0	1.00
Apr 93 - Jul 93	10	2	2	0	1.00
Jul 93 - Oct 93	11	6	3	1	0.67
Total		61	41	3	0.721

The graph of the birth dates for mala subsequently detected as independent young included on Figure 5.3 suggests a possible relationship between major rainfall events and episodes of recruitment to the population. The apparent absence of recruitment of independent young from births in April, May and June 1993 following the major rainfall event in Jan-Feb of that year is an artefact of sampling. Young born during that period would not be detected as independent young until the July, August and September period which was after the completion of intensive trapping at the site. The subject of enhanced survival of young to independence will be examined further in section 5.3.7.

5.3.6 Sex ratios

Data on the comparative sex ratios for the captive and release populations are shown in Table 5.10. In captivity the ratio of male to female births was near parity whilst for the release population the recorded higher proportion of male births was approaching significance. Interestingly the ratio of male to female animals detected as independents within the release population was also near parity suggesting a higher loss of male young due to either mortality or dispersal.

Table 5.10
Chi-square test for differences in sex ratios between captive births, births in the reintroduced population and reintroduced births detected as independent young

Situation	Sex	Observed No. O	Expected No. E	O - E	$\frac{(O - E)^2}{E}$	P
Captive	Males	60	63.5	3.5	0.1929	> 0.5
	Females	67	63.5	3.5	0.1929	
		127			$\chi^2=0.3858$	
						(df = 1)
Reintroduced (all births)	Males	23	18.0	5.0	1.3888	< 0.1
	Females	13	18.0	5.0	1.3888	
		36			$\chi^2=2.7778$	
						(df = 1)
Reintroduced (Independents only)	Males	5	6.0	1.0	0.1667	> 0.5
	Females	7	6.0	1.0	0.1667	
		12			$\chi^2=0.3333$	
						(df = 1)

5.3.7 Survival of animals born *in situ*

Between October 1989 and September 1993 a total of 15 independent *in situ* bred

mala, consisting of 7 males and 8 females, were captured at the Sangster's Bore study area. Survival timelines similar to those constructed for released animals were generated to examine the survival patterns of these individuals (Fig 5.4). The lines represent the range of dates over which each animal was known to be alive, based on a birth date extrapolated from body measurements and subsequent detection of the animal by radio-tracking and trapping. On that basis, like the timelines for the released animals, these will tend to underestimate actual survival times.

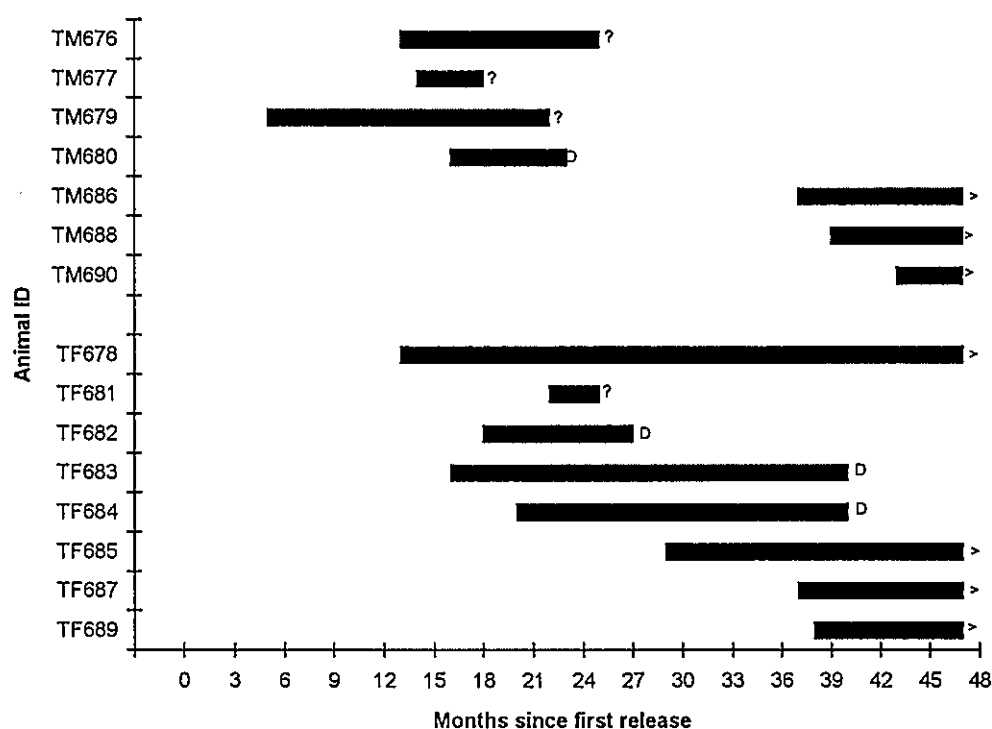


Figure 5.4 Survivorship timelines for *in situ* bred mala recorded at the Sangster's Bore site between October 1989 and August 1993. Lines commence on the date of birth, extrapolated from body measurements, and end on the last date each animal was known to be alive. D indicates confirmed death, ? indicates last known date of contact status unknown, arrow indicates known to be alive at last sampling.

It can be seen that there was considerable variation between individual animals and periods in terms of survival. Known survival times range from 3 months for one female up to 33 months for another. As with the release group, the confirmed mortalities of animals in the last quarter of 1991 relate to predation by feral cats. It is probable that a proportion of the animals whose status is recorded as unknown for that same time also fell prey to cats.

Figure 5.5 shows the estimated comparative survivorship for *in situ* bred male and female mala, for each consecutive 3-month sample period over the course of the study. Despite the small numbers of animals involved in these calculations, survivorship of the *in situ* bred animals was greater than 60% for all 3-month sample periods except Apr-Jun 91 to Oct-Dec 1991, which corresponds with the period of maximum cat predation on the population. The overall mean survivorship for the *in situ* bred animals between April 1990 to September 1993 was 0.92, compared with 0.77 for the released animals. There was no statistical difference between the values of mean survivorship (Fisher's exact test: $P=0.11$).

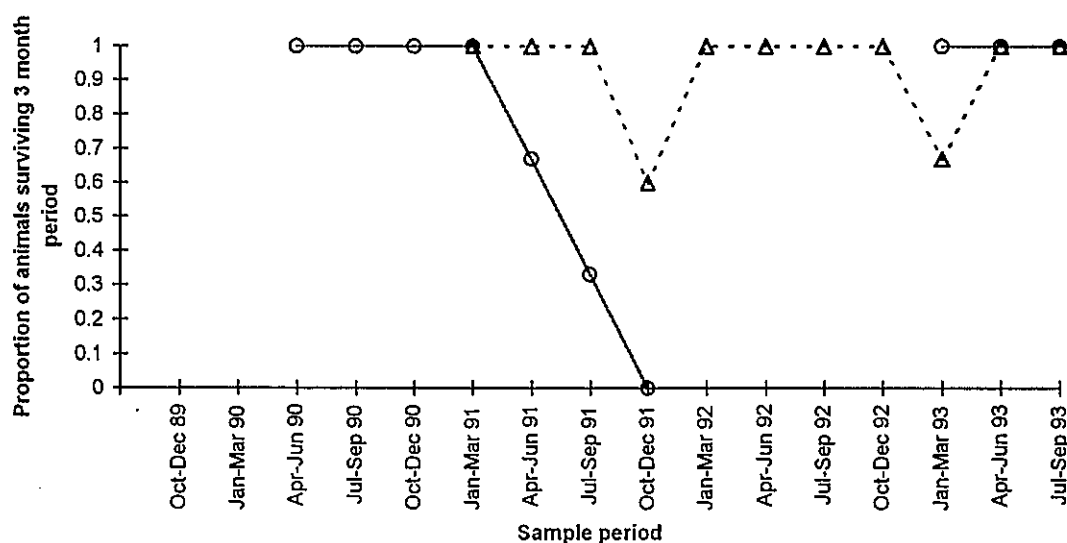


Figure 5.5 Changes in the 3-monthly survivorship for *in situ* bred male and female mala within the population between October 1989 and September 1993. Survivorship expressed as probability that an individual which is alive at time t_0 will survive to the start of the next 3-month period

Mean survivorship for *in situ* females over the period of the study was higher than the value for males, being 0.93 and 0.8 respectively; however, the difference was not statistically significant. Due to the small number of *in situ* bred animals involved in the study, no attempt was made to estimate or interpret any influence of age on survivorship.

As indicated in a previous section, the number of independent young captured during this study was low when compared with the number of pouch young detected with females, suggesting either low survival between early pouch-life and independence or low trapability. The plot of birth dates for *in situ* bred animals against rainfall (Fig 5.3) suggests that

there may be some link between survival to independence and major rainfall events. This relationship is explored further in Table 5.11, which shows the relative survival rates for pouch young born during months which have had in excess of 50mm of rainfall in either of the 2 months immediately preceding, or following the birth (wet months), compared with pouch young born during months which have had less than 50mm of rainfall in either of the 2 months immediately preceding, or following, the birth (dry months). Rainfall events greater than 50mm had previously been associated with episodes of recruitment to the population (Fig. 5.3), and appear to influence changes in diet (Chapter 7). This probably relates to the plant growth response to rainfall events of this size. A lag period of 2 months was chosen, as it represents approximately half the average pouch life for mala.

Table 5.11

Comparative survival rates to independence for pouch young born in wet and dry months
(Wet months are those with rainfall of > 50mm within 2 months pre or post the birth month)

Stage of dependence	Number of individual mala young recorded for:	
	wet months (n=26)	dry months (n=22)
No. recorded as dependent pouch young	24	16
No. recorded as independent young	9	3
% surviving to independence	37.5	18.8

Over the 48 months of the study, a total of 26 months were categorised as wet months and 22 months as dry months. The respective rates of survival to independence for *in situ* bred pouch young were 37.5% for the wet months compared with 18.8% for the dry months. Due to the small sizes of the samples there was no statistical difference between the values ($\chi^2 = 1.61$, 1 df, $P > 0.20$).

5.3.8 Population growth

Known-to-be-alive estimates for the captive and *in situ* bred components of the reintroduced population were derived from survival timelines. Figure 5.6 shows the pattern

of growth for the reintroduced population, and distinguishes the relative contributions of sequential releases of additional captive-bred animals and recruitment of *in situ* bred animals. The significant decline in the population associated with predation by feral cats is clearly evident between July 1991 and April 1992. Despite the two major periods of decline in the population, the mean rate of increase (r) calculated for the population over the length of the study was 0.104. This rate was, however, supported by the ongoing sequential release of captive animals into the population.

