Population Modelling the Yellow-footed Rock-wallaby (*Petrogale xanthopus xanthopus*) in space and time.

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Abstract

Conservation biology is primarily concerned with the amelioration of species decline. The Yellow-footed Rock-wallaby (*Petrogale xanthopus xanthopus*) is a medium-sized Macropod that inhabits the semiarid rangelands of South Australia and New South Wales. Its conservation status is Vulnerable C2a(i). In this study, population modelling, spatially explicit habitat modelling and Population Viability Analysis (PVA) have been used to better understand the factors that affect the abundance and distribution of the *P. x. xanthopus* in South Australia. The processes that drive the population dynamics of a species operate at different scales. As such this research involves a collection of several inter-related and scale-specific empirical studies that provide insights about the population dynamics of *P. x. xanthopus.* Each of these studies captures environmental, demographic and behavioural process acting on the population at different scales. These include the analysis of relative abundance data derived from an aerial census, mark recapture sampling of demographic parameters in relation to rainfall patterns and a collection of habitat models derived at different scales using presence-absence data. Spatially explicit PVAs enable the population dynamics of a species to be modelled in space and time. Using these data, a PVA is conducted to explore and rank the importance of the factors that threaten this species and help guide their future monitoring and management. Movement is also a key issue when considering problems such as isolation and inbreeding. Given that little is known about the dispersal behaviour of this species, a range of different dispersal behaviours are also simulated in the PVA using random and non-random mating algorithms, to estimate the potential for inbreeding.

Declaration

I declare that this thesis does not incorporate without acknowledgement any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge it does not contain any materials previously published or written by another person except where due reference is made in the text.

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CHAPTER 1

General Introduction

1.0 Introduction

Conservation biology is primarily concerned with the amelioration of species decline. It has evolved as a multidisciplinary science, bringing together the fields of ecology, genetics mathematics, geography, animal behavior, chemistry, philosophy and sociology (Burgman and Lindenmayer, 1998). It is a relatively new synthesis involving the study of human impacts on biodiversity and the evaluation of management solutions usually using models (Caughley and Gunn, 1996; Shultz et al, 1999).

The body of theory related to the conservation of species has its roots in the development of the equilibrium theory of island biogeography (MacArthur and Wilson, 1967), metapopulation models (Levins, 1970) and source-sink theory (Pulliam, 1988). Lidicker (1995) defines a metapopulation as an assemblage of local populations or "demes" of the same species connected by dispersal. As metapopulation persistence requires a balance between local extinction and recolonisation (Hanski, 1996), the persistence of metapopulations is related to the problem of connectivity (Hansson, 1995). In this study, metapopulation dynamics and the problem of connectivity are explored for a single species, the Yellow-footed Rock-wallaby (*Petrogale xanthopus xanthopus*).

The processes that drive the population dynamics of a species operate at different scales. For example, a metapopulation occupying an entire landscape may maintain a relatively constant population level while local populations fluctuate according to local environmental conditions and the presence of other species. Hence scale is an important issue in the science of conservation biology and researchers must have a clear understanding of scale-dependent processes. This also emphasises the importance of appropriate data collection strategies that consider spatial and temporal scales (Bissonette and Broekhuizen, 1995; Merriam 1995; Pickett and White 1986; Forman and Gordon 1986). Accordingly, data have been collected and analysed in this study across a range of scales and the discussions following acknowledge the scale domains of each data collection strategy.

Over the last two decades, mathematical models have been increasingly used in predictive population ecology (Stephens et al, 2002). Population Viability Analysis (PVA) is a computer modelling tool used to assess how stochastic events through environmental, demographic and genetic processes affect the probability of extinction of a population sometime into the future (Lindenmayer et al, 1993; Lindenmayer and Possingham, 1994; Possingham et al, 1993; Beissinger, 2002; Caswell, 2001; Marmontel et al, 1996; Morris and Doak, 2002; Reed et al, 2002). The causes of decline in complex environments where there may be many threatening processes, are often difficult to measure empirically. As empirical studies often require a long-term commitment, there is also a very real danger that the species may become extinct during experimentation. A primary role for PVA is to assess these threats in relation to the probability of extinction and facilitate input into a formal decision making process that guides future management and monitoring strategies (Possingham, 2001). In this study, a novel spatially-explicit individual-based PVA approach is presented, which models individual behaviour and explores the genetic and demographic consequences of a range of ecological processes for *P. x. xanthopus* to help guide the management and highlight priorities for future research.

The analysis of the relationship between a species and its environment falls more generally under the guise of habitat modelling or species distribution modelling. Increasingly ecologists are being required to produce estimates of species distributions for conservation and biodiversity programmes or seek to find potential past, present and future habitats in the landscape to better target restoration efforts (Lehmann et al, 2002). Habitat models are also used to represent the landscape in spatially-explicit PVAs. In this study, several new approaches will be used to model the distribution of this species and provide a habitat quality landscape in the PVA.

1.1 *Petrogale xanthopus xanthopus*

P. x. xanthopus is a medium-sized Macropod that inhabits the semiarid rangelands of South Australia and New South Wales. A second sub-species *P. x. celaris* occupies a smaller area in Queensland. The first extensive research and regional field survey of *P. x. xanthopus* in South Australia was conducted in 1980 and 1981 by Copley (1981) for the Nature Conservation Society of South Australia, with the aim of establishing the geographical range of *P. x. xanthopus*. Comparing this work with historical data suggested that the species had declined since early European records, despite maintaining its former geographical extent in South Australia (Copley, 1981). The factors that are thought to have contributed to this decline include competition from

introduced herbivores and predation, primarily from foxes (Copley and Alexander, 1997; Hornsby, 1995a; Lim et al, 1987; Lim and Giles, 1987).

This species has been chosen as the focus of this research for several reasons. Firstly, its conservation status is Vulnerable C2a(i). This rating applies when the population size is estimated to number fewer than 10,000 mature individuals and no subpopulation is estimated to contain more than 1000 mature individuals (IUCN, 2003). Secondly, the species has been designated a key indicator of rangeland health in the Flinders Ranges, Olary Hills and Gawler Ranges of South Australia, as part of a rangelands restoration program in South Australia called *Bounceback*. *Bounceback* is a priority Natural Heritage Trust (NHT) rangelands project with considerable funding also provided by the Department for Environment and Heritage (DEH), South Australia. Finally, the biology of the species is relatively well known compared with many other species. For example, in South Australia there have been several behavioral studies conducted by Hornsby (1978; 1981; 1995a; 1995b; 1997), ecological studies by Lim (1987) and Lim et al (1987), habitat and distribution studies by Copley (1981; 1997; 1983), and studies related to diet in South Australia by Copley (1983) and Lapidge (1997; 2001). Interstate, there have been ecological studies by Sharp (1997a; 1997b; 2002; 2000), biological studies by Poole (1985), genetic research by Eldridge (1997) and genetic studies related to population structure by Pope (1993) and Pope et al (1996).

Extensive aerial monitoring of the species has also been carried out by the DEH since 1980 over much of the geographical range of the species (Alexander et al, 1993). This information is used by DEH to measure the response of the species to management strategies. While these data appear to indicate an increase in the abundance of *P. x. xanthopus* in response to management strategies in some areas, there remains other areas where threat abatement strategies are being applied but there has only been a limited response. Additionally, despite all of the studies previously listed, little is known about the dispersal behavior of this species (Sharp, 2002) when the degree of connectivity between local populations may be important for maintaining metapopulation viability. This also places some doubt about the utility of using population trends alone to guide the management of the species.

1.2 Research Aims

In this study, population modelling, habitat modelling and Population Viability Analysis (PVA) are used to better understand the factors that affect the abundance and distribution of *P. x. xanthopus* in South Australia. The aim of this study is to critically analyse a range of empirical data collected at a different scales and use population modelling to guide future management and monitoring of *P. x. xanthopus*.

1.3 Thesis Outline

This study includes a collection of three interrelated empirical studies that measure the population dynamics of *P. x. xanthopus.* Each of these studies captures different environmental, demographic and behavioural process acting on the population at different scales. They include the analysis of population summary data derived from an aerial census of the species over a large geographical area, detailed mark recapture sampling to estimate demographic parameters and a collection of habitat models derived at different scales using presence-absence data from aerial and ground observations. The latter part of this thesis describes a PVA that is used to explore and rank the importance of input parameters representing different ecological processes to help guide future monitoring and management of the species. Data derived from the results presented in the earlier chapters are used in the PVA model in Chapter 6.

The aim of Chapter 2 is to present a range of summary population parameters that have been derived from the aerial survey of *P. x. xanthopus* by the DEH. DEH has been conducting aerial surveys of *P. x. xanthopus*, since the early 1980's. These surveys have been conducted over a large geographical area of South Australia. In semiarid environments, rainfall patterns directly affect the herbivory. Hence, these population trends have been modelled in relation to rainfall patterns. The utility of using summary population parameters in affecting management priorities for this species is also discussed.

The primary aim of Chapter 3 is to compare a range of demographic parameters at two sites in the Flinders Ranges that are under different pest management strategies. Moreover, Chapter 3 attempts to answer the following questions:

1. Does survival differ between sex, stage and location?
2. Does rainfall, as a surrogate of food resource availability, affect survival?
3. Does animal condition vary with location?
4. Does fecundity vary with location?
5. Does fecundity vary with rainfall?

Here, age-specific survival and fecundity are estimated for two sample populations using a mark recapture method.

In Chapter 4, habitat models for *P. x. xanthopus* are presented at two different scales. At one scale an aspatial approach is presented based upon presence-absence data and habitat characteristics collected in the field at 150 sites from 2000 to 2002 in the Flinders Ranges South Australia. Spatially explicit habitat models are also presented at a broader scale. Here several models are tested including some novel approaches that deal with interactive explanatory variables, non-linear correlations and categorical variables. These include Regression Trees and Generalised Additive Models (Austin, 2002) as well as data mining methods called Multivariate Adaptive Regression Splines (Friedman, 1991) and Polynomial Multivariate Adaptive Regression Splines (Stone et al, 1997). Spatial autocorrelation is also modelled explicitly in this study following the work carried out by Besag (1972) and Augustin et al (1996). The prediction surfaces of two of these approaches are then derived in a Geographical Information System (GIS). All spatially explicit habitat models use presence-absence data based on aerial survey data, ground survey data and biophysical data including climate, vegetation community and topographical data. In Chapter 6, the prediction surface is also used to underpin a spatially explicit PVA model of this species. A second aim of Chapter 4 is to assess any change of status of *P. x. xanthopus* at the sites visited by Copley (1981) in 1980.

Incidence functions focus on patch processes rather than demographic processes. For large populations, models that employ incidence functions are generally more appropriate to describe extinction and colonisation probabilities in terms of patch size and isolation (Hanski, 1994). In contrast, PVAs that employ a bottom-up approach by including biological parameters such as

fecundity, survival, dispersal and disturbance events are more appropriate for smaller populations (Ball, 2000; Beissinger and Westphal, 1998). This is the approach taken in this study.

In Chapter 5 a novel dual-sex, individual-based spatially explicit PVA is described. This has been written using the C++ programming language and interfaced with a GIS. Individual-based PVAs that simulate the fate of both sexes are thought to be better suited than single sex population models for small population studies where the distance between potential breeding partners may adversely affect the population's viability (Allee et al, 1949; Turchin, 1998). While this PVA is used to specifically model *P. x. xanthopus* (in Chapter 6), the application has been written in a generic form, such that other semi-arid mammals in possible future studies can also be modelled.