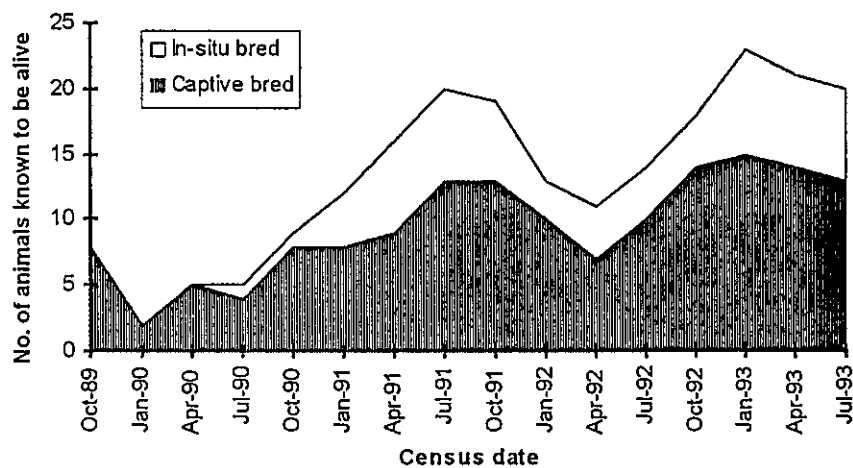


Figure 5.6 Graphical representation of known-to-be-alive estimates of total reintroduced population at the Sangster's Bore release site between October 1989 and September 1993.

The highest proportions of *in situ* bred animals in the population correspond with the pulses of recruitment associated with major rainfall events in the study area in Jan-Feb 1991 and Jan-Feb 1993. The maximum estimate of the known-to-be-alive population was 23 animals in Jan 93. It is probable that the actual population was consistently higher than the known-to-be-alive estimates, because of a combination of factors including trap shyness and dispersal by individual animals beyond the range of the established trapping effort.

5.4 Discussion

The most positive outcome of this study has been the demonstration that it is

logistically possible to reintroduce captive-bred hare-wallabies. Of the 51 captive-bred animals translocated during this program only 2 mortalities were attributed to the act of transfer. Whilst there was enormous variation in the subsequent survival of individual animals, the maximum survival period of 37 months recorded for one female suggests that under appropriate conditions the released animals were able to survive, and adapt to their new circumstances. The analysis of survival and fecundity data presented in this chapter has also served to increase our understanding of the factors which can influence the establishment, persistence and growth of a population.

Predation was clearly the major cause of mortalities within the reintroduced population over the period of this study. Whilst the total number of animals lost to predation was not extreme when considered over the 48 month span of the program, the vast majority of these deaths occurred over short spaces of time (Gibson *et al.* 1994). The overall effect on the release population in such instances was catastrophic, because given the small size of the population there was limited potential for the population to recover. This pattern is similar to that reported for reintroduction attempts involving other medium sized mammals on the Australian mainland (Short *et al.* 1992, Johnson *et al.* 1996, Christensen & Burrows 1995). Of 40 Burrowing Bettongs released in the Gibson Desert by Christensen & Burrows (1995), 11 were confirmed as having been killed by cats, and within 60 days after release no live animals could be detected.

The dynamics of small populations such as those employed in reintroductions are largely determined by the unpredictable fortunes of individual members (Caughley & Sinclair 1994). In situations where a population has been driven to a very low level because of a change in its environment, such as predation or fire, it then becomes far more susceptible to chance events simply as a result of its size. The obvious consequence of this is an increased probability of the population not persisting, but being driven to extinction. McCallum *et al.* (1995) modelled the impact of predation on a translocation of the Bridled Nailtail Wallaby. Not surprisingly, their models suggested that even moderate levels of predation substantially increased the probabilities of extinction of small translocated populations. These models differed significantly, however, in their portrayal of predation events compared with what occurred in the mala reintroductions. Both in the current program and other attempts in the Tanami, predation by foxes and cats was highly episodic rather than chronic as depicted in the models. In this way the reintroduced

population was subjected to relatively short episodes of intensive predation pressure rather than a constant predation pressure. The nature of these episodes was unpredictable and hence provided little information to direct predator control efforts.

There is a growing body of theoretical literature relating to the viability of populations in relation to their size and structure (Lacy & Clark 1990, McCallum 1995, Possingham 1996). Most such presentations are based on some form of Population Viability Analyses (PVA), which attempt to predict the probability that a population will become extinct within a certain time frame, given a set of assumptions about factors that affect a species and a specific management regime. Such an approach was applied by McCallum (1995), specifically to investigate the probability of success of a translocation for the Bridled Nailtail Wallaby, as a function of the size and structure of the initial translocated population. The results of this modelling suggest that a release of 10 pairs would be sufficient to reduce the chance of extinction from purely demographic stochasticity to less than 10%. The limitations of such models are that by their nature they depend on estimates of a large number of parameters, most of which are likely to be poorly known for an endangered species. This is particularly so in relation to estimates of survival in the field which have been shown in the present study to vary considerably, even in the absence of predation events, from those derived from captive populations. The total lack of information on the age-specific fecundity rates, and to a lesser extent survival rates for males, have to date limited the effective application of this type of analysis to the mala. Despite such limitations these models can be used as a tool for exploring the effects of certain combinations of environmental and demographic parameters on a population. In this way they can be usefully employed as an aid in planning a reintroduction program, and establishing the basis for testing modelled hypotheses much in the same way as the framework presented in Chapter 2.

Whilst two mortalities were attributed to dispersal into unfavourable habitats, there was no evidence to suggest that this was any type of homing behaviour, or that any particular group of animals was predisposed to such behaviour. What it does demonstrate is that the phenomenon of overdispersal is possible, and hence habitat selection is important as released animals may not persist or survive in unfavourable habitats. The initial incident of dispersal into unfavourable habitat occurred in relation to the first release, when groups of 4 animals (2 males and 2 females) were acclimatised together in each release pen. Nocturnal observations of these animals during

the holding phase, and subsequent examination of the carcass for the dispersing animal, suggest that there were a significant number of aggressive interactions between animals in the holding pens. It is possible that the pattern of post-release dispersal displayed by this animal was a consequence of these aggressive interactions. Whilst there was some evidence of aggression between free-ranging animals, detected as scarring and missing patches of fur on trapped animals, there was no evidence that this influenced patterns of dispersal (this is explored further in Chapter 6.). Due to the relatively small size of the reintroduced population, even at its peak, animals were most likely being introduced into an unsaturated environment and hence any aggressive interactions might be expected to be reduced compared with a more saturated environment.

The absence of any detectable differences in survival associated with age or sex may have been influenced by both low sample sizes and low average survival times, as distinct age and sex-specific survival rates have commonly been recorded in studies of macropods (Caughley 1966) and other mammals (Owen-Smith 1993). The observed pattern of significantly higher survival probabilities based on time-since-release (and hence independent of age) for females than males may, in fact, reflect the tendency for female-biased sex ratio among adult populations of macropods (Caughley 1966).

The maintenance and/or gains of body weight by released animals both immediately post-release and during subsequent captures, provides some evidence of their ability to cope with the release environment. It also demonstrates that the soft-release techniques adopted during this program suited the animals, and that no extra conditioning to the environment was required. Despite the presence of supplementary food, animals might have been expected to lose condition following release, due to both increased stress and energetic demands associated with locating food and shelter. The lack of any detectable change in body condition related to seasonal conditions is most likely related to the presence of the supplements, which were more heavily utilised by the released animals during dry periods (this is discussed further in Chapter 7).

There was no apparent seasonal influence on reproduction detected during this study, with a substantial proportion (72%) of females being detected in reproductive condition across all sample periods. The regular detection of pouch young does, at the very least, indicate that

released animals were capable of detecting mates, and that fertile matings and births had occurred. Overall the reproductive potential of the reintroduced population was very close to that recorded for the captive population; however, due to the apparently high rates of juvenile mortality, this potential was not realised in the reintroduced population.

The low rates of recruitment for pouch young to independence observed during this study are similar in pattern, if not in their magnitude, to those recorded for other macropod species. Johnson (1989) reported that mortality rates of young Red-necked Wallabies *Macropus rufogriseus* were low during pouch life and peaked just after permanent pouch evacuation. Clancy and Croft (1992) reported a similar pattern for *Macropus robustus*, in which fewer than half of the detected pouch young survived more than a short period after leaving the pouch. Whilst both studies reported high rates of juvenile mortality, neither provided any evidence of the environmental factors influencing its magnitude. Work completed by Delaney (1993) on the tropical rock-wallaby *Petrogale assimilis*, recorded survivorship rates for pouch young as low as 15% during unfavourable (dry) years. During such periods almost no young survived to sexual maturity. The subsequent improvement in offspring survival recorded during favourable (wet) years suggests that recruitment occurred principally in pulses, with a higher proportion of young from females surviving during favourable years. Newsome (1965) noted similar patterns of survival in Red Kangaroo in central Australia, and used this to generate a numerical response curve relating pouch-young survival to a derived index of aridity (Fig 5.7).

The male-biased (0.56F:1M) sex ratio of mala pouch young recorded at birth in the reintroduced population is similar to that recorded for other mammal species, whose females are philopatric and relatively long-lived (Johnson 1989). In his review of dispersal and philopatry in the macropodoids, Johnson (1989) suggested that a relative increase in the number of males produced might be a selection response to the increased cost to females of producing daughters that did not disperse and would therefore be likely to compete with their mothers for resources. Similar arguments have been used to explain male-biased sex ratios in *Antechinus* spp. (Cockburn *et al.* 1985) and a number of eutherian mammals (Clutton-Brock *et al.* 1982, Johnson 1988). The subsequent near-parity of the sex ratio for mala detected as independent recruits to the reintroduced population is likely to reflect the tendency for males to disperse from their natal range, a fact reinforced by telemetry studies

reported in Chapter 6. This dispersal-related change in the sex ratio was presumably due to either increased mortality in dispersing animals or dispersal beyond the trapping effort conducted during this study.