Movement is also a key issue when considering problems such as isolation and inbreeding. Consequently, the model incorporates a range of dispersal modes. For example, passive dispersers randomly move through the landscape, whereas active dispersers actively search for suitable habitats. Finally, an inbreeding sub-model is described. This allows one to gain better insights about the effects of landscape and movement on inbreeding depression. An inbreeding coefficient is simulated in two ways. Following the work carried out by Daniels et al (2000), the first approach involves tracking the mean kinship coefficient, a relative estimate of inbreeding, from a simulated pedigree tree of a target population. The second approach assumes random mating and uses Wright's (1969) equation to estimate relative inbreeding.

In Chapter 6 the PVA application is used to model *P. x. xanthopus* population dynamics using data presented in earlier chapters. This is not intended to provide definitive estimates of expected extinction times, but to focus on the parameters that most affect the viability of the species. The first aim of Chapter 6 is to use PVA to explore how small changes in survival affect the probability of extinction and compare mark recapture estimates of survival collected in this study and Sharp's (2000) study. The second aim of this chapter is to use sensitivity analysis to assess what factors are most likely to affect the viability of a metapopulation of *P. x. xanthopus* in the Northern Flinders Ranges of South Australia. This requires the habitat model derived in Chapter 4. Sensitivity analysis in this context is used to set priorities for further monitoring and management. The dispersal behaviour of this species is largely unknown. Hence the third aim of Chapter 6 is to explore different dispersal behaviours and how they are likely affect inbreeding.

In Chapter 7, an overall summary of the findings in this study is provided including an assessment of the utility of PVA to guide future monitoring and management of *P. x. xanthopus.* Future model refinements and priorities for further research are also discussed.

CHAPTER 2

An analysis of the aerial survey of the Yellow-footed Rock-wallaby (*Petrogale xanthopus xanthopus*) in South Australia.

2.0 Introduction

The Department for Environment and Heritage, South Australia (DEH) has been monitoring *Petrogale xanthopus xanthopus* on a regional scale in South Australia for over a decade. Wildlife managers generally use population monitoring to ascertain the response of a species (or group of species) to a particular management strategy (Southwell, 1989). At a regional scale, aerial surveys of *P. x. xanthopus* have been favoured above other survey techniques for estimating relative abundance. This is largely because of the cost associated with field surveys and the relatively inaccessible country in which *P. x. xanthopus* is found.

Relative abundance measures, such as growth rates, can be used to describe population trends. These measures can be derived from a finite series of abundance indices (Caughley, 1977a). They provide a more general level of abstraction and summarise the underlying population processes (McCallum, 2000).

The aim of this chapter is to explore a range of summary population parameters that have been derived from the aerial survey of *P. x. xanthopus* by DEH. In semi-arid environments, rainfall patterns directly affect the herbivory. Hence, these population parameters have been modelled in relation to rainfall patterns. This is followed by a discussion about the utility of using summary population parameters in affecting management priorities for this species.

2.1 Biases in Aerial Surveys

Caughley (1977a) lists three approaches that estimate abundance: the population size, where a population can be delineated within a distinct boundary; an absolute density, in the absence of a boundary; and a density index. Ascertaining population size is not appropriate for most macropod populations and absolute density estimates are expensive particularly over large areas. For this reason density indicies are preferred (Hone, 1988). A density index is a proportional estimate (called a relative estimate) of abundance (Caughley, 1974). This may have a linear or non-linear relationship with the absolute density of a population (Southwell, 1989).

Aerial sightability indexes are usually negatively biased and result from environmental factors, survey design factors and observability (Caughley, 1974; Caughley et al, 1976; Southwell, 1989). These biases are therefore systematic in nature. There is also an important statistical distinction between precision and accuracy (McCallum, 2000). Precision is said to be a measure of the variation between replicate counts over the same area (Caughley, 1989). Conversely, accuracy refers to the systematic biases in the counts. Caughley (1989) provides a useful overview of different approaches taken to deal with systematic biases.

Precision depends upon the extent of observation uncertainty and process uncertainty (Hilborn and Mangel, 1997). Here observation uncertainty refers to random errors in the recorded measurements caused by the observer and observation methodology. Process uncertainty refers to variation in species behavior, demographic and environmental stochasticity. However, the distinction between accuracy and precision can be vague and random errors at one spatial or temporal scale may exhibit systematic trends at another spatial or temporal scale. For example, the demographic and environmental stochasticity in census data may exhibit systematic trends that can be correlated with other measurements.

The accuracy and precision of aerial surveys has been the subject of discussion in much of the literature (see Caughley, 1974; Caughley, 1977b; Caughley, 1989; Caughley et al, 1976; Hill et al, 1985; Hone, 1988; Pollock and Kendall, 1987; Stoll et al, 1991). The early development of wildlife aerial sampling methods probably began in the mid-1960's in Tanzania according to Jolly and Watson (1979). Aerial surveys in Australia were first applied to macropods in the early 1960s (Southwell, 1989). The factors that affect aerial counts of macropods include vegetation density (Caughley et al, 1976), the time of day (Hill et al, 1985; Short and Hone, 1988), observer experience, aircraft height, speed, light, turbulence, wind, shadow intensity (Caughley, 1989;

Caughley et al, 1976; Grice et al, 1990), cloud cover (Short and Bayliss, 1985), the hazing of aircraft Perspex (Caughley, 1989), the direction of flight (Bayliss and Giles, 1985; Caughley, 1989; Hill et al, 1985), transect strip width (Caughley et al, 1976), the clustering or dispersion of the population (Cook and Jacobson, 1979; Cook and Martin, 1974; Newsome et al, 1981) and habitat (Short and Bayliss, 1985). In addition, many of these factors are correlated (Caughley, 1989).

These effects necessitate a consistent sampling methodology with repeatability to improve precision and a derived sightability correction factor to improve accuracy (Caughley, 1977b; Caughley, 1989). Until recently most of the work by these authors has focused on improving the accuracy of aerial surveys with less emphasis on understanding and improving the precision of aerial surveys even though the latter is more important for monitoring population trends (Caughley, 1989; Southwell, 1989). Most methods of estimating aerial sightability accuracy have usually involved comparing field (ground) estimates with the aerial counts and applying a calibration factor to the aerial counts (Pollock and Kendall, 1987). These calibration factors obviously vary between methodologies, habitats and the census species.

2.2 The aerial survey of *Petrogale xanthopus xanthopus*

2.2.1 The monitoring framework in South Australia

As mentioned in Chapter 1, the first extensive research and regional field survey of *P. x. xanthopus* in South Australia was conducted between 1980 and 1981 by Peter Copley for the Nature Conservation Society of S.A (Copley, 1981). The aim of this survey was to ascertain the presence of *P. x. xanthopus* (Copley, 1983). From historical evidence, this work suggested that the species had declined since early European records despite maintaining its geographical extent in South Australia (Copley, 1981; Copley, 1983; Copley and Alexander, 1997). However, this field survey was also able to establish a framework from which aerial survey work could be conducted by DEH (Copley and Alexander, 1997). Of the eleven key colonies identified, colonies in the Olary Hills and Gawler Ranges were identified as 'most at risk' with some colonies in the Flinders Ranges identified as threatened (Alexander, 1994). The aerial surveys were therefore designed to provide regular monitoring of the relative abundance of these colonies and their response to threat abatement management strategies, (Alexander et al, 1993; Copley, 1983; Copley and Alexander, 1997).

The aerial surveys first commenced in 1981 in the Olary Hills and the Southern Flinders Ranges between Quorn and Hawker. They recommenced for the period from 1989 to present except 1994 (De Preu, 2000) and in the Olary Hills (Copley and Alexander, 1997) up until 2000. Aerial surveys also commenced in 1993 in the Flinders Ranges National Park and surrounds. In 2000 this was extended to the Gammon Ranges National Park. Intermittent surveys have also been conducted in 1995, 1999 and 2000 in the Gawler Ranges with some work in the Mt Remarkable National Park more recently.

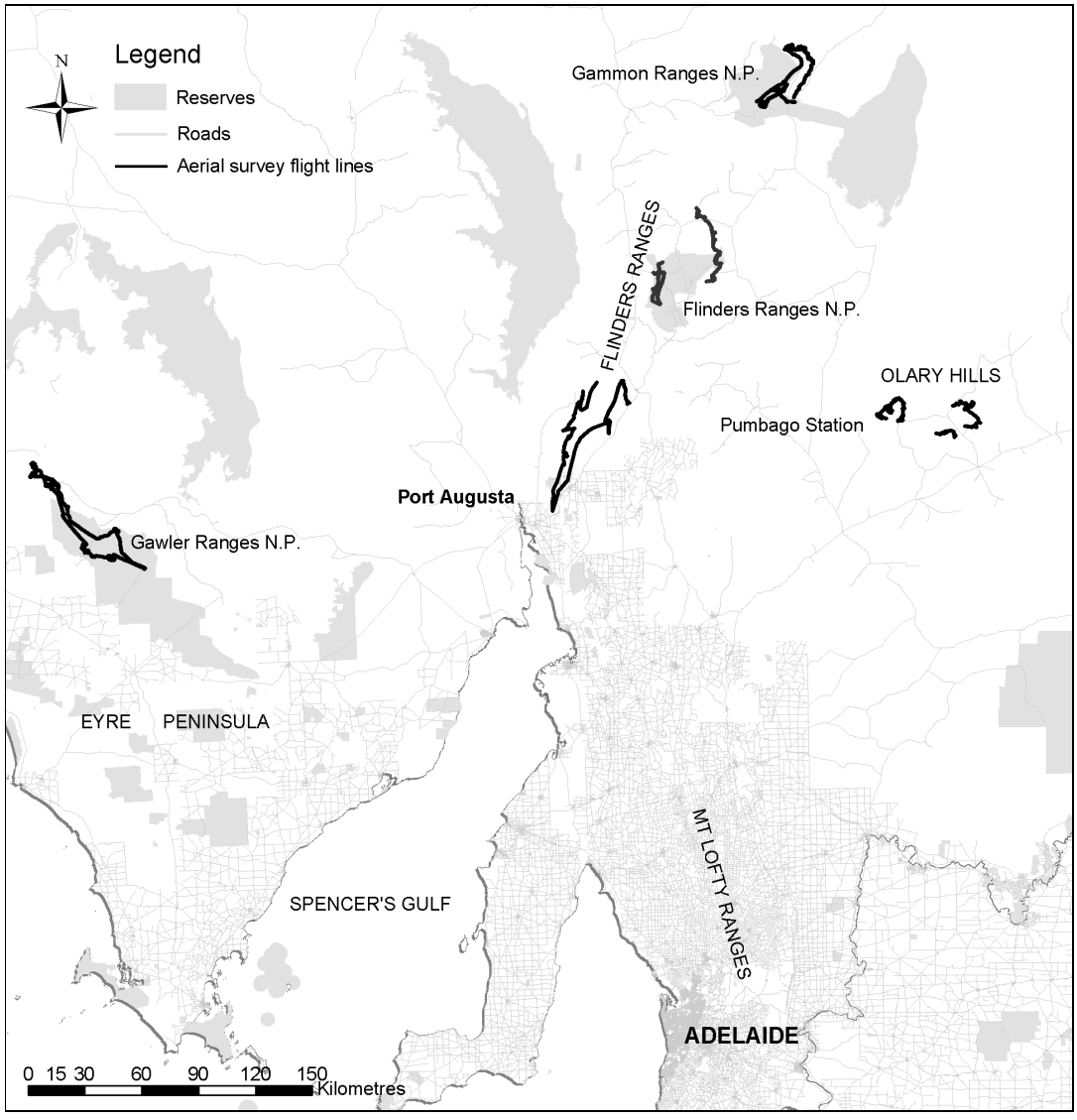


Figure 2.1 Aerial Survey Routes in S.A.

By 1993, an integrated feral pest control program had commenced in the Flinders Ranges National Park and surrounds (Alexander et al, 1997). This program continues to the present day and includes goat, fox and rabbit control. The continued aerial survey of the route between Quorn and

Hawker where there is little or no feral pest control is intended to provide baseline data for the comparison of *P. x. xanthopus* response in treatment areas (Alexander, 1994).

2.2.2 Route Consistency

The flight routes from 1993 (shown in Figure 2.1) to present have remained largely consistent. Minor deviations in flight routes occurred in 1997 in the vicinity of Buckaringa Hill in the Southern Flinders Ranges. In 1998, the route also varied slightly in the vicinity of Balcorachina Creek and Eregunda Creek, north of the Flinders Ranges Nation Park to include more appropriate habitat and one of the mark and re-capture sites for comparison. The route has also continued to expand at Plumbago Station in the Olary Hills in an attempt to follow the growing dispersion of *P. x. xanthopus* in this area. As the original objective was to measure population growth over the entirety of Plumbago Station (a widely dispersed array of hills), there was a very real danger that any apparent flattening of population growth (indicating carrying capacity) might have been an artifact of a the flight route not accounting for the geographical expansion of the population.

2.2.3 Electronic Recording

In 1996, a GPS electronic census system was trialed and then fully implemented in 1997 by DEH. The system consists of four components: data entry keypads for each observer connected to a computer pen-tablet and GPS receiver and a computer software application (see Plate 2.2). The electronic hardware was manufactured by Walkom (1996) and the software application called 'Flystat' was written by Lethbridge (1996). The software application records the key entries for up to three observers along with GPS positions using a Trimble SV6 six channel GPS. The keypads are strapped to the legs of each observer enabling them to enter their observed counts by pushing buttons on the pads (see Plates 2.1 to 2.3). This removes the need for observers to look away from the ground or memorise the counts. This system is also used by DEH for aerial surveys of Cape Barren Geese (*Cereopsis novaehollandiae*) and substitutes successfully in the role of an electronic logging and out-of-bounds alarm system for aerial fox baiting.

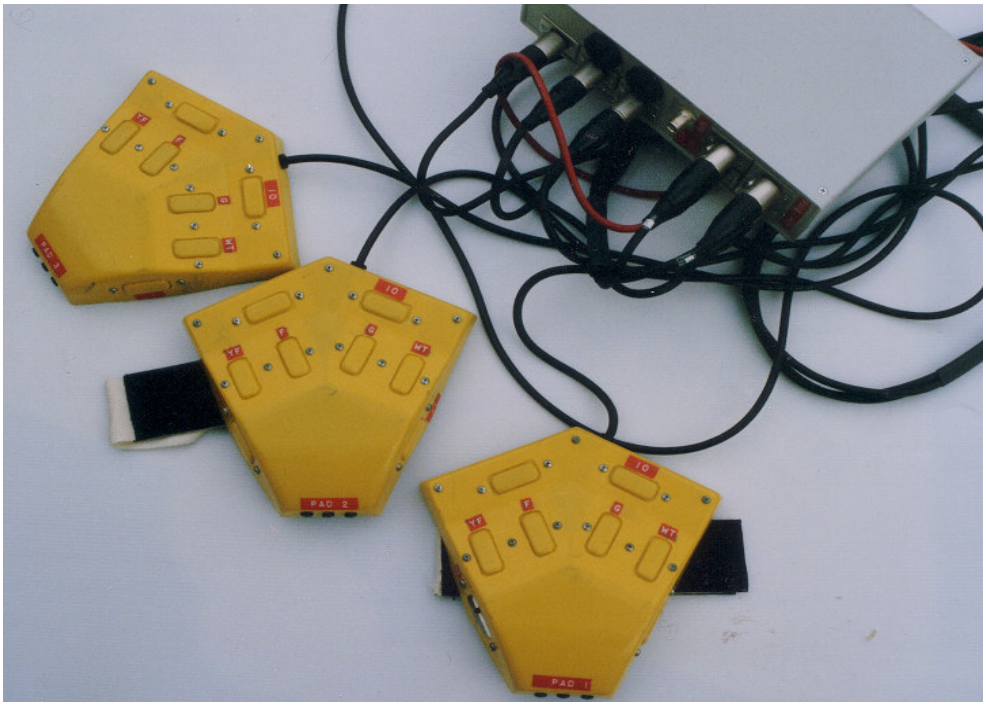


Plate 2.1 GPS Electronic Census System – keypads and main control box.



Plate 2.2 GPS Electronic Census System – pen-computer and key pad with front observer in-flight.



Plate 2.3 GPS Electronic Census System – rear observer with key pad in-flight

2.2.4 The Aerial Sightability for *Petrogale xanthopus xanthopus*

Most transect sampling approaches are either fixed width transects or distance sampling techniques. The latter uses probability functions that relate sightability with distance to derive an effective strip width (Buckland et al, 1993). However, helicopter surveys of *P. x. xanthopus* are not strip transects and, given that any distance estimation is impossible, a probability associated with sighting distances cannot be estimated. As the habitat occupied by *P. x. xanthopus* is largely linear, the raw counts are instead spatially grouped into four kilometre sections rather than dividing them by an area.

A key influence on the power to detect population trends lies in the variability of the index being used (Gibbs, 2000). However, only one study has been carried out which attempted to calculate an aerial sightability factor (the accuracy of observations) for *P. x. xanthopus.* This work was carried out by Lim (1987) in Middle Gorge in the Southern Flinders Ranges of South Australia. The correction factor ranges between 4.61 and 5.85 indicating the variability (or precision) of sightability. Unfortunately, Lim's (1987) study was carried out over a relatively small area (< 2km) and no other studies since this time have attempted to explore this variability for *P. x. xanthopus* aerial sightings.

2.2.5 Survey Design and Standardisation in South Australia

In order to reduce many of the biases discussed in 2.1, DEH has attempted to ensure that the surveys in S.A. adhere to a standard methodology (Copley and Alexander 1997). In the rocky and rugged terrain where *P. x. xanthopus* is found the sightability from the air is reduced (Clancy and Close, 1997). Aerial census in this terrain therefore requires slow and low flying aircraft. For this reason, helicopters are preferred over fixed wing aircraft. They are also more maneuverable and easily able to maintain low air speeds (Beasom et al, 1981; Kufeld et al, 1980; Stoll et al, 1991). However, despite these gains, the ground to helicopter distance will constantly fluctuate in steep rocky terrain in order to maintain acceptable safety margins. This affects sightability.

The census is flown in late June or early July of each year on clear mornings when the weather is cool and the animals are most likely to be found near the top of hills sunning themselves (Alexander, 1996). As the survey period may be lengthy, two successive surveys on two consecutive days along the same route are flown in opposing directions. Apart from sites around the centre of the route, the pass of two flights in opposing directions over each site is generally at different times of the morning. This attempts to reduce biases associated with the time of day while also providing some repeatability. Where possible the census work is not undertaken in the rain and in most cases the surveys are not conducted in strong wind conditions (>10 knots). However, conditions do change during the survey and weather conditions can become variable. To a lesser degree some biases associated with the aircraft's approach to each habitat type have also been removed by taking the maximum count of animals in each 4km section (Alexander, 1996). Observers are also trained and checked for consistency against a more experienced observer. Aircraft speed is kept constant at approximately 50 knots.

Abundance estimates reported by DEH have traditionally used Lim's (1981) sightability correction, derived in Middle Gorge, S.A., to present estimates of abundance over the entire survey area. However, the assumption that one sightability correction is valid over an entire landscape is fundamentally flawed. While a major improvement would be to publishing relative abundance measures, these measures still assume that the same fraction of the population is seen from one year to the next. This assumption is also untested.

2.3 Modelling Population Trends

2.3.1 General definitions

As previously mentioned, attempting to estimate true abundance from aerial surveys is difficult. Alternatively, relative abundance can be used to measure population trend. An important measure of trend is the rate of increase 'r'. This can be measured from a finite series of population estimates (Caughley, 1977a). As previously mentioned, this measure is a more general level of abstraction (McCallum, 2000) providing a summary of the population processes which underlie it. These underlying processes require vital rate measures such as fecundity, mortality, immigration and emigration (Southwell, 1989), and require more detailed investigations at a local level. The general formula for the rate of increase is described in Equation 2.1.

$$r = \ln(N_{t+1} / N_t) \qquad \textbf{Equation 2.1}$$

Here r is the rate of increase, N_t , N_{t+1} are the abundance estimates or indices of abundance at time t and $t+1$ respectively.

Caughley (1977a) describes the observed rate of increase $\bar{r}$ as the mean exponential rate of increase over a period of time. Here $\bar{r}$ is the slope of the natural logarithm of the abundance measures (or indices) over time. This measure does not consider fluctuations during that period, which may be highly autocorrelated and influenced by environmental and demographic stochasticity (McCallum, 2000).

The intrinsic rate of increase r_m is described by Caughley (1977a) as the rate of increase a population can attain when there is no shortage of resources. It is the maximum exponential rate at which a population with a stable age distribution grows. The term r_s however, refers to the intrinsic rate of increase for a given level of resources, hence this term describes the exponential rate at which a population grows with a stable age distribution appropriate to its current rates of age-specific survival and fecundity (Caughley, 1977a).

The observed rate of increase can be evaluated over a given period using linear regression to evaluate trend (Gerrodette, 1987; McCallum, 2000). However, the calculation a rate of increase over a period for a population in semi-arid environments in the face of environmental stochasticity may fail to reveal the interaction of ecological and environmental processes. Age distribution and demographic autocorrelations will also violate the assumptions of linear regression and affect the estimation $\bar{r}$ (Zar, 1996).

2.3.2 Numerical Response Models

In fluctuating environments it may be more appropriate to adopt an indirect approach and model rate of growth in relation to resource availability (McCallum, 2000). This approach uses numerical response models. Numerical response models focus on the effect that resources have on the consumer as opposed to functional response models, which focus on the effect consumers have on resources (Caughley and Sinclair, 1994). Numerical response models attempt to relate population trend (the rate of increase) with the level of resource (Caughley and Sinclair, 1994). Bayliss (1987) and Caughley (1984) describe a technique using the Ivlev (1961) numerical response model or Mitscherlich model (Cairns, 1989) for kangaroos where a time-lagged interval of rainfall is used as a surrogate estimate of resource availability or pasture biomass.

The Ivlev (1961) model is a nonlinear inverted exponential equation and takes the following form.

$$r = -a + c(1 - e^{-dV}) \qquad \textbf{Equation 2.2}$$

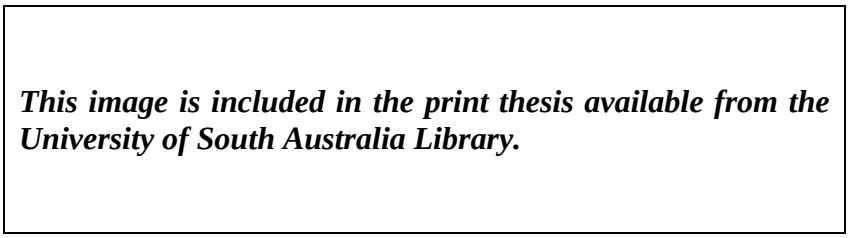
Here r is the rate of increase of the species, a is the maximum rate of decrease of a population in the absence of resources, c is the rate at which a is ameliorated by increasing the amount of resources and d is a measure of the demographic efficiency of the population (Bayliss, 1987). The demographic efficiency may be thought of as the ability of a population to increase when resources are in short supply (Caughley and Sinclair, 1994). The variable V represents resource abundance or a surrogate measure such as rainfall. The model asymptotes to a maximum or intrinsic rate of increase r_m where $r_m = c - a$. The intrinsic rate of increase r_m indicates the maximum growth rate possible for this population (Bayliss, 1987).