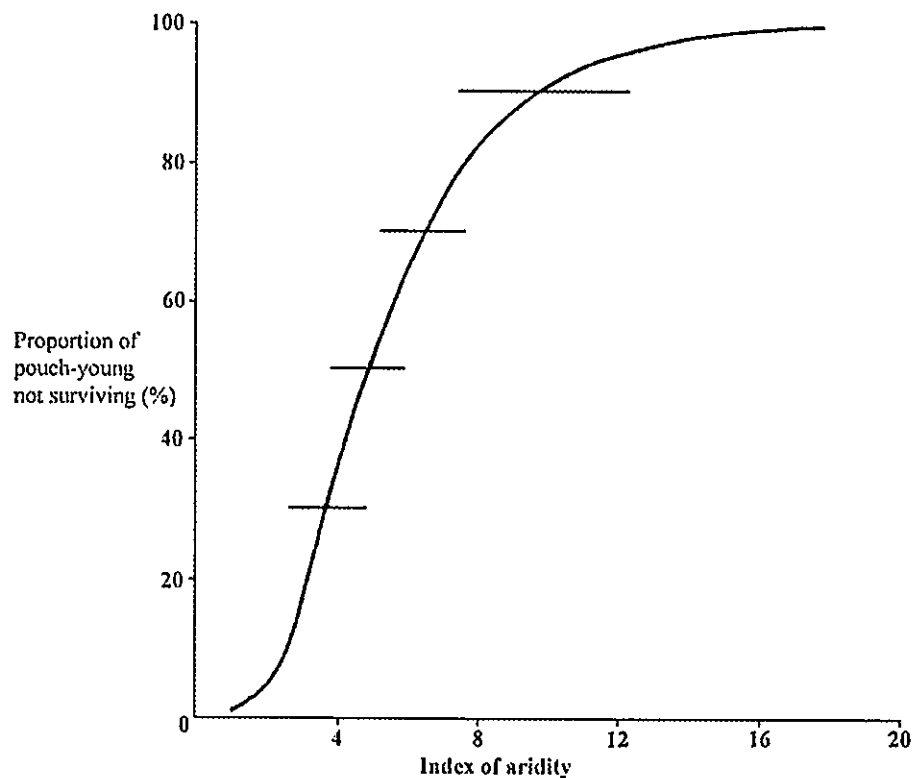


Figure 5.7 Theoretical regression of the proportion of pouch-young which do not survive to become young-at-foot on the increase in the index of aridity during life in the pouch. (Adapted from Newsome 1965)

From the analysis presented in this chapter we can now better understand the factors influencing the persistence and dynamics of the reintroduced mala population. What becomes immediately apparent is that survivorship is the prime factor influencing population persistence/growth for this reintroduced population. Even under the most favourable conditions experienced during the present study, both with respect to rainfall and predators, juvenile survival rates were low and hence natural recruitment to the population was slow. This slow recruitment rate obviously becomes more critical when added to periodic catastrophic declines associated with predation. The resulting population dynamic is extremely fragile, and at the population sizes present during this study is extremely prone to

extinction. The mean rate of increase calculated for the population, whilst positive at 0.10, was entirely dependent on the continuing sequential release of additional captive-bred animals at the site.

Chapter Six

Dispersal and Site Fidelity

6.1 Introduction

The patterns of dispersal and site fidelity by captive-bred and *in situ* bred mala within the reintroduced population will have significant effects on the long term survival and dynamics of the population. An understanding of the nature of these patterns, and the factors which influence them, will provide scope for improving the success rate for establishment of captive-bred animals back into the wild. It will also provide information that can be used to identify suitable sites for future reintroductions, based on observed patterns of movement and habitat use by captive-bred and *in situ* bred animals.

Howard (1960) described two types of dispersal: 'Innate dispersal' and 'Environmental dispersal'. Innate dispersal was defined as a spontaneous movement, the root of which lay in the genetics of the individual animal rather than any external influence. In contrast, environmental dispersal was defined as a response to unfavourable conditions, such as food or shelter availability. In general, environmental dispersal is considered less random than innate dispersal, as animals will tend to either move away from unfavourable conditions or towards favourable conditions (Caughley 1980). Since many components of an animal's environment undergo considerable changes over time, there is likely to be a significant temporal component to environmental dispersal (Howard 1960). The spatial and temporal patterning of important resources in the environment is, therefore, likely to be the major factor influencing the patterns of dispersal and site fidelity by animals being reintroduced to a site.

The analysis presented here is not intended as a study of home-range use patterns and movements in the standard sense of studies conducted on a range of species. It has been designed to investigate characteristics of dispersal from and fidelity to the release site. The results will have implications for interpreting survival of animals, selection of future release sites, and understanding the factors which affect the establishment, growth and dispersal of a reintroduced population.

Throughout this chapter reference will be made to both patterns of dispersal and dispersion by released hare-wallabies, each of which has a distinct meaning in the ecological literature. The word dispersal will be used in two contexts: firstly, to indicate the movement of individual captive-bred animals from their point of release to a home-range site (post-release dispersal), and secondly in reference to the movement by juveniles from their natal home-range to an independent home-range (juvenile dispersal). Dispersion will be used to describe the spatial pattern of spread of both individual fixes and centres of activity for the release group being monitored.

6.2 Methods

6.2.1 Base map

Because of the remoteness of the Tanami area, limited large scale map information was available for the release site. A base map of the site was therefore produced using available aerial photography and a Geographic Positioning System.

Detailed overlays were produced from 1 : 10000 aerial photography defining dominant landscape, drainage and vegetation systems within the release area. Overlays were then digitised using the ARCEDIT module of ARC/INFO (ESRI) to produce a single base map combining all attribute information. Real-world scaling was achieved by transforming the base map with reference to control points located on the ground using a Geographic Positioning System. These control points were also used to register and align animal fix maps during the data capture stage.

6.2.2 Data capture and entry

Four types of locational fix data were obtained for all radio-collared animals. These were :

- i. Triangulated daytime fixes
- ii. Physically located daytime fixes
- iii. Triangulated night-time fixes
- iv. Night-time capture locations

The methods used to obtain these locational data are described in the general methods section of this thesis (Chapter 4).

Locational fixes for each individual animal were initially plotted manually onto stable base maps of the release area. Whilst this operation was more time consuming than automated procedures, it permitted greater interpretation and inspection of raw data. This greatly facilitated the identification and correction of system or operator errors in data collection.

Individual maps of animal fixes were then digitised by Nicole de Preu, Andrew Foster and the author, using the ARCEDIT module of ARC/INFO (ESRI) to produce fix files of digital coordinates. Attribute information associated with each locational fix, including date, time and location type, were linked to coordinate files using the ARCINFO module of ARC/INFO (ESRI), after data had originally been input using DBASE III+.

6.2.3 Data analysis

Preliminary analysis of animal locational data was conducted by Nicole de Preu, using AML (Automated Motor Language) programs within ARC/INFO (ESRI) which were produced by Angus Duguid (CCNT). This included calculation of minimum convex polygon home-range areas, arithmetic centres of activity and dispersion of locational fixes between habitat types.

Detailed analysis of locational data was conducted by the author using the commercially produced software packages RANGES IV (Kenward 1990) and Excel 4.0. No attempt was made within this study to compare the relative merits of various predictors of home-range. The two predictors adopted to describe movements and dispersal by hare-wallabies, Harmonic Mean Model (HMM) and Minimum Convex Polygon (MCP), are used within their well-documented limitations (Boulanger and White 1990, White and Garrott 1990). HMM was chosen as the prime description of home-range area for this study, on the basis of its capacity to define contours of activity, and its documented lower bias in simulation trials against the four other commonly used home-range estimators (Boulanger and White

1990). MCP was used to permit direct comparisons with the many past home-range studies of macropods in which it has been applied. Differences in the home-range characteristics were examined between sexes and captive-bred and *in situ* bred animals using analysis of variance (Zar 1984). In general, statistical significance at the 5% level was used as the basis for establishing if samples were significantly different. Due to the small sample sizes involved in some comparisons, significance at the <10% level was interpreted as indicating a strong tendency towards significance.

Because of the nature of the release program and differences between individuals in the survival times (and hence the effective period that telemetry locations could be collected), Incremental Area Analysis (IAA) (Kenward 1990) was performed to determine the minimum number of fixes required to provide reasonably robust estimates of home-range. IAA provides a plot of the sequential increase in range size attributable to the addition of each new fix. Locational fixes for each animal were randomly sorted before constructing incremental area curves. The curves for all individual animals tracked during the study were combined to derive a composite incremental area plot. The desired number of fixes is achieved when range size reaches an asymptote (Kenward 1990).

In order to avoid many of the problems associated with the influence of sample size on calculations of home-range area, most of the analyses presented in this chapter focus on components of range use and movements which were independent of area. These include measurement of distances between home-range centres and ratios of core-range area to total-range area. The Harmonic Mean Centre (HMC) was chosen to estimate the activity centre of individual range areas. The HMC of an areal distribution is located where location points exhibit the highest clustering, and gives an approximation of the true activity centre.

6.3 Results

6.3.1 Tracking effort and performance

Over the course of the study all of the 51 animals released at the Sangster's Bore site were fitted with radio-telemetry collars. Due to the enormous variation in their survival times, the number of locational fixes collected for individual animals was similarly variable. During

initial releases some technical difficulties were encountered, in relation to wallabies chewing on whip antennae fitted to the telemetry collars. Modification of the collar package and antennae assemblies by the manufacturer (Sirtrack) reduced this problem to virtually nil, and subsequent rates of collar failure were low. Signal strength varied considerably in relation to the shelter sites used by animals, but signals were received up to distances of 5 km using 6m fixed-point towers.

6.3.2 Incremental area analysis

Incremental area analyses on sets of locational fixes, collected from animals released during the course of the study, indicate that robust estimates of home-range size require approximately 50 fixes. This is depicted in the composite plot of the number of fixes against percentage of range area (Fig 6.1). Whilst there is some increase in area above 50 fixes it was considered that 50 fixes would provide reliable estimates of home-range, as beyond this point there was little addition to total home-range area with the addition of extra fixes. In all subsequent analyses referring to measures of home-range area, only those individual animals with 50 or more fixes were included.

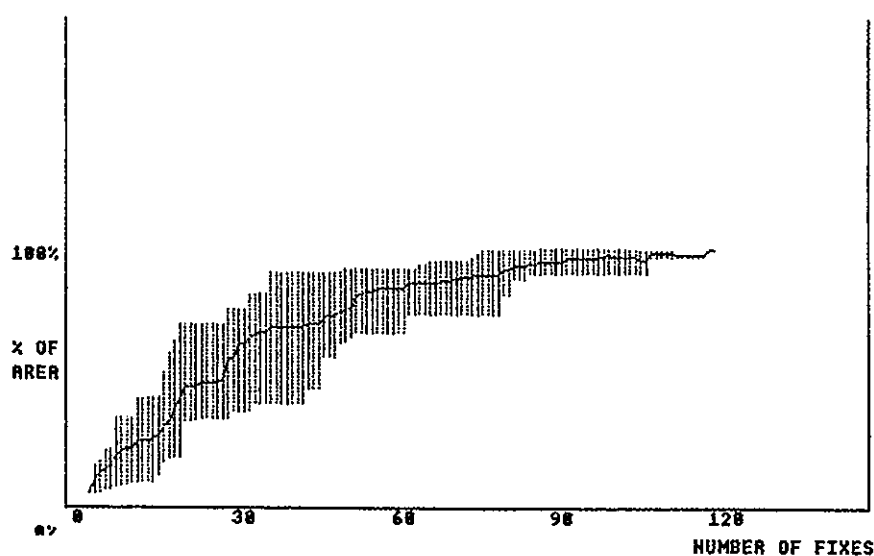


Figure 6.1 Incremental area analysis showing the effect of number of fixes on estimates of home-range size. (Shading indicates range around the mean value)

6.3.3 Post-release dispersal

First-night dispersal distances, measured as the distance between the centre of the release pen and the daytime shelter site for the day immediately post-release, were calculated for 11 of the animals released during the study (Table 6.1). Whilst several more animals were tracked following release, many were excluded from this analysis, as their first accurate post-release fix was not collected consecutive to their release date. The mean value for males ($n=3$) was slightly higher than that recorded for females ($n=8$), but the difference was not significant.

Initial post-release dispersal by released animals was further investigated by calculating 6-month home-range areas for males and females, for which sufficient fixes (50+) were collected. The 95% Harmonic Mean home-range areas as shown in Table 6.2 are extremely similar for both males and females. The 95% HM home-range was adopted on the assumption that approximately 5% of the movements by animals would be exploratory, and hence outside their normal home-range area.

Table 6.1

Distance between release pen and first daytime nest site for male and female animals at Sangster's Bore with greater than 50 independent locational fixes[#].
(ANOVA used to compare mean distances between males and females)

Distance between the release pen and the first daytime nest site for:				Sig. F Statistic
Males (n=3)		Females (n=8)		
Animal Number	Distance (m)	Animal Number	Distance (m)	
TM093	530.5	TF196	276.2	
TM303	118.6	TF198	223.6	
TM308	416.3	TF200	47.1	
		TF202	558.9	
		TF203	116.4	
		TF205	556.4	
		TF208	306.0	
		TF231	12.0	
Mean	355.1 + 212.6	Mean	262.3 + 209.8	0.5301

[#] Remaining release animals excluded from this analysis as 1st daytime location not consecutive to release date.

Table 6.2

Comparative values for the initial 6-month home-range area estimate, based on the 95% Harmonic Mean Contour measured for males and females with greater than 50 independent locational fixes.

(ANOVA used to compare mean distances between males and females)

Comparative 95% Harmonic Mean Home-ranges measured during initial 6 months following release for:					
Males			Females		
Animal No.	Number of fixes	95% HMC (ha)	Animal No.	Number of fixes	95% HMC (ha)
TM083	111	72.25	TF176	107	93.42
TM093	55	59.92	TF178	118	63.77
TM098	58	36.29	TF200	102	43.42
TM307	50	57.56	TF204	55	61.57
			TF215	52	36.1
Mean		56.50			59.66
					F Statistic
					0.0583
					Probability
					0.8161

The similarity in initial dispersal by males and females is reinforced by the comparative distances between the centre of the initial 6-month home-range and the release pen (Table 6.3). Whilst the mean value for males is substantially higher than that for the females, this is mainly due to the large displacement of Male TM098.

Table 6.3

Comparative values for the distance between the centre of the initial 6-month home-range estimate, based on the 95% Harmonic Mean Contour and the centre of the release pen measured for males and females

(ANOVA used to compare mean distances between males and females)

Comparative distance between range centre and release pen measured during initial 6 months following release for:					
Males			Females		
Animal No.	Number of fixes	Distance (m)	Animal No.	Number of fixes	Distance (m)
TM083	111	100.4	TF176	107	133.3
TM093	55	281.3	TF178	118	258.5
TM098	58	955.7	TF200	102	207.5
TM307	50	107.7	TF204	55	238.6
			TF208	39	189.5
			TF215	52	94.4
Mean		361.27			186.97
					F Statistic
					1.1399
					Probability
					0.3168

6.3.4 Site fidelity

In order to examine patterns of longer-term dispersion or fidelity to the release site, sequential analysis of 6-month blocks of fixes was conducted for those males and females for which sufficient fixes had been collected over time. The parameters selected to examine this phenomenon were:

- the absolute areas of home-ranges,
- the distances between the point of release and established range centres,
- the ratios of core home-range areas to total area ranged, and
- the degree of overlap between consecutive 6-month home-range areas.

The comparative 95% harmonic mean (HM) ranges for those animals for which sufficient locational fixes were obtained are given in Table 6.4. There were no significant differences between the 95% HM for males and females for the first 6-month block. However, for the second block, the male 95% HM ranges were significantly larger than those of females ($P < 0.05$). For the third block, the male 95% HM ranges showed a strong tendency towards being larger than those of females ($P < 0.1$). These differences clearly suggest a tendency for males to range further than females, and is graphically illustrated in Figures 6.2 and 6.3, which display the plotted 95% HM ranges for Male 083 and Female 176 respectively. The differences between consecutive 6-month HM range areas were not significant for either males or females, indicating that neither sex consistently expanded its range over time.

The comparative male and female dispersal patterns for range centres relative to the point of release are shown in Table 6.5. Whilst the mean value for the distance between the centre of the first 6-monthly HM range and point of release is larger for males than females, the difference was not significant, as the value is heavily weighted by the large initial dispersal by male TM083. There were no significant differences between males and females in the dispersal of consecutive home-range centres, nor between consecutive ranges for either sex.

Table 6. 4

Comparative areas in hectares of 95% Harmonic Mean Range for consecutive 6-month blocks of fixes, measured for male and female mala released at Sangster's Bore.
(Only animals with >50 fixes are included in each 6-month block)

	Area of 95% Harmonic Mean Range measured for:				
	1st 6 months	2nd 6 months	3rd 6 months	4th 6 months	5th 6 months
Females					
TF176	93.42	48.57	26.39	-	-
TF178	63.77	2.92	14.69	19.03	20.98
TF200	43.42	38.01	7.30	-	-
TF204	61.57	31.07	-	-	-
TF208	44.09	39.36	-	-	-
TF215	39.36	13.40	-	-	-
Mean	53.32	28.89	16.13		
Males					
TM83	72.25	153.13	67.43	107.79	-
TM93	36.29	168.15	160.22	-	-
TM98	59.92	46.29	-	-	-
TM307	57.56	34.44	-	-	-
Mean	56.51	100.50	113.82		
Sig. F Stat	0.835	0.039	0.069	-	-

Table 6.5

Comparative distances between the centres of consecutive 6-month home-ranges, using Harmonic Mean Range estimate, and the centre of the release pen measured for male and female mala.

	Distances in metres between the centre of the release pen and the centre of the Harmonic Mean Range measured for:				
	1st 6 months	2nd 6 months	3rd 6 months	4th 6 months	5th 6 months
Females					
TF176	133	120	121	-	-
TF178	258	265	174	289	116
TF200	207	142	389	-	-
TF204	239	191	-	-	-
TF208	189	569	-	-	-
TF215	94	230	-	-	-
Mean	187	252	228		
Males					
TM83	100	122	118	542	-
TM93	281	351	258	-	-
TM98	956	228	-	-	-
TM307	108	240	-	-	-
Mean	361	235	188		
Sig. F Stat	0.317	0.852	0.757	-	-

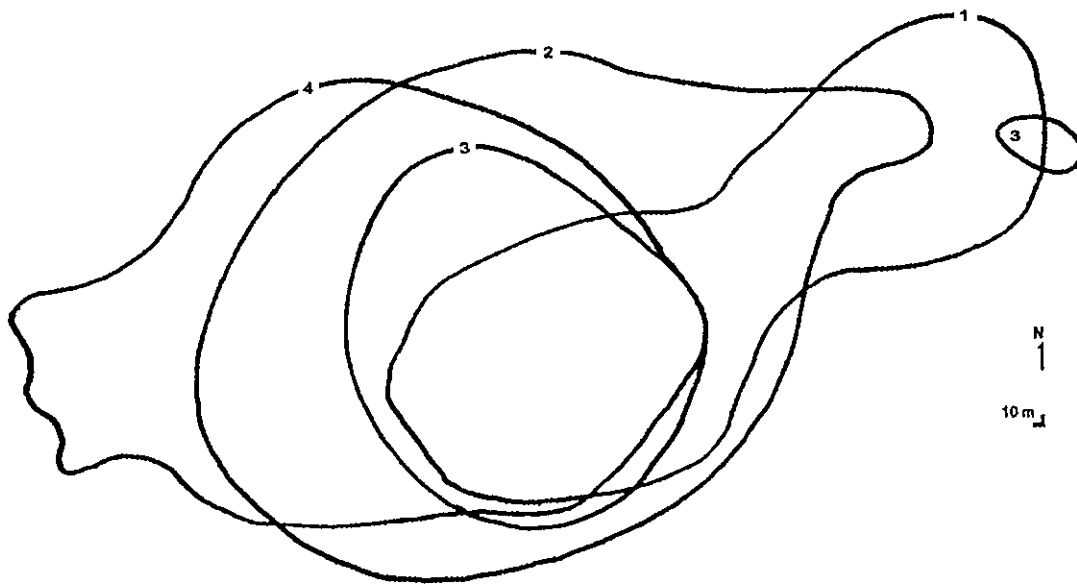


Figure 6.2 Consecutive 6-monthly 95% harmonic mean range area boundaries for Male TM083. (1: 1st 6months, 2: 2nd 6months, 3: 3rd 6months, 4: 4th 6months)