This type of model is biologically meaningful because inferences can be made about the biological processes it underpins by interpreting the parameter estimates (Ratkowsky, 1983).

2.3.3 Modelling rainfall and the Rate of Increase for *Petrogale xathopus xathopus*

Copley and Alexander (1997) summarised findings from Lim et al (Lim et al, 1987) and Hornsby (unpublished data). Based upon ground counts, these surveys suggested a correlation between the number of *P. x. xanthopus* sighted and rainfall.

A more extensive analysis of the rate of increase in relation to rainfall was conducted by Sharp and Norton (2000). These authors modelled the annual rate of increase derived from aerial counts of *P. x. xanthopus* from 1980 to 1995 in western NSW and related this to lagged intervals of rainfall using polynomial models and the Ivlev numerical response model.



Source: Sharp & Norton (2000).

Figure 2.2 A graphical representation of the Ivlev numerical response model for *P. x. xanthopus* in western NSW.

Here r = -2.0 + 2.3205 $(1 - e^{-0.0082\,V})$ (Sharp and Norton, 2000). The adjusted r value accounts for variations in the periods between census

Sharp and Norton (2000) found a lower intrinsic rate of increase (r_m = 0.32) than expected compared with biological estimates calculated from known annual reproductive output (1.65-1.95 per annum) and sex ratios from several other studies. Using sex ratio data from Middle Gorge in the Flinders Ranges, South Australia measured by Robinson et al (1994) and unpublished data by Sharp the expected values of r_m were between 0.51 and 0.79 suggesting the "rates of recruitment were not primarily regulated by absolute resource availability" (Sharp and Norton, 2000, p77).

However, r_m is an averaged value and in this case was derived from few data. The annual rate of growth will also exceed r_m in some years due to demographic stochasticity, particularly when high birth pulses in one season precede another season of high survival rates. Hence with few data and in the absence of confidence intervals, it would be premature to derive any conclusions from this value of r_m. The Ivlev (1961) model, being a numerical response model, also does not account for density dependence

Interestingly, there was no fox or goat control at this site. They also noted the unusually low value of –2.0 for the maximum rate of decrease when compared with other macropod species. However, this could merely be an artifact of the lack of data at the lower rainfall end of the model.

2.4 Methods

2.4.1 Study Sites

As previously mentioned, DEH carry out an annual census of *P. x. xanthopus* over much of the northern rangelands of South Australia. This study focuses on four subsets of the total survey area, namely the Wilkawillina Gorge zone in the northern Flinders Ranges, the Depot Flat zone in the central Flinders Ranges, the Hawker zone in the central Flinders Ranges and Plumbago Station zone in the Olary Hills (see Figure 2.3). The primary motivation for selecting these sites is the length of the periods these have been surveyed. These sites also have contrasting threat abatement strategies. Plumbago Station has been surveyed since 1989 and has had an integrated pest control system (fox, rabbit and goat control) in place since the early 90's, the central Flinders Ranges sites have also been surveyed since 1989 but have had no integrated pest control in place although some fox and goat control is known to take place at times, and Wilkawillina Gorge has been surveyed since 1995 with integrated fox, rabbit and goat control progressively intensified since 1995. Wilkawillina Gorge also contains two out of three mark-recapture sites for comparison. Parameters derived from the mark-recapture study are discussed in Chapter 3. The central Flinders Ranges has been divided into the Depot Flat and Hawker zones because rainfall is know to be higher in the south and closer to Depot Flat. Consequently, rainfall gauges at Deport Flat and Hawker were used respectively in the analysis that follows.

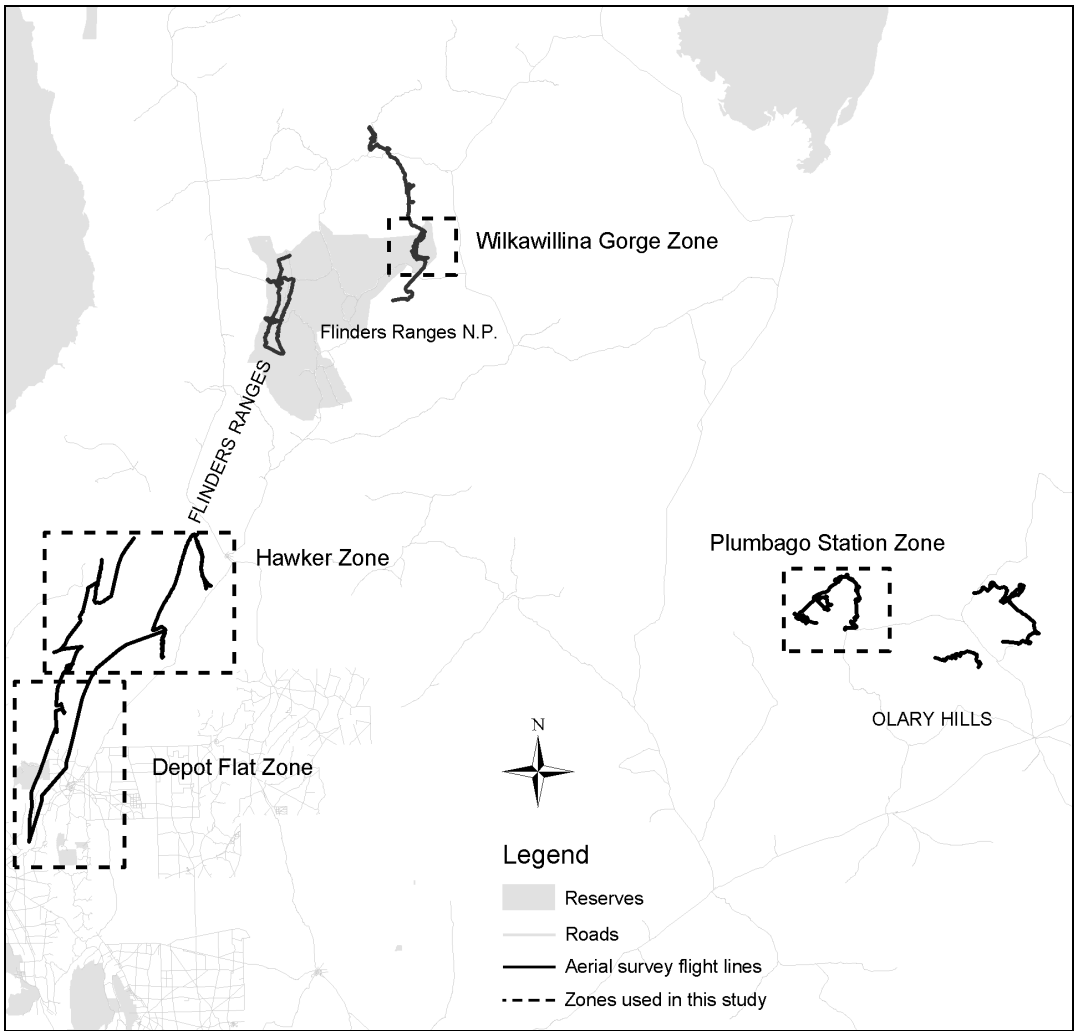


Figure 2.3 The four of the aerial survey zones analysed in this study

Enlargement of Figure 2.1 showing the Hawker, Depot Flat, Plumbago Station and Wilkawillina Gorge zones.

2.4.2 Determining Rate of Growth over a Period

The data in Tables 2.1, 2.2 and 2.3 has been provided by DEH for aerial surveys over the period from 1989 to 2002. The rates of growth *r* in Tables 2.1, 2.2 and 2.3 are calculated using Equation 2.1.

Autocorrelation in time series data can violate the assumption of independence which underpins linear regression. Nevertheless linear regression may still be able to sufficiently indicate trends providing caution is exercised with the statistical confidence one is likely to derive from this approach. Equation 2.3 is the general form of the regression. Here N_t refers to the maximum counts obtained in four kilometre linear sections along the route from two surveys flown in opposing directions in late June/early July of each year.

$$\ln(N_t) = \bar{r}t + c \qquad \textbf{Equation 2.3}$$

Here c , the intercept represents the population at time zero. Obviously a population prediction at time zero is fictitious and as such, will be ignored. The mean exponential rate of increase $\bar{r}$, is the slope of the linear regression.

Table 2.1 Sightings in the Southern Flinders Ranges (provided DEH.)

This image is included in the print thesis available from the University of South Australia Library.

Table 2.2 Sightings in the Flinders Ranges National Park: Wilkawillina Gorge (provided by DEH.)

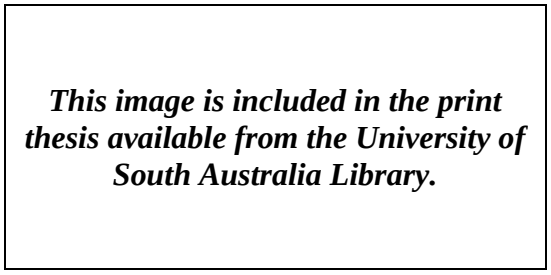
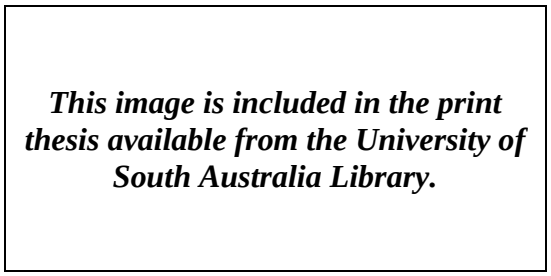


Table 2.3 Sightings in the Olary Hills: Plumbago Station (provided by DEH)



Plumbago Station was not surveyed in 1994 and 2001. Consequently some rates of growth could not be derived. Similarly, in 1992 and 1994 the Depot Flat zone and Hawker zone were not flown. The natural logarithm values of N_t from the four zones in Tables 2.1, 2.2 and 2.3 were plotted and regressed using Equation 2.3.

2.4.3 Measuring Autocorrelation

Temporally autocorrelated data can be analysed using autocorrelation plots (Box et al, 1994). This technique assumes an equal interval between data points. Missing data are tolerated providing they are explicitly stated. This tool can therefore be used to check for independence in univariate data by computing the autocorrelation of the data values at varying time lags. If independent, the temporally lagged correlations should not be significantly different from zero.

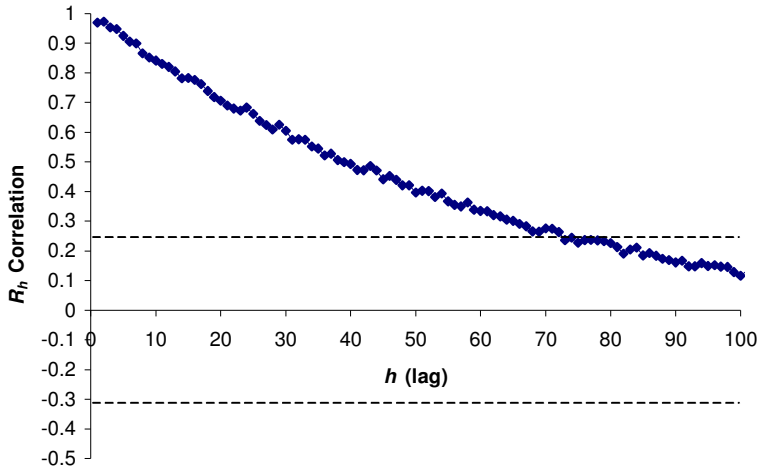


Figure 2.4 Example of simulated autocorrelated data up to an approximate lag of 70.