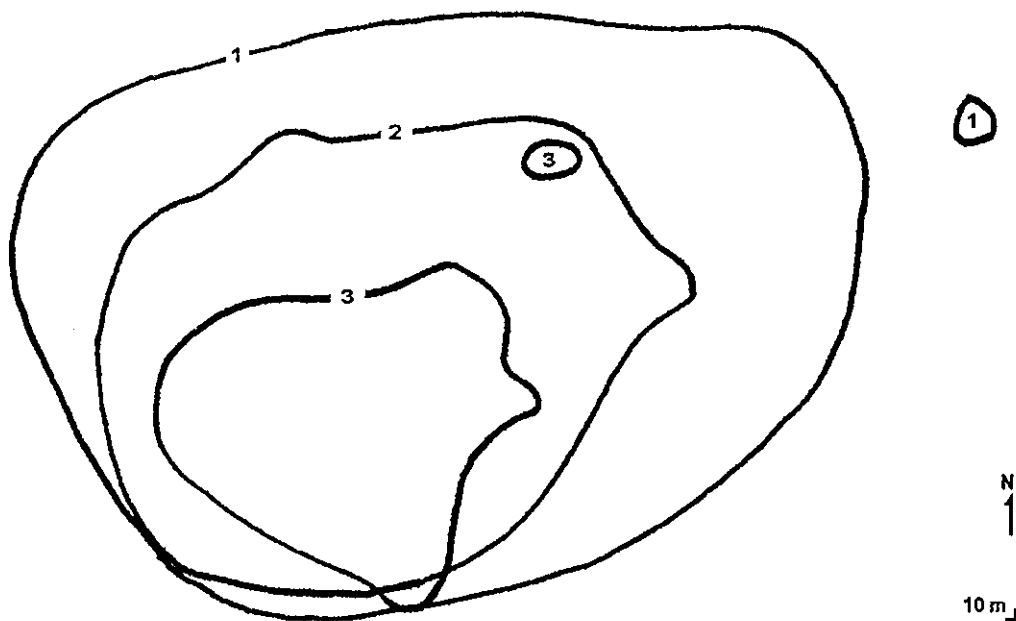


Figure 6.3 Consecutive 6-monthly 95% harmonic mean range boundaries for Female TF176. (1: 1st 6months, 2: 2nd 6months, 3: 3rd 6months, 4: 4th 6months)

Table 6.6 gives the comparative ratios of the 100% HM range estimate to the 95% HM range estimate for consecutive 6-month range-areas for male and female mala. This ratio is intended to reflect the relative extent of exploratory movement being undertaken by each sex and, by examining it over a period of time, investigate the temporal component to it. There was a significant difference in the ratios for males and females for the 1st of the 6-month blocks, suggesting a tendency for greater exploratory behaviour by males during that period. This is particularly relevant given that the 95% HM range areas for males and females were found not to differ for this period (Table 6.4). There were no significant differences between males and females for the remaining 6-month blocks, nor between the consecutive 6-month blocks for each sex.

Table 6.6
Comparative ratios of 100% Harmonic Mean range estimate to 95% Harmonic Mean range estimate for consecutive 6-month home-ranges measured for male and female mala.

	Ratio of 100% HMR to 95% HMR measured for:				
	1st 6 months	2nd 6 months	3rd 6 months	4th 6 months	5th 6 months
Females					
TF176	2.12	2.75	1.79	-	-
TF178	2.24	2.53	2.52	3.35	1.03
TF200	2.58	2.36	5.03	-	-
TF204	1.35	1.65	-	-	-
TF208	1.21	1.95	-	-	-
TF215	1.49	1.33	-	-	-
Mean	1.83	2.09	3.11		
Males					
TM83	3.66	1.67	1.79	1.47	-
TM93	1.88	2.12	1.14	-	-
TM98	1.71	1.01	-	-	-
TM307	3.35	5.24	-	-	-
Mean	2.65	2.51	1.46		
Sig. F Stat	0.089	0.483	0.291	-	-

Data describing the proportional overlap of the initial 6-month 95% Harmonic Mean range area and the next subsequent 6-month range area for captive-bred male and female mala are presented in Table 6.7. The proportion of the initial range area contained within the next subsequent range area was significantly greater in females than males. This suggests a greater stability in range boundaries for females compared with males. These patterns of overlap for

the consecutive home-range areas for a male and female mala are also illustrated in Figures 6.2 and 6.3 respectively. This is likely to be related to both the exploratory movements revealed in Table 6.6, and possibly the constant state of flux associated with the maintenance of male dominance hierarchies and mating systems.

6.3.5 Factors influencing dispersion of released and *in situ* bred mala

The patterns of dispersion of both released and *in situ* bred hare-wallabies were investigated in relation to several factors considered likely to influence dispersion, including: (i) locations of supplementary feeding points, (ii) vegetation communities, and (iii) the presence of other animals.

Table 6.7
Proportional overlap of the initial 6-month home-range area and the subsequent 6-month home-range area using 95% Harmonic Mean range estimate measured for captive-bred male and female mala with greater than 50 independent locational fixes

Proportion of overlap between initial 6-month 95% Harmonic Mean home-range and 2nd 6-month home-range measured for:							
Males			Females			F Statistic	Probability
Animal No.	Number of fixes	Proportion overlapping	Animal No.	Number of fixes	Proportion overlapping		
TM083	111	38	TF176	107	100		
TM093	55	24	TF178	118	100		
TM098	58	98	TF200	102	100		
TM307	50	100	TF204	55	93		
			TF215	52	100		
Mean		64.8			98.6	3.7208	0.0951

The mean distances between the centres of the night and day life-time home-ranges, including all the locational fixes collected for an animal over the course of the program, and the nearest supplementary feeding station for captive-bred and *in situ* bred mala are presented in Table 6.8. Whilst the mean distances were larger for *in situ* bred animals than captive-bred animals for both night and day ranges, the differences were not significant, due to the small sample of *in situ* bred animals, and the large variability. Separation of fix centres from food

hoppers differed significantly between night and day for captive-bred (but not *in situ* bred) animals; they were further from feeding stations during the day. The centre of the daytime range for the captive-bred animals was significantly further from the feeding station than the night range. This is not surprising for an animal which feeds at night, and hence has its night activity focussed towards feeding areas. The non-significance of this comparison for the *in situ* bred animals suggests that either no distinct separation occurs, and/or that animals are less focussed on the feeding stations. The patterns of use of supplementary feeders were further investigated using dietary analysis, and the results are discussed in Chapter 7.

Table 6.8

Mean values for the distance between the centres of the night and day lifetime home-range areas and the nearest feeding stations measured for captive-bred and *in situ* bred mala.

Home-range type	Distances in metres measured for:		F Statistic	Probability
	Captive-bred (n=14)	<i>In situ</i> bred (n=3)		
Night	157.3	392.9	0.730	0.500
Day	232.6	462.7	0.282	0.758
F Statistic	3.257	8.421		
Probability	0.021	0.106		

Table 6.9 describes the relative distribution of locational fixes between the two major habitat associations at the release site. When data were pooled for both sexes there was a significant difference between the proportion of fixes located in each habitat, with 69% occurring in the *Triodia pungens*-dominated habitat compared with 31% in the more open caliche areas. In light of the higher relative abundance of caliche-dominated habitat at the site, this suggests a strong preferential use of the *Triodia pungens* habitat. This is similar to the pattern described from previous studies of habitat-use by mala (Lundie-Jenkins 1994).

The influence of the presence of other animals on the patterns of dispersion of captive-bred mala was investigated by constructing histograms to display the proportional frequencies of the separation distances between simultaneously located male and female animals. This parameter was derived by first calculating the distances between individual animals for whom

simultaneous locational fixes had been obtained. For the purposes of this analysis, the locations for two individual animals were considered to be simultaneous if they were recorded within 5 minutes of each other. The resultant data-set contained the instantaneous separation distances for collared animals within the release population. Because of differences in the number of simultaneous fixes recorded for males and females, and from day and night tracking, the absolute frequencies for each class of separation distance were converted to proportions. These proportions were then used to construct histograms, to enable any patterns in relation to the separation of individuals to be investigated.

Table 6.9
Proportional distribution of day and night locational fixes
between the major vegetation types measured for captive-bred male and female mala.
(The figures in brackets are the proportional occurrence of *T. pungens* and swale habitat
within the study area.)

	Mean proportion of Locational fixes occurring in the two major vegetation types					
	<i>T. pungens</i> -dominated		F Statistic Probability	Caliche swale		F Statistic Probability
	Day	Night		Day	Night	
Males (n=10)	70	74	0.60	30	26	0.60
Females (n=13)	65	67	0.70	36	33	0.70
F Statistic Probability	0.42	0.50		0.41	0.50	
Pooled Mean (n=23)	69 (27%)			31 (73%)		0.0013

For both male and female animals, frequency histograms of daytime separation distances were clearly skewed to the right, relative to histograms of nocturnal separation distances. This is illustrated in Fig. 6.4, which depicts a histogram of the differences in the proportional frequency of same-sex separation distances from simultaneous locations between daytime and night-time locations for both male and female mala. Where the bars project below the zero line, the proportional frequency of simultaneous locations within that distance class is greater for the night-time locations than the daytime locations. Conversely, where the bars project above the line the proportional frequency of simultaneous locations within that distance class is greater for the daytime locations than the night-time locations. The skewness

displayed by both sexes is indicative of a tendency for greater separation between individual animals of the same sex in daytime shelter sites than in nocturnal feeding sites.