In the example in Figure 2.4, the dashed lines represent 95% confidences around zero autocorrelation (temporally independent data). Here up to a lag of approximately 68, the data are temporally autocorrelated ($\alpha = 0.05$). The horizontal axis is the time lag *h*. The autocorrelation coefficient R_h ranges from –1 to +1 and is define by Equation 2.4.

$$R_h = \frac{C_h}{C_0} \qquad \textbf{Equation 2.4}$$

Here C_h is known as the autocovariance, defined by Equation 2.5 and C_0, is the variance of Y_t.

$$C_h = \frac{1}{n}\sum_{t=1}^{n-h}(Y_t - \overline{Y})(Y_{t+h} - \overline{Y}) \qquad \textbf{Equation 2.5}$$

Here *n* are the number of data, Y_t are the univariate measurements and *h* is the lag. This test is important because most standard statistical tests assume the data have been randomly sampled. Partial autocorrelation is the correlation between the values of a series with the values lagged by 1 or more cases, after the effects of correlations at the intervening lags have been removed.

2.4.4 Relating Rate of Growth to Resource Availability

The rates of growth in Tables 2.1, 2.2 and 2.3 were also modeled against a range of lagged rainfall periods using the Ivlev (1961) model (Equation 2.2). Monthly rainfall data were obtained from the Australian Bureau of Meteorology on the 'Climate Data Australia' database, version 2.2 (2002). These data were obtained for rainfall gauges nearest to the centre of each of the zones. These locations are provided in Table 2.4.

Table 2.4 Location of currently operating rainfall gauges and their distance to the centre of the census zone (latitude and longitude are in AGD84).

Station Number	Station Name	Latitude	Longitude	Distance to Centre	Census Zone
17097	Angorichina Station	S31˚ 05'	E138˚ 44'	25km	Wilkawillina
19002	Depot Flat	S32˚ 15'	E137˚ 58'	16km	Depot Flat
19017	Hawker P.O.	S31˚ 48'	E138˚ 25'	15km	Hawker
20050	Plumbago Station	S32˚ 04'	E139˚ 53'	8km	Plumbago
17054	Wirrealpa Station	S31˚ 07'	E138˚ 57'	19km	Wilkawillina

Equation 2.2 is a non-linear growth model and consequently the parameters *a*, *c* and *d* cannot be solved using linear regression. However, simple non-linear equations can be solved by transforming either one or more of the variables (Smyth, 2002). Both the data and the arrangement of parameters in the model can be non-linear. For example, in Equation 2.2 the parameter *a* appears to enter the model linearly while parameters *c* and *d* are more likely to enter the model non-linearly (Smyth, 2002). This is called parameter-effects non-linearity (Ratkowsky, 1983). The extent of non-linearity in the model and data combination is known as 'intrinsic non-

linearity' and when this is high, an acceptable convergence to a single set of parameter estimates may be difficult (Ratkowsky, 1983). However, provided intrinsic non-linearity is low and the parameters-effects non-linearity is not extensive, model non-linearity can be reduced by either reparameterisation techniques (Ratkowsky, 1983), data transformations, model separation (separable least squares - Smyth, 2002) or a combination of all of the above. The quest to find convergence to single parameter estimates can be confounded when the parameters are highly correlated (Ratkowsky, 1983). This is clearly evident in Equation 2.2.

Biases in the residuals were tested with a range of reparameterisation combinations on parameters *a*, *c* and *d* in Equation 2.2 using Monte Carlo simulation. Parameters *a* and *c* were transformed to the exponents e^a and e^c respectively. Because parameter *d* in equation 2.2 is known to be between 0 and 1, in order to keep it positive, the transformation $e^{(0-d)}$ is suggested by Ratkowsky (1983).

If all parameters are transformed Equation 2.2 becomes:

$$r = -e^{\alpha} + e^{\beta}(1 - e^{-(e^{(0-\lambda)}V)}), \qquad \textbf{Equation 2.6}$$

where $a = e^{\alpha}$, $c = e^{\beta}$ and $d = e^{(0-\lambda)}$.

Estimates of the parameters α, β and λ, denoted $\hat{\alpha}$, $\hat{\beta}$ and $\hat{\lambda}$, can be found in Equation 2.4 by iteratively incrementing candidate parameters an equal amount and determining the minimum corresponding sum of the squares of the residuals in the data. Estimates of the original parameters, denoted $\hat{a}$, $\hat{c}$ and $\hat{d}$, can then be derived from the estimates $\hat{\alpha}$, $\hat{\beta}$ and $\hat{\lambda}$, using the relationships $\hat{a} = e^{\hat{\alpha}}$, $\hat{c} = e^{\hat{\beta}}$ and $\hat{d} = e^{(0-\hat{\lambda})}$.

2.4.5 Monte Carlo Simulation

Improving the detection of trends in population parameters may be achieved by either increasing replication and/or increasing the monitoring period. Both approaches have cost implications. The latter approach runs a risk with populations that are rare or endangered and declining, that significant trends will take longer to become apparent than the population will survive (Allen, 1980). In this case the sampling effort should be increased. Understanding the confidence intervals of model parameters and the strategies that will more likely increase the power of these estimations is critical. However, when data are few, ascertaining parameter confidence intervals using the standard parametric approach, involving for example a Students t test, is generally weak and relies on the loose assumption that the sample data are indicative of the total population (Manly, 1997). Khaemba et al (2001) suggest that these tests, like the data, are often subject to biases. Violations of the linear assumptions that underpin the derivation of these confidences is also evident in non-linear growth models (Smyth, 2002) such as the Ivlev (1961) equation. In any case these statistical measures do not help us to explore strategies that might improve model/parameter power.

Monte Carlo simulation modeling allows one to explore the effects of certain assumptions and hence becomes a useful planning aid, allowing fieldwork to focus on critical questions (McCallum, 1994). Moreover, Monte Carlo simulation modeling allows one to explore different survey methodologies using artificial replication (Khaemba et al, 2001). Replication by simulation also allows one to explore the likely power of parameter estimates for different survey methodologies (Manly, 1997).

Monte Carlo simulation involves generating random samples using a computer pseudo-random number generator to test an observed statistic or the power of a model's parameters (Manly, 1997). Manly (1997) discusses two types of testing under the more general Monte Carlo testing. These are bootstrapping and randomization tests. The randomization test and the bootstrap test both use the sample data and resample it or compare it with another random dataset multiple times for distribution testing. These approaches assume all of the sample data has an equal likelihood of occurrence. Other types of Monte Carlo simulation involve creating new artificial sample data providing there is some *a priori* knowledge about the sampling variations (Press et al, 2002).

2.4.6 Bootstrapping

Bootstrapping uses the sample frequency as the best estimate of the underlying probability distribution of the whole population (Manly, 1997). This distribution is used to generate a new set of resampled data points or an 'artificial' population. A number of resamples *n* is drawn from the sample population according to a uniform random distribution with replacement where *n* is made to be the same as the number of data points in the sample population. The resampling process is continued a large number of times so that inferences can be made about the resulting parameter distributions. Bootstrapping is a non-parametric approach that has the advantage over many other Monte Carlo simulation approaches of not making any assumptions about the errors of a distribution (Efron and Tibshirani, 1993; Gavaris, 1999; Indurkhya et al, 2001).

Bootstrapping in more complex models can involve re-sampling the sample pairs (or triplets) X and Y or by resampling the residuals (Manly, 1997). Bootstrapping has three disadvantages. It cannot be used to predict the likely confidences or power for a number of samples greater than *n.* Bootstrapping also assumes the sample data are a typical sub-set of the total population (Manly, 1997). This is particularly problematic when data are few and it may become unstable. Finally it assumes that each sample is equally likely to occur (Manly, 1997).

However, in the Ivlev (1961) model, the samples do not have an equal probability of occurrence because the frequency of rainfall is not uniformly random, nor is it a normal distribution in this area. For this reason a weighted parametric bootstrapping approach that determines parameter confidences is preferred. Here the data are not uniform randomly selected with replacement but randomly selected according to a nominated rainfall distribution, which in this area is closer to a log-normal distribution. A program was written in Borland C++ to carry out the weighted bootstrapping. Each sample is drawn by first is drawing a rainfall deviated from a log-normal generator with a nominated mean and variance. The sample θ_j with the closest rainfall to the log-normal deviate is then used as the j^{th} bootstrap sample $\hat{\theta}_j^*$. This sample is replaced and the process is repeated up to *n* samples. The Ivlev equation is then fitted to the resample data and the resulting parameters are stored to file. The process is repeated for *s* simulations.

2.4.7 Parameter distributions

The properties of the resulting parameter distributions obtained by bootstrapping are usually unknown. To deal with this Efron (1979) introduced a method where the percentiles at either end of the distribution are used to obtain the confidence interval. For example a 90% confidence interval is between the 5% percentile and the 95% percentile. However, a biased parameter distribution may result where the median of the distribution does not agree with the parameter estimate (Manly, 1997, see Figure 2.5). For this reason, Efron (1981) proposed a bias-corrected (BC) and accelerated (BCa) percentile method of calculating confidence intervals. Indurkhya et al (2001) also found this method performed well with outliers. In this study the BC percentile technique has been used (Chaudhary and Stearns 1996).

For *j* bootstrap replicates $\hat{\theta}_j^*$, the median bias $\hat{z}$ adjustment for $\hat{\theta}^*$ is given by equation 2.7.

$$\hat{z} = \Phi^{-1}[Q] \qquad \textbf{Equation 2.7}$$

Here Φ is the standard normal distribution function and Q is the proportion of $\hat{\theta}_j^*$ bootstrap replicates less than the parameter estimate (Briggs et al, 1999). The bias-corrected confidence intervals are then obtained from distribution at the percentiles using Equations 2.8a and 2.8b.

$$LowerPercentile = (2\hat{z} - z_{\alpha/2}) \qquad \textbf{Equation 2.8a}$$

$$UpperPercentile = (2\hat{z} + z_{\alpha/2}) \qquad \textbf{Equation 2.8b}$$

Here $z_{\alpha/2} = \Phi^{-1}(\alpha/2)$, the cumulative distribution of the standard normal variate. For example $\alpha/2 = 0.05$ in each tail for say a 90% confidence interval (see Figure 2.5). If the median of the bootstrap parameter distribution is equal to the parameter estimate, then $Q = 0.5$ and $\hat{z} = 0$ hence no percentile adjustment will take place (Briggs et al, 1999; Gavaris, 1999).