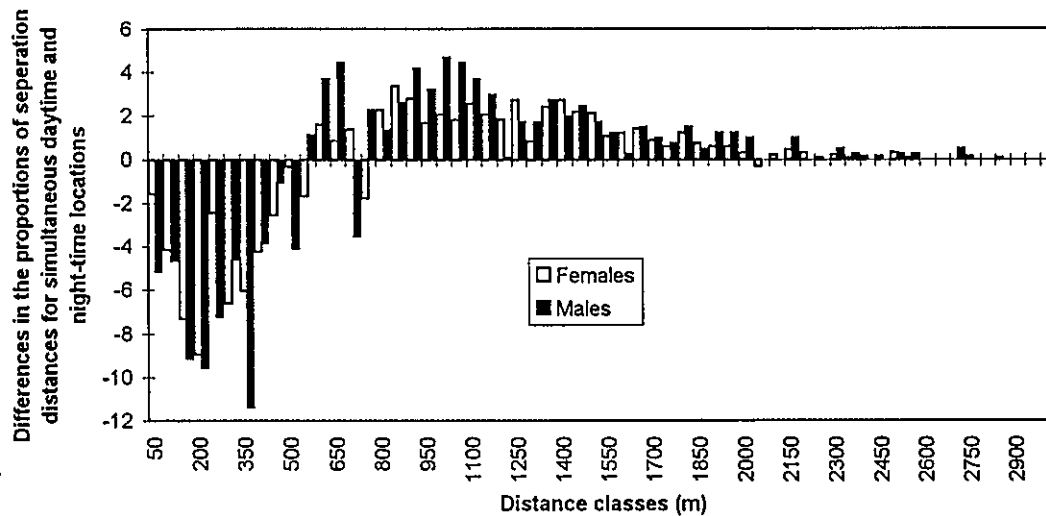


Figure 6.4 Differences in the proportional frequency histograms of separation distances from simultaneous locations between daytime and night-time locations for male (closed bars) and female (open bars) mala.

The relative tendencies of male and female animals to be located near other individuals of the same sex were further compared by constructing histograms, which displayed the differences between male and female mala in the proportional frequencies of separation distances for both simultaneous daytime and night-time locations (Figs 6.5 & 6.6). Fig. 6.5 shows the differences between the distribution of daytime separation distances for female and male mala. In regions where the graph extends above the zero line, the proportional frequencies for females are higher than the corresponding male values, and below the line male values are higher. The pattern that emerges shows a higher proportional frequency of female separations than male separations in the ranges 50-300m and 1150-1600m, and a higher proportional frequency of male separations than female separations in the ranges 500 - 1100m and 1800-2000m. The presence of two peaks for both sexes is an artefact of clumping the data from the two separate release areas. Thus the female peak at 1150-1600m, and the male peak at 1800-2000m, are separation distances between animals that have established home-ranges in the vicinity of different release pens. If we exclude these outer peaks, the remaining peaks

show a relatively larger proportion of the female separations fell within the 50-300m distance class, and a relatively larger proportion of the male separations fell within the 500-1100m distance class. This pattern suggests a greater tendency for females compared with males to occupy daytime shelter sites near animals of the same sex.

The difference histogram derived from simultaneous night-time locations for female and male animals (Fig. 6.6) does not show any discernible pattern in relative distribution of separation distances. The absolute size of the differences between the proportional frequencies for some distance classes are 2-3 times larger than the differences derived from daytime locations. However, the differences in the dominance of values for females and males virtually changes direction with each consecutive distance class. In excess of 90% of the simultaneous night-time locations for both sexes recorded separation distances less than 1200m compared with a greater spread of values for the daytime locations. If we assume that the principal night-time activity by animals relates to foraging, then it is likely that the variability in this pattern is a consequence in seasonal changes in food availability. The absence of paired peaks within the histogram for night-time locations may indicate a tendency for less separation of feeding areas compared with daytime shelter sites.

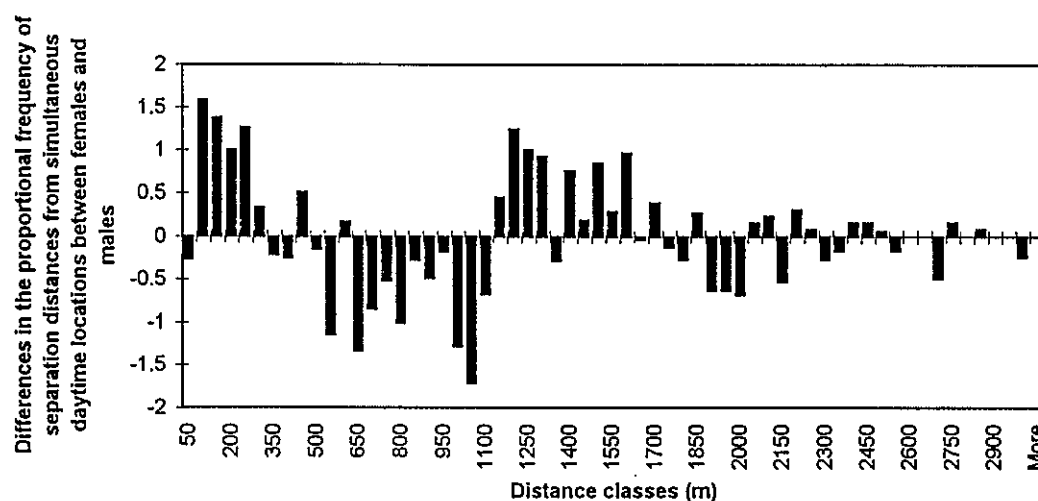


Figure 6.5 Differences between the frequency histograms for male and female mala for the proportional frequency of the same-sex separation distances from simultaneous daytime locations.
(For distance classes where the female proportion is larger, the bars project above the zero line, and where the male proportion is larger the bars project below the zero line)

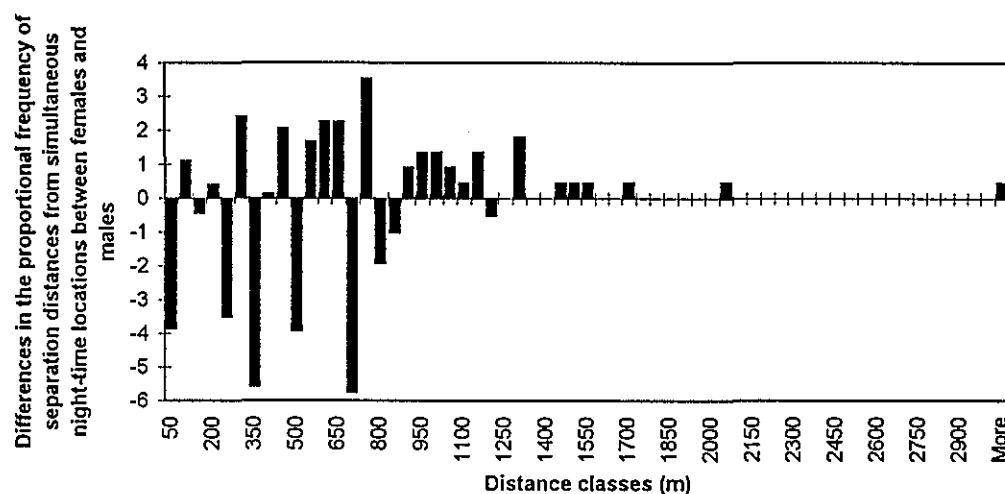


Figure 6.6 Differences between the frequency histograms for male and female mala for the proportional frequency of the same-sex separation distances from simultaneous night-time locations.
(For distance classes where the female proportion is larger, the bars project above the zero line, and where the male proportion is larger the bars project below the zero line)

6.3.6 Juvenile dispersal

Data describing the patterns of dispersal by independent young from their maternal home-ranges were collected for two mothers, each of whom reared a young of each sex whose dispersal was monitored by telemetry. This limited data set showed a non-significant tendency for males to disperse further from the maternal home-range, and to occupy an area including less of the mother's original and post-natal home-ranges (Table 6.10). In both cases the male young ranged over a greater area following independence, and occupied less of the natal home-range compared with the female young. Examples of this difference are graphically illustrated in Figures 6.7 & 6.8. Histograms of the relative frequency of different separation distances between females and their male and female offspring, determined from simultaneous locations, further illustrate the different patterns of juvenile dispersal encountered during this study (Fig 6.9). This pattern of dispersal by independent male offspring could, in part, account for the apparent change from a sex ratio that is male-biased at birth, to near parity for independent young.

Table 6.10

Separation distance between the Harmonic Mean centre of home-range areas for two mothers and their monitored independent young, measured over the same time period.

	Distance between range centres, in metres, measured for:		Mean	Sig. F Stat.
	Male young	Female young		
TF176	1211	254	732.5	0.3997
TF178	262	184	223.0	
Mean	736.5	219		
Sig. F Stat.	0.3903			

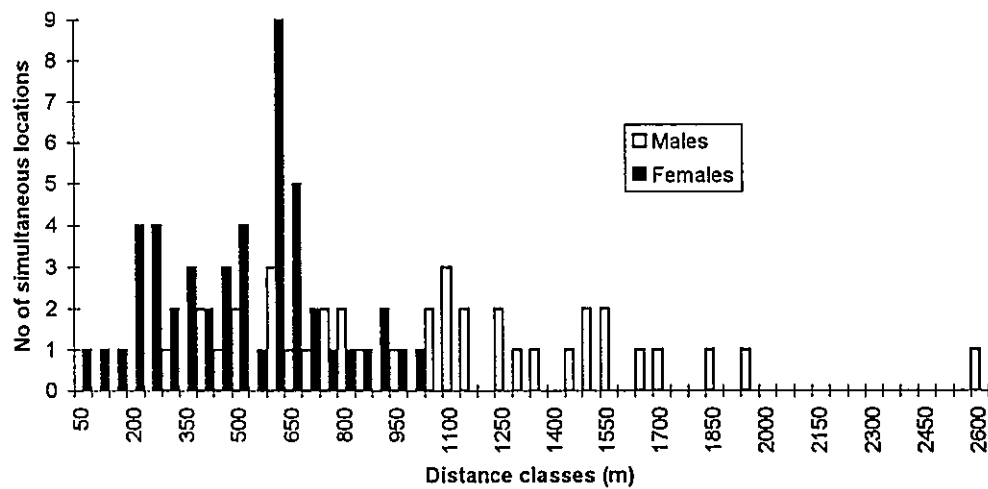


Figure 6.9 Frequency histogram of separation distances for simultaneous locations, for mothers and their male and female offspring.