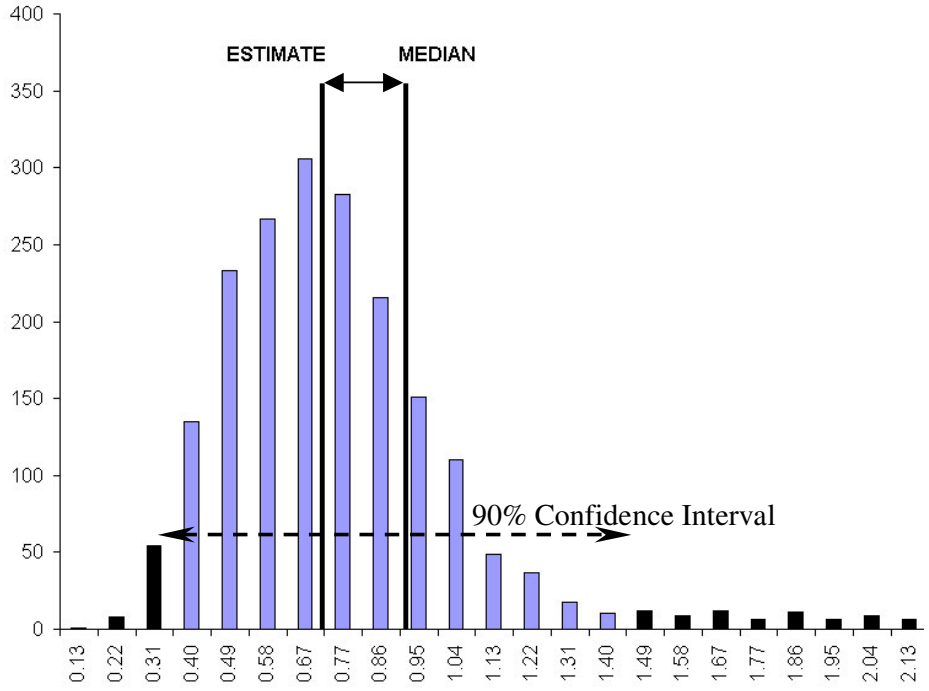


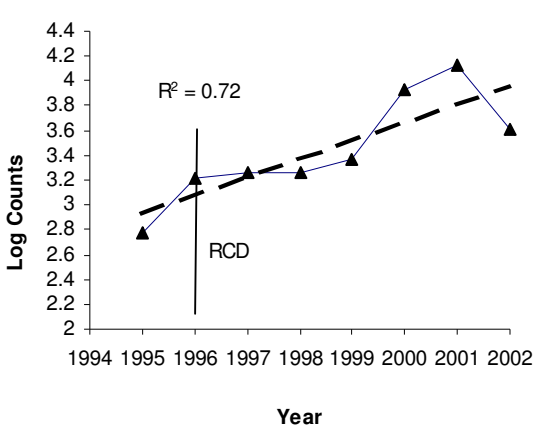
Figure 2.5 Example of bias in the percentile estimates of Confidence Interval

A bias-corrected percentile algorthim was coded in Borland C++ and incorporated in the bootstrap code described earlier. This algorithm was adapted from algorithm AS 214 in Fortran code obtained through StatLib and published by the Royal Statistical Society. The C++ code also incorporates other statistical algorithms from this source including AS 111, the percentage points of the normal distribution (Beasley and Springer, 1977); and AS 66, the normal integral (Hill, 1973).

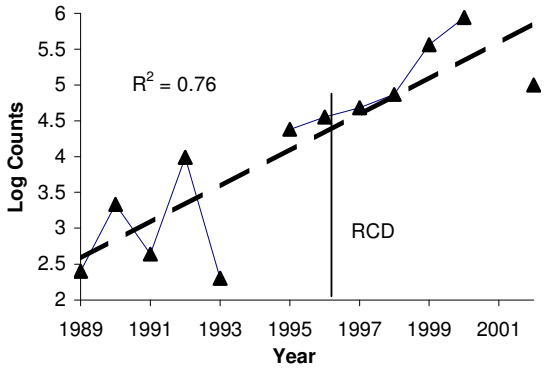
2.5 Results

2.5.1 Observed rate of Increase from Time Series

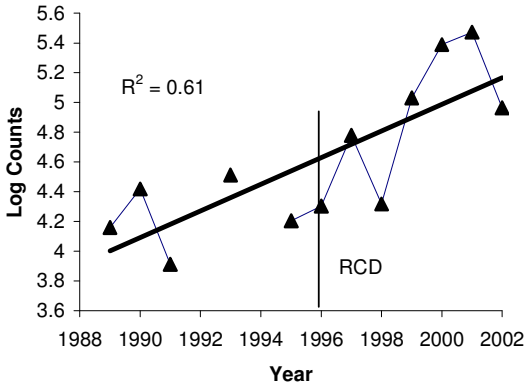
The natural logarithm of the observed counts of *P. x. xanthopus* for four zones in South Australia were regressed using Ordinary Least Squares regression (OLS). These are graphed in Figure 2.6. As some of the assumptions of linear regression are likely to be violated, caution should be exercised when using these results. Despite this, the graphs in Figure 2.6 do provide some indication of trends. The RCD (Rabbit Calicivirus Disease) outbreak in November 1995 is thought have had the greatest impact on rabbits in South Australia (Holden, 2000) and as such, may have had an impact on native herbivores. This event has been marked on the graphs in Figure 2.6. The R^2 values indicate the amount of variation explained by the OLS regression.



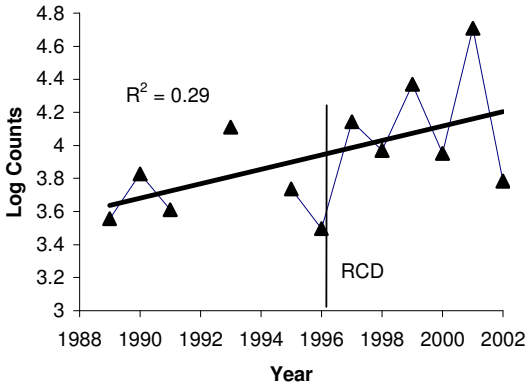
Wilkawillina Gorge ($\bar{r}$ = 0.15)



Plumbago Station ($\bar{r}$ = 0.25)



Depot Flat ($\bar{r}$ = 0.09)



Hawker ($\bar{r}$ = 0.04)

Figure 2.6 The logarithm of *P. x. xanthopus* observed counts for each year and zone in South Australia.

$\bar{r}$ is the mean exponential rate of increase which is the slope of the line derived from Ordinary Least Squares regression. The outbreak of Rabbit Calicivirus Disease (RCD) occurred in November 1995 and has been marked with a vertical bar.

2.5.2 Autocorrelation

If the data are not subject to excessive noise or stochastic events, autocorrelation should be evident in the population trend data. The following Box-Jenkins autocorrelation plots (Figures

2.7a to 2.7d) have been derived using the statistical package SPSS 11.5.0 (SPSS Inc, 2002). These plots indicate the presence of observation noise and stochasticity in the data as well as indicating the presence of autocorrelation. In Figures 2.7a to 2.7d, the autocorrelation factor (ACF) refers to correlations between the log counts in any given year and the log counts lagged by one or more years (SPSS Inc, 2002). These correlations are positive or negative. Correlations for up to 10 years of lags are shown in these graphs. The partial autocorrelation factor (Partial ACF) indicates correlations between the log counts in any given year and the log counts lagged by one or more years, after the effects of correlations at the intervening lags have been removed (SPSS Inc, 2002). The 'dash-dot' lines indicate the 95% confidence interval lines around temporally uncorrelated data.

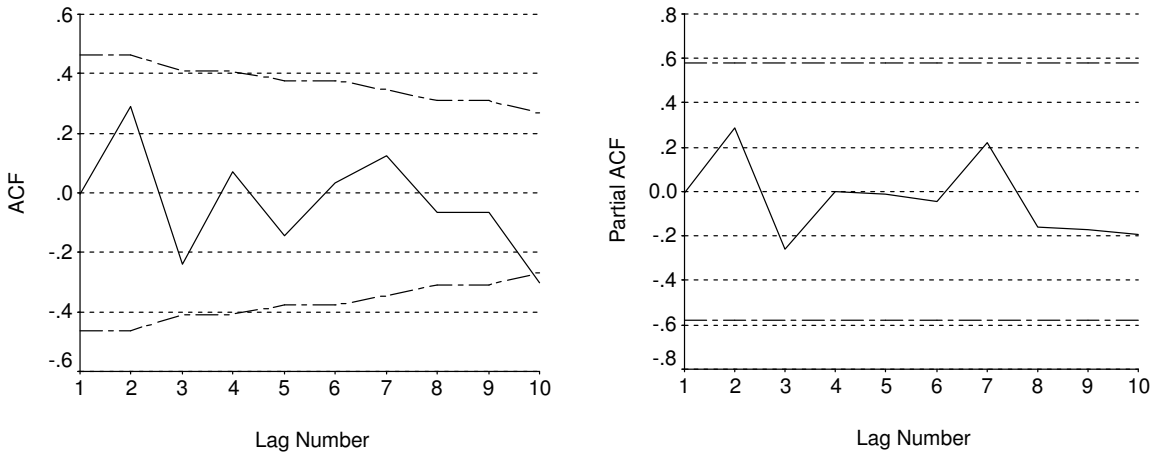


Figure 2.7a Hawker autocorrelation and partial autocorrelation factors

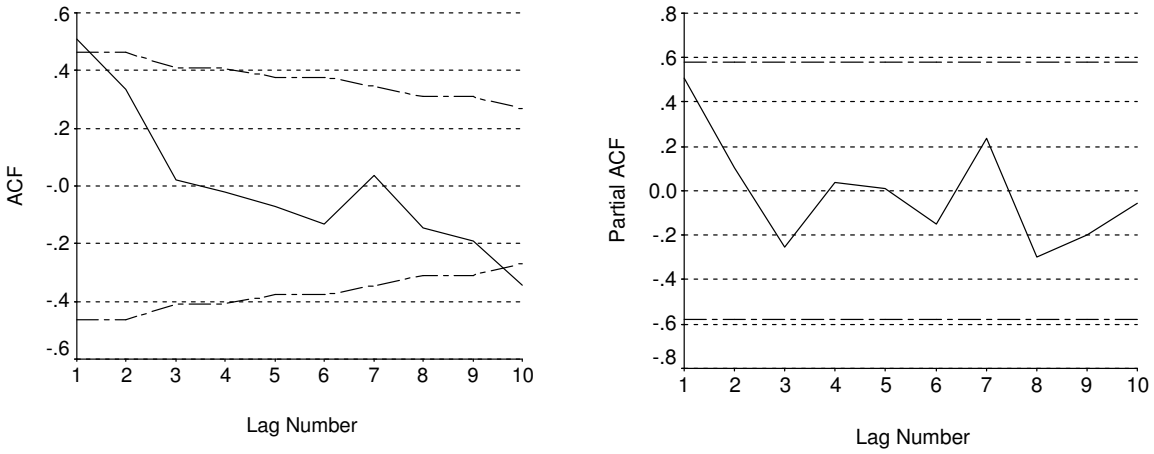


Figure 2.7b Depot Flat autocorrelation and partial autocorrelation factors

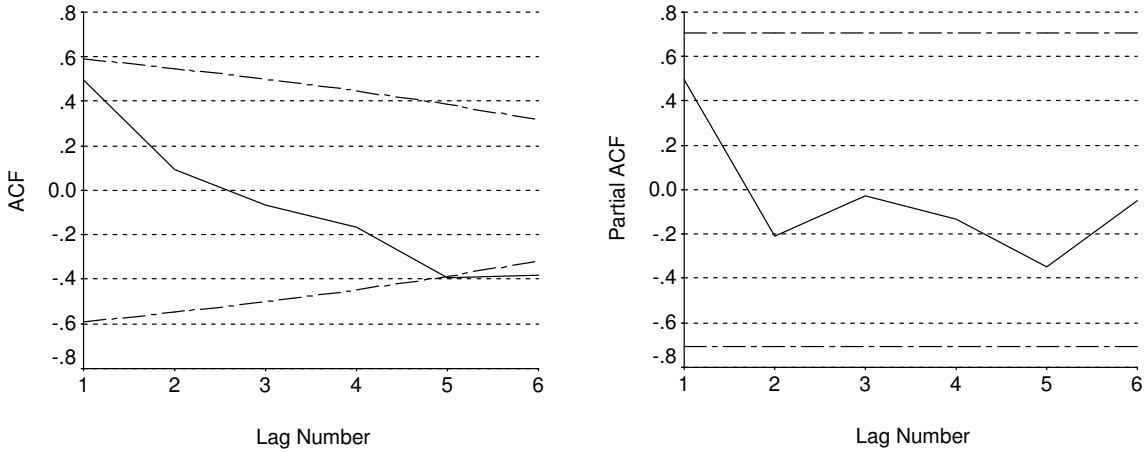


Figure 2.7c Wilkawillina Gorge autocorrelation and partial autocorrelation factors