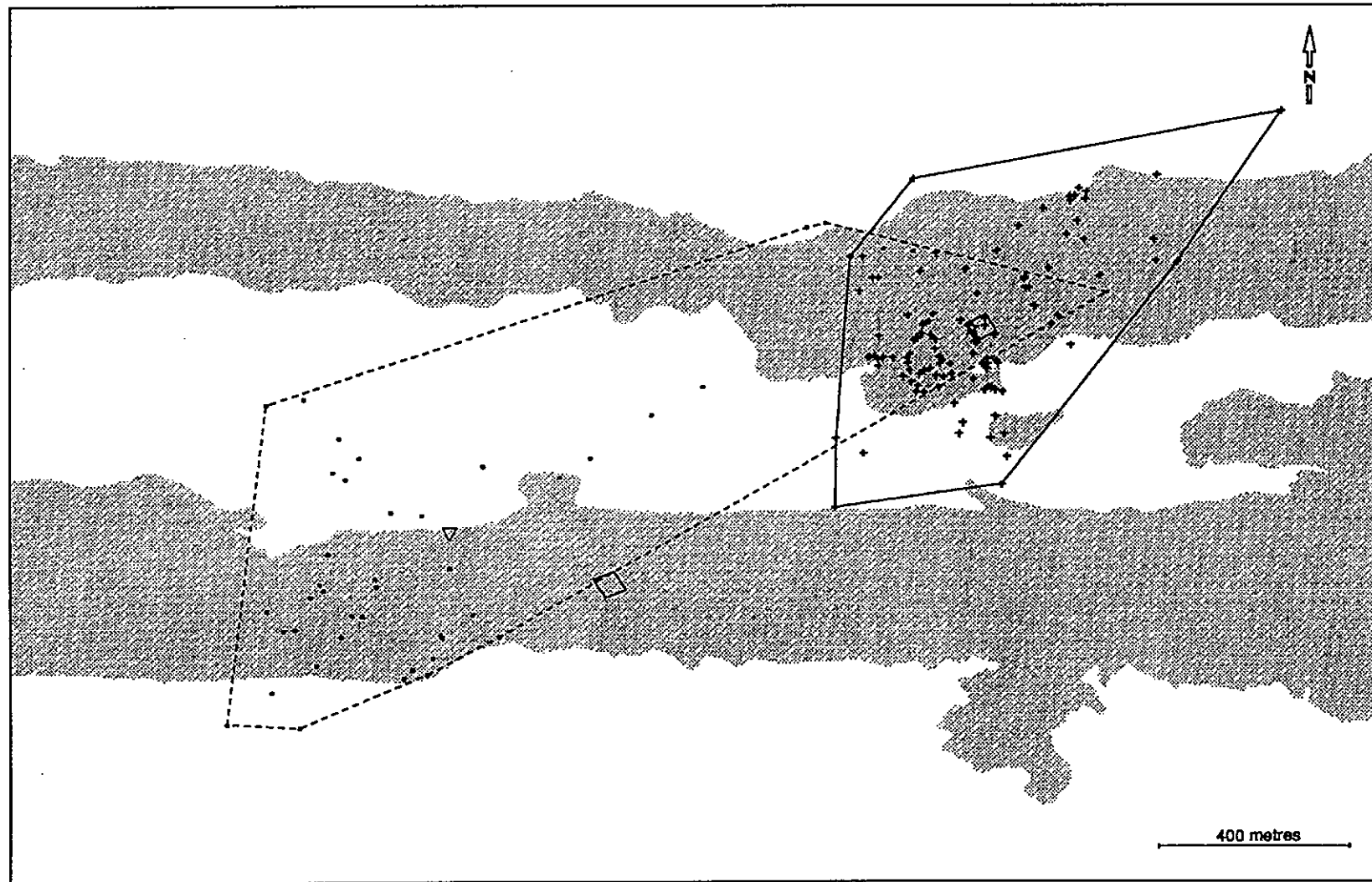


Figure 6.7 Relative location of the home-range areas for Female TF176 and her male offspring TM679 determined from locations recorded from the first capture of the offspring as an independent. Home range displayed as the Maximum Convex Polygon (MCP). (Female TF176: MCP = —, Fixes = +; Male TM679: MCP = - - -, Fixes = •; □ = release pens.)

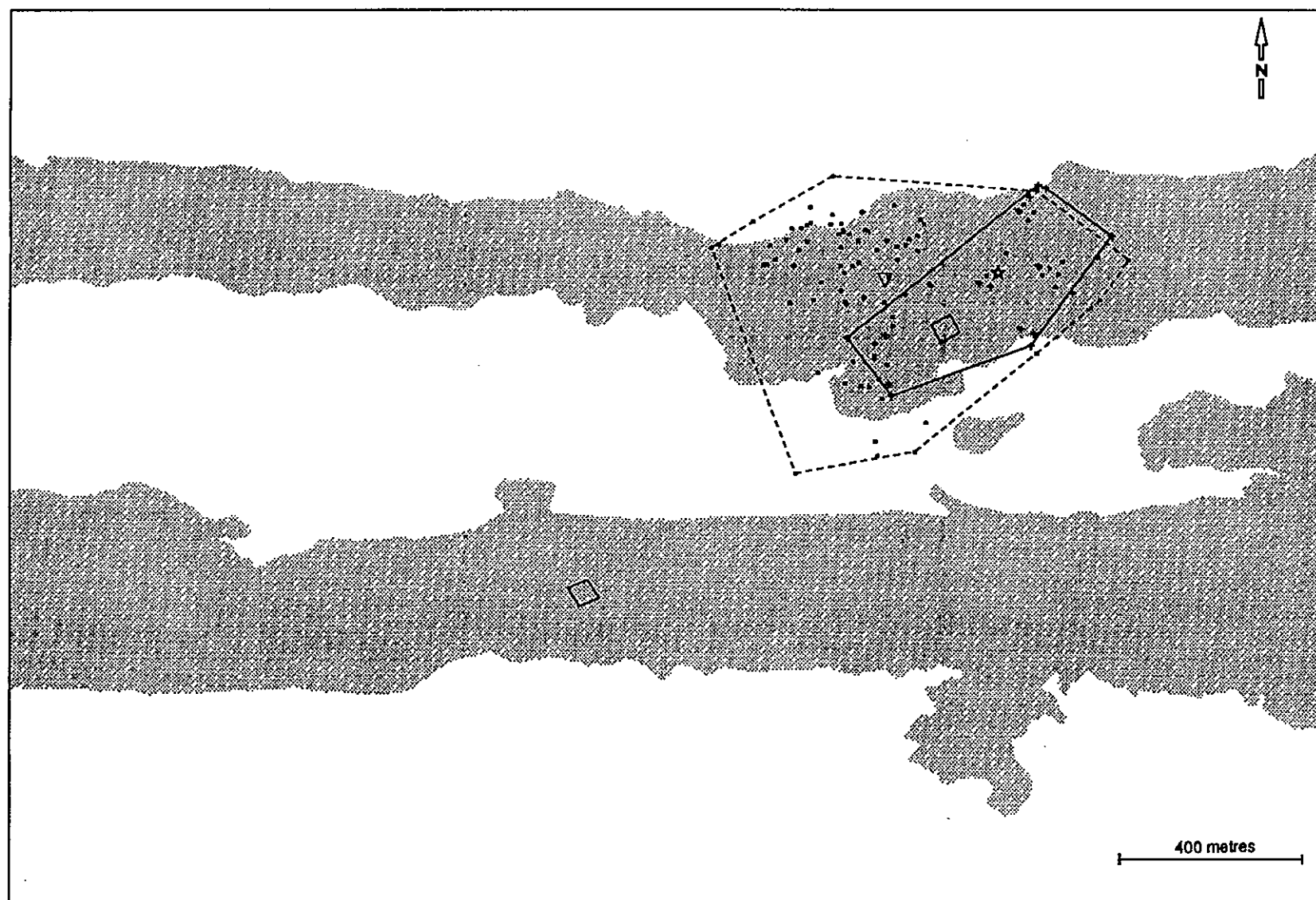


Figure 6.8 Relative location of the home-range areas for Female TF176 and her female offspring TF678 determined from locations recorded from the first capture of the offspring as an independent. Home range displayed as the Maximum Convex Polygon. (MCP). (Female TF176: MCP = — , Fixes = + ; Female TF678: MCP = - - - , Fixes = •, □ = release pens.)

6.3.7 Population dispersion and density

By combining locational fixes collected for all animals during periods throughout the study, it was possible to generate population range areas which estimated the total dispersion of the reintroduced population. During the period of most extensive tracking between January 1991 and January 1993 the collared animals, including both captive-bred and *in situ* bred animals, were spread over an average area of approximately 252 ha. Figure 6.10 displays the calculated population range against known-to-be-alive estimates of the population size, derived in Chapter 5. Except for the final dispersion estimate in January 1993, the estimates of population dispersion closely tracked the known-to-be-alive estimates for the population. This difference may be an artefact of the reduced tracking effort expended towards the latter stages of the program. Whilst the total number of fixes included in the estimate easily exceeds 50, the mean number of fixes for individual animals which comprise this total is lower than for the other periods. The mean density calculated for the period for which dispersion data were available was 0.066 ± 0.007 mala/ha or 6.65 ± 0.75 mala/km².

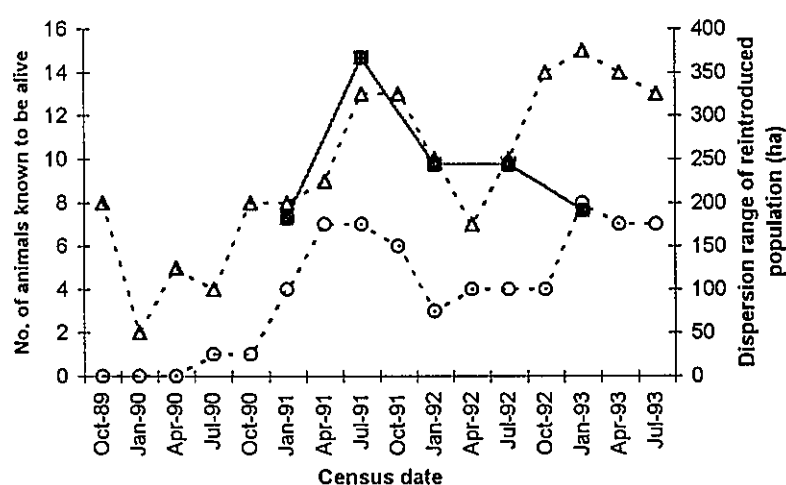


Figure 6.10. Estimated population dispersion of the reintroduced mala population for the period Jan 1991 to Jan 1993 plotted against known-to-be-alive estimates for the population. (Total population : Δ , *In situ* population : ○, Dispersion range : ■)

6.4 Discussion

The approach adopted during the present study has been to examine the characteristics of post-release dispersal, site fidelity, dispersion of individuals within the population and juvenile dispersal in the context of an establishing reintroduced population. For this reason, much of the information has been presented in a fashion that does not lend itself to comparisons with the more general forms of home-range analysis presented in the ecological literature. Whilst there is a body of published literature in relation to patterns of home-range use and movements by macropods, there is a dearth of information in relation to the fine-grained movements of macropods, in past reintroductions. This dichotomy is equally evident when the review is extended to include other groups of Australian mammals. The reasons for this lack of published information in relation to reintroductions appears to be :

- (i) The poor survival rates of animals released in the majority of reintroductions.
- (ii) The lack of an effective post-release monitoring of animals in early reintroduction programs.
- (iii) A reluctance by investigators to publish the results of reintroductions that were considered to have failed due to excessive mortalities.