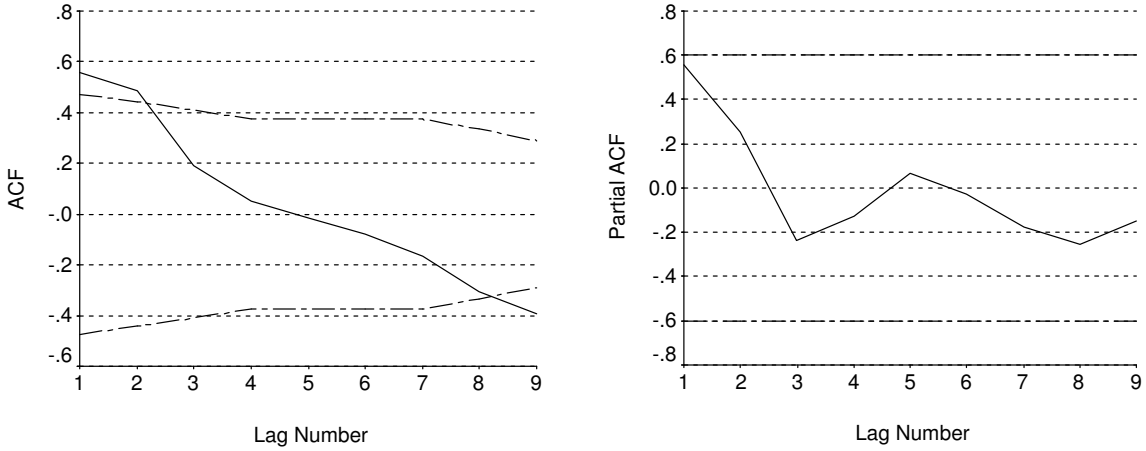


Figure 2.7d Plumbago Station autocorrelation and partial autocorrelation factors

Plumbago Station and Depot Flat indicate significant autocorrelation ($\alpha = 0.05$) in the early lags where they exceed the 95% interval lines. Other sites do not display any significant departure from temporally uncorrelated data. However, the magnitude 95% interval lines is also likely to reflect a combination of observation noise and stochastic events in the observations. Hence much of the measurable temporal autocorrelation in the data may have been swamped by noise.

2.5.3 The Ivlev Model

A range of rainfall intervals and lags from the time of survey (approximately late June of every year) were tested for their fit of the rates of growth using the technique discussed in Section 2.4.4. Candidate rainfall events for up to 12 months interval and 15 months lag were tested. Extracts of these results are presented in Tables 2.5a, 2.5b, 2.5c and 2.5d. In each table the three highest R^2 values are bolded and underlined.

Table 2.5a Ivlev (1961) fit and selected parameters at Depot Flat.

The intrinsic rate of increase r_m, maximum rate of decrease a and R^2 goodness of fit test of the Ivlev (1961) model, for a range of monthly rainfall intervals at Depot Flat from 1989 to 2002 (n=9).

Depot Flat															
		Interval (months)													
		3			**4**			**5**			**6**			**7**	
		r_m	a	R^2	r_m	a	R^2	r_m	a	R^2	r_m	a	R^2	r_m	a	R^2
Lag (Months)	**0**	0.19	0.72	0.20	0.26	0.75	0.39	0.24	0.74	0.31	0.24	3.69	0.35	0.27	4.21	**0.46**
	1	0.19	0.81	0.20	0.13	0.72	0.12	0.17	2.67	0.10	0.25	5.05	**0.44**	0.26	5.36	0.34
	2	0.19	0.83	0.24	0.28	5.05	0.35	1.01	0.95	**0.53**	0.37	1.89	0.33	0.15	3.26	0.17
	3	0.18	2.86	0.06	0.64	1.16	**0.50**	0.35	2.14	0.30	0.17	3.06	0.14	0.14	3.06	0.08
	4	0.42	2.00	0.39	0.22	3.71	0.18	0.17	15.69	0.13	0.12	1.86	0.03	0.06	0.11	
	5	0.15	2.67	0.17	0.15	14.18	0.18	0.12	2.32	0.05	0.06	0.28		0.06	0.11	

Table 2.5b Ivlev (1961) fit and selected parameters at Plumbago Station.

The intrinsic rate of increase r_m, maximum rate of decrease a and R^2 goodness of fit test of the Ivlev (1961) model, for a range of monthly rainfall intervals and lags at Plumbago Station from 1989 to 2000 with the 1993 outlier removed (n=8).

Plumbago Station (1993 outlier removed)															
		Interval (months)													
		3			**4**			**5**			**6**			**7**	
		r_m	a	R^2	r_m	a	R^2	r_m	a	R^2	r_m	a	R^2	r_m	a	R^2
Lag (Months)	**0**	0.71	0.73	**0.49**	0.63	1.00	**0.55**	0.62	11.18	0.34	0.62	12.46	0.44	0.64	11.49	**0.56**
	1	0.65	0.72	0.40	0.57	5.05	0.14	0.56	11.18	0.18	0.62	12.46	0.41	0.59	11.81	0.23
	2	0.50	2.32	0.03	0.47	3.95	0.04	0.59	11.81	0.30	0.51	10.02	0.11	0.40	0.05	
	3	0.43	0.28	0.01	0.54	2.22	0.10	0.46	8.97	0.02	0.40	0.05		0.40	0.05	
	4	0.40	0.05		0.38	0.05		0.38	0.05		0.38	0.05		0.40	0.05	

Table 2.5c Ivlev (1961) fit and selected parameters at Wilkawillina Gorge (Wirrealpa Gauge).

The intrinsic rate of increase r_m, maximum rate of decrease a and R^2 goodness of fit test of the Ivlev (1961) model, for a range of monthly rainfall intervals and lags at Wilkawillina Gorge using the Wirrealpa Station Rainfall Gauge from 1995 to 2002 (*n*=7).

Wilkawillina Gorge – Angorichina Rainfall Gauge

		Interval (months)														
		3			**4**			**5**			**6**			**7**		
		r_m	a	R^2	r_m	a	R^2	r_m	a	R^2	r_m	a	R^2	r_m	a	R^2
Lag (Months)	**0**	0.45	0.47	**0.67**	0.32	0.64	0.43	0.31	1.00	0.59	0.32	1.19	0.52	0.27	4.21	**0.71**
	1	0.32	0.25	0.27	0.31	1.21	0.56	0.32	1.72	0.50	0.27	4.96	**0.68**	0.32	1.59	0.30
	2	0.30	0.95	0.57	0.30	1.59	0.49	0.26	4.75	**0.68**	0.29	1.60	0.27	0.28	5.05	0.25
	3	0.26	0.22	0.15	0.28	4.47	0.56	0.27	1.86	0.20	0.25	4.47	0.13	0.26	4.75	0.14
	4	0.21	1.00	0.10	0.55	0.18	0.05	0.12	0.05		0.12	0.05		0.12	0.05	
	5	4.86	0.19	0.08	0.12	0.05		0.12	0.05		0.12	0.05		0.12	0.05	

Table 2.5d Ivlev (1961) fit and selected parameters at Wilkawillina Gorge (Angorichina Gauge).

The intrinsic rate of increase r_m, maximum rate of decrease a and R^2 goodness of fit test of the Ivlev (1961) model, for a range of monthly rainfall intervals and lags at Angorichina Station from 1995 to 2002 (*n*=7).

Wilkawillina Gorge (Angorichina Station gauge)

		Interval (months)														
		3			**4**			**5**			**6**			**7**		
		r_m	a	R^2	r_m	a	R^2	r_m	a	R^2	r_m	a	R^2	r_m	a	R^2
Lag (Months)	**0**	0.43	0.51	**0.80**	0.31	0.51	**0.68**	0.24	0.51	**0.64**	0.24	3.71	**0.61**	0.25	4.47	**0.51**
	1	0.30	0.37	0.53	0.26	0.49	0.62	0.26	3.22	0.51	0.22	4.47	0.37	0.40	7.58	0.49
	2	0.27	0.48	0.61	0.28	2.32	0.48	0.25	4.47	0.36	0.36	6.77	0.35	0.12	0.14	
	3	0.20	0.34	0.07	0.20	3.26	0.11	0.26	4.75	0.13	0.12	0.08		0.12	0.14	
	4	0.11	0.05		0.12	0.05	0.00	0.12	0.05		0.12	0.05		0.12	0.05	
	5	0.12	0.05		0.12	0.05	0.00	0.12	0.05		0.12	0.05		0.12	0.06	

Table 2.5e Ivlev (1961) fit and selected parameters at Hawker

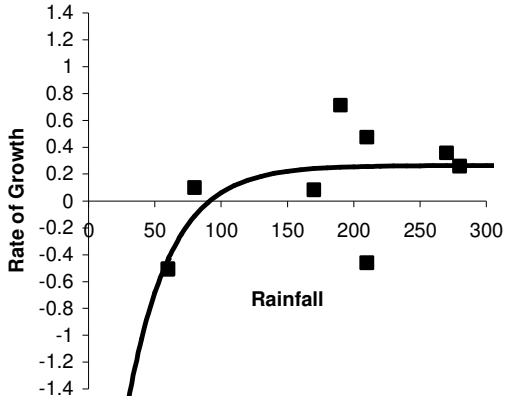
The intrinsic rate of increase r_m, maximum rate of decrease a and R^2 goodness of fit test of the Ivlev (1961) model, for a range of monthly rainfall intervals and lags at Hawker from 1989 to 2002 (n=9).

Hawker															
		Interval (months)													
		3			4			5			6			7	
		r_m	a	R^2	r_m	a	R^2	r_m	a	R^2	r_m	a	R^2	r_m	a	R^2
Lag (Months)	0	0.16	0.51	0.12	0.22	1.23	**0.47**	0.21	1.57	**0.49**	0.26	5.36	**0.48**	0.26	1.96	**0.40**
	1	0.22	1.21	0.38	0.21	1.86	0.44	0.23	4.75	0.29	0.23	3.06	0.35	0.11	0.84	0.05
	2	0.21	1.33	0.42	0.22	4.47	0.27	0.64	1.12	0.38	4.25	0.51	0.09	0.04	6.73	0.02
	3	4.97	0.26	0.13	0.87	0.86	0.39	4.28	0.48	0.10	0.06	0.81	0.02	0.07	0.81	0.03
	4	0.57	1.06	0.42	0.13	1.46	0.07	0.09	1.57	0.06	0.10	1.13	0.05	0.16	2.86	0.10
	5	0.07	0.91	0.02	0.07	0.91	0.03	0.06	0.72	0.02	0.14	2.86	0.08	0.09	16.20	0.09

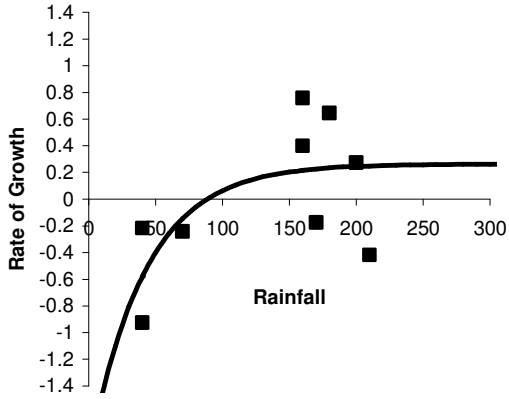
Other lag/interval combinations well outside of these ranges were also tested. However, all had significantly lower R^2 values and have consequently been omitted from Tables 2.5a-e. In Tables 2.5a to 2.5e, the highest R^2 values are highlighted in bold and underlined. It was decided to remove the 1993 outlier count for Plumbago Station. This effectively doubled the R^2 values. It is considered that the maximum rate of increase r_m is a useful indicator variable in comparative studies. It is derived from the Ivlev (1961) model through the relationship $r_m = c - a$. This is the maximum rate of increase where there are theoretically no limitations on resources. Parameter a and r_m are shown in Tables 2.5a to 2.5e by way of comparison. However, as previously mentioned the interpretation of r_m should be treated with caution, because r_m is effectively an averaged value and the Ivlev (1961) model does not account for density dependence. This value also fails to separate processes such as predation from say competition or resource limitation. The use of rainfall as a surrogate variable may also fail to adequately describe resource availability because of the range of likely vegetation responses to rainfall in different land systems. Interestingly, parameter r_m is more stable than a for a range of R^2 values in each area. This is probably due to the intrinsic dependency between parameters a and c.