The best documented exceptions to this generalisation relate to recent reintroduction programs for the Numbat (Friend 1990, Friend and Thomas 1994), Eastern Barred Bandicoot *Perameles gunnii* (Duffy *et al.* 1995) and the Brush-tailed Phascogale *Phascogale tapoatafa* (Soderquist 1995). Where possible these studies and the results from overseas reintroductions will be compared with the findings of the present study.

The absence of any significant difference between male and female mala, in the three elements of initial post-release dispersal measured during this program, is different to the trends recorded in most published studies of macropod movements, which have tended to find greater values for dispersal and home-range area for male animals. Male Eastern Barred Bandicoots reintroduced to Gellibrand Hill Park in Victoria were found both to travel further than females and to take longer to disperse (Duffy *et al.* 1995). Similarly Soderquist (1995) found large initial dispersal distances (> 6 km) by male Brushtailed Phascogales during experimental reintroductions conducted in Gippsland, Victoria. The fact that sex-related

differences are detected in mala for comparisons conducted outside this initial acclimatisation period, suggests that initial post-release behaviour is probably influenced by habitat and environmental factors that act equally on males and females. It also suggests that during this phase, social organisation and interaction may be less influential. Baker (1982), in reviewing migration and dispersal in a range of species, suggested that dispersing individuals tend to explore and assess unfamiliar habitats, and settle in the most favourable sites. The fact that during the current program animals were being introduced into an unsaturated environment may also have affected the lack of any significant difference between males and females.

The sole parameter for which there were significant differences between male and female mala during the initial 6 months following release, was the ratio of the 100% Harmonic Mean Range (HMR) to the 95% Harmonic Mean Range (HMR). This ratio was calculated to examine any differences in the tendencies of the different sexes to explore. Such an examination was based on the assumption that 5% of the movements by individual animals will be exploratory and outside the bounds of their normal home-range area. The significantly higher value of this ratio for male mala compared with females during the initial 6-month period, combined with the fact that the sizes of the male and female 95% HMR for the period were not significantly different, suggests that males undertake a greater amount of exploratory movement. Wolf (1994) suggests that the characteristics of exploratory behaviour displayed by an individual are dependent upon the resource being sought. He extended this to propose that for females of polygynous species the resource was likely to be an aspect of the habitat such as food, whereas for males it would include searching for mating opportunities, and hence was likely to require movement over larger areas. The differences in the 95% HMR areas for males and females determined for periods outside the initial 6-month period are likely to be associated with this same phenomenon.

Site fidelity is an extremely difficult characteristic to define for any species, as it is clearly a combined artefact of the resource needs and behavioural characteristics of individual animals. The very fact that site fidelity is related to resource needs means that there will be some degree of both spatial and temporal variability in the relative attachment an animal has for a particular site or habitat. Such variability is clearly evident in the measurements for the dispersion of home-range centres, for both male and female animals, from the point of release.

The within-sex variance for both sexes was extremely high for all periods, and there were no distinct patterns in relation to either sex or time-since-release. In order to examine fidelity to the release site, this variability should, however, be distinguishable from any consistent unidirectional movement by an animal, which might suggest low fidelity or rejection of a site. Whilst there were 2 cases of animals dispersing into unfavourable habitats immediately following release (Chapter 5), in the majority of cases there was no evidence of animals continuing to disperse away from their point of release. Females, in fact, showed a tendency for substantial overlap (>90%) between consecutive 6-month home-range areas. The lower tendency for home-range overlap by male mala may again be related to greater amount of exploratory behaviour by males leading to larger shifts in consecutive range areas. The fact that the released animals did not show any continued dispersal from the release site indicates that the immediate environment provided them with the various resources they required for survival.

The observed partitioning of activity between the two different vegetation communities at the release site is similar to that described from faecal pellet surveys conducted by Lundie-Jenkins (1993) on the wild population of mala which previously occupied the site. Whilst the data from the present study is not as detailed, it is still apparent that movements and dispersal by animals are influenced by vegetation cover. The distinct partitioning relates to the relative resource needs satisfied by the different communities. The mature dense spinifex cover of *Triodia pungens* fulfils the daytime shelter requirements of the mala and provides protective cover for long-range movements by animals. In contrast, the more open caliche vegetation acts principally as a nocturnal feeding area, and hence its pattern of use is far more concentrated. Confirmation of this pattern of habitat use has implications in relation to the location of release sites. Location of a release site in an area containing habitat known to be favoured for movement and shelter by mala would presumably promote more natural and gradual dispersal by *in situ* bred animals. Sites where the available cover is greatly fragmented or extremely dense would tend to restrict dispersal, as casual observations suggest mala are less likely to move through either very open, or overgrown, vegetation.

In addition to the influence of habitat, it was apparent that the location of supplementary food sources, and the proximity of other animals, had some effect on the dispersion of individual animals within the population. The tendency for animals to locate with

respect to artificial food sources has been previously examined for bandicoots (Broughton & Dickman 1991) and sugar gliders (Smith pers. comm.). Both studies found tendencies by resident animals to shift both their home-range areas, and centres of maximum activity, to utilise artificial food resources placed in their respective environments. As mala are nocturnal feeders, it is not surprising that the night-time ranges of the animals released at Sangster's Bore were significantly more closely aligned to the supplementary food sources than ranges plotted from locations of daytime shelter sites. It does, however, serve to confirm the pattern suggested by other data whereby mala tend to be relatively solitary animals, occupying discrete individual shelters, and aggregating on favoured resource patches. The proportional frequency histograms of separation distances between individual animals' daytime and night-time locations, for both male and female mala, provide further evidence of this pattern. This separation appeared to be less distinct for the *in situ* bred animals, as was their tendency (insignificant because of small sample sizes of *in situ* bred animals) to locate adjacent to a supplementary feed point.

Examination of the influence of other animals of the same sex on the patterns of dispersion within the population revealed a trend towards greater separation distances between the daytime shelter sites of males than of females. No such relationship was reflected in a similar analysis of night-time locations. The increased separation of males is likely to reflect some population structuring, and is supported by observations of aggression between male mala at the release site. On a number of occasions during trapping operations, male mala captured in nearby traps showed scarring and hair loss similar to that seen in captive males as a result of fighting. The occurrence of such conflicts within the reintroduced population is surprising given the low densities at which animals occurred within the release area, and the lack of any physical barriers to dispersal by animals. The fact that there was no pattern in the separation distances for night-time locations is again suggestive of the tendency for mala to aggregate at night on rich resource patches. The dispersal of both the supplementary feeding points and natural feeding areas within a release area will clearly influence the extent to which this aggregation occurs.

The characteristics for the home-ranges and spacing behaviour of mala recorded during this reintroduction program closely fit the Type 2 social type described by Croft (1989), and

hence is similar to that determined for Long-nosed Potoroo *Potorous tridactylus* (Kitchener 1973) , Brush-tailed Bettong *Bettongia penicillata* (Christensen 1980) and Red-necked Pademelon *Thylogale thetis* (Johnson 1980). Croft (1989) generalised that the common features of these type 2 species were that they are often solitary but aggregate on favoured resource patches, use closed shelter sites, are nocturnally active and forage in or close to cover. Whilst the present study did not examine the existence of dominance hierarchies amongst males, there was some evidence that higher ranked males had larger home-ranges centred on the densest part of the overall reintroduced population. During the first 3 years of the program, this dominance appeared to be held by a single male (TM083) who consistently maintained the largest home-range of the males monitored. During the last 6 months of monitoring described in this thesis, the range area for TM083 showed a dramatic reduction in size and a substantial shift to the periphery of the population's range. This coincided with the establishment of a large home-range area, central to the population's range, by a younger male. Such a pattern is also consistent with the Type 2 social structure described by Croft (1989)

Despite the small number of dispersal events by juvenile mala monitored during the current study, it is apparent that there is a tendency for male offspring to disperse further from the natal home-range than females. In his review of dispersal in macropodoids, Johnson (1989) concluded that dispersal appeared to be predominantly by sub-adult males. Of the nine species considered in his review dispersal was male-biased in eight. The exception to this trend was *Potorous tridactylus* in which males and females were equally likely to disperse. Whilst the patterns themselves are obvious enough, the proximate causes of dispersal by juveniles are, however, not easy to discern. Johnson suggested that natal dispersal in macropods may be triggered by some aspect of the maturation process itself, as it regularly coincided with the attainment of sexual maturity. He also argued that there was little direct evidence that dispersal by sub-adult animals is initiated by extrinsic stimuli. Observations of captive mala (Lundie-Jenkins 1993) have recorded significant levels of aggression between females and sub-adult male offspring, although this may be an artefact of captive containment. In captivity this aggression has resulted in serious injuries to sub-adult male offspring, which are limited in their ability to avoid the mother's aggression due to containment. In order to clarify the process, more detailed monitoring of females and young than conducted in the present study would be required.

Measures of the total dispersion of the reintroduced population may provide a basis for estimating the area of habitat required to establish a viable population. The mean population dispersion estimate of 252 ha, containing an average density of translocated mala of 6.65km^{-2} , suggests that an area of between 750 to 7500 ha would be required to establish a viable population of 50-500 mala. This calculated range takes account of the two alternate hypotheses in relation to minimum viable populations which propose either 50 (Caughley & Sinclair 1994) or 500 (Franklin 1980). The close correlation between the estimate of population dispersion and known-to-be-alive estimates for the population further strengthens the claim for applying the data as a basis for estimating the area of suitable habitat required at a potential release site in order to establish a viable population. Differences in both the level and patterning of productivity at sites will influence the dispersion of released individuals, and hence the dispersion described from this study is a reflection of the manner in which this spinifex system satisfies the needs of the mala.