It is expected that rainfall lags of between seven and ten months would influence the birth pulse contribution to the rate of growth firstly because new-borns spend approximately 200 days in pouch and are not be seen for more than 6.5 months and secondly birth pulses are likely to be influenced by conditions of up to a few months prior. However, no models had a high R^2 values

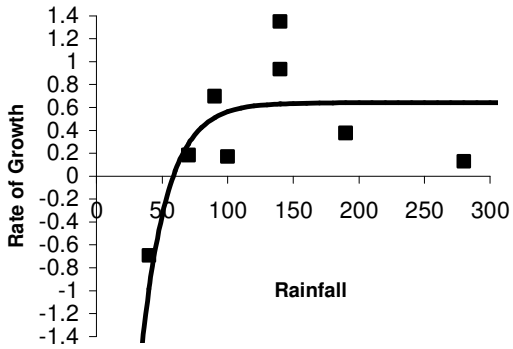
after about seven months. Overall models having a seven months interval and zero months lag rainfall were the best fit of the data. While this lag is likely to have some birth pulse influence, it is more likely to summarise many superimposed demographic phases with more direct influences from juvenile and adult survival. The graphs of these models for each site are displayed in Figure 2.8.



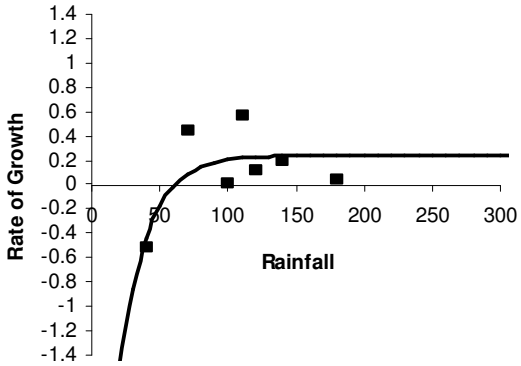
Depot Flat: : 7 month interval, no lag, a=4.16, c=4.42, d=0.031, r_m=0.26, R^2=0.46, F = 2.55, $F_{0.05\ (2,6)}$ = 5.14



Hawker: : 7 month interval, no lag, a=1.94, c=2.20, d=0.024, r_m=0.26, R^2=0.40, F = 1.99, $F_{0.05\ (2,6)}$ = 5.14



Plumbago Station: 7 month interval, no lag, a=11.52, c=12.16, d=0.050, r_m=0.64, R^2=0.56, F = 3.24, $F_{0.05\ (2,5)}$ = 5.79



Wilkawillina Gorge: 7 month interval, no lag, (Angorichina Station gauge), a=4.46, c=4.70, d=0.048, r_m=0.24, R^2=0.51, F = 2.04, $F_{0.05\ (2,4)}$ = 6.94

Figure 2.8 Comparison of Ivlev Plots for each site

2.5.4 Weighted Bootstrap Tests of the Ivlev Models

Weighted bootstrap tests were conducted for each model in each area. As previously mentioned, parametric tests are unsuitable measures of confidence interval because they assume the distribution of the data is known. Parameter distributions were therefore derived from bootstrap replicates for each model. The bias-corrected percentile method was chosen because it avoids the assumption of normality and also deals with bias in the replicate distribution. For each bootstrap test, 2000 simulations were run with the parameter confidence intervals recorded after the accumulation of every ten simulations. Histograms of the 1000 bootstrap parameter replicates were inspected for homoscedasticity and skewness.

The percentile estimates of parameters *a* and *b* were wide in all models. This was exacerbated when there were fewer sample points. The bootstrap confidence interval estimates for the intrinsic rate of growth $r_m = c - a$ and *d* were the best overall, exhibiting the least skewness and homoscedasticity. These are thought to be more reliable indicators of population trends and coincidentally seem to be more useful biological summary indicators. As previously mentioned, the intrinsic rate of increase r_m indicates the highest average growth rate when resources are unlimited and *d* is a measure of the demographic efficiency of the population (Bayliss, 1987). Figure 2.9 shows the intrinsic rates of growths for each site and Figure 2.10 shows parameter *d* for each site. The parameters in Figure 2.9 and 2.10 use the seven months interval, zero lagged Ivlev models from Figure 2.8 and show the weighted bootstrap bias-corrected 5% and 95% percentiles derived from 1000 bootstrap replicates. The rainfall mean and variance for seven months interval from November to May at each site were used to weight the bootstrap calculations. Each zone's rainfall mean and variance were calculated for the period of each site's census and two years prior. This was considered to be more appropriate than calculating a rainfall mean and variance at each site over the entire period of rain gauge recordings. The periods over which the mean and variance were derived are 1994-2002 at Wilkawillina Gorge using the Angorichina Station gauge, 1988-2002 at both Hawker and Depot Flat, and 1985-2000 at Plumbago Station.

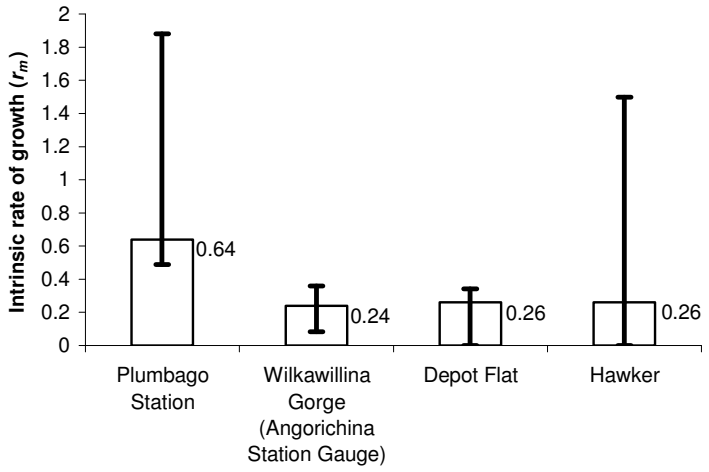


Figure 2.9 Summary of Intrinsic Rates of Growth (r_m) for the seven months interval, zero lagged Ivlev models from Figure 2.8

Error bars indicate the weighted bootstrap 5% and 95% bias-corrected percentiles derived from 1000 bootstrap replicates.

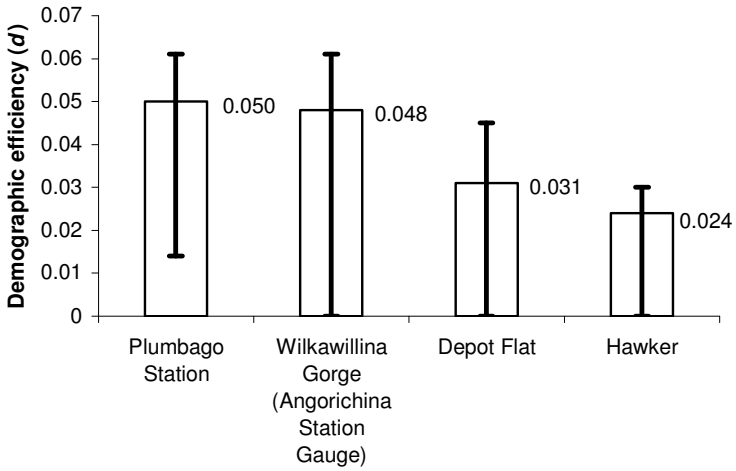


Figure 2.10 Summary of demographic efficiency (*d*) for the seven months interval, zero lagged Ivlev models from Figure 2.8

Error bars indicate the weighted bootstrap 5% and 95% bias-corrected percentiles derived from 1000 bootstrap replicates.

2.5.5 An Alternative Mean Rate of Growth

As an alternative to using regression to determine the mean rate of growth, Burgman et al (1993) suggest using a Monte Carlo simulation approach. In this study the Ivlev models at each site have been used to generate a mean rate of growth. Using a log-normal deviate generator, 5000 simulated rainfalls were generated and substituted in the Ivlev equations graphed in Figure 2.8 to calculate a mean rate of growth and variance. The rainfall mean and variance used to generate these log-normal deviates have been calculated from existing records but only for the period in which the census was conducted. These results are summarised in Table 2.5.

Table 2.5 Simulated mean rates of growth

Site	Simulated $\bar{r}$	Simulated $\sigma_{\bar{r}}^2$
Plumbago Station	0.49	0.108
Wilkawillina Gorge	0.17	0.011
Depot Flat	0.19	0.023
Hawker	0.15	0.023

2.5.6 Dispersion

A useful application of the GPS aerial recording system is the ability to analyse changes in the spatial dispersion of the sample data. Figure 2.11 shows a flight route obtained using the electronic GPS system 'Flystat' (Lethbridge, 1996) from Wilkawillina Gorge to Eregunda Creek.

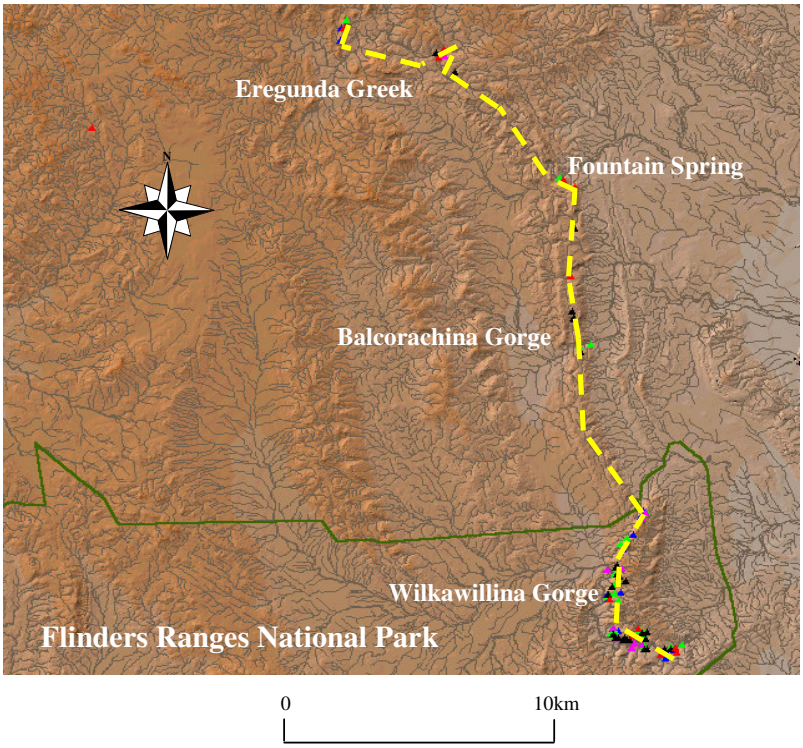


Figure 2.11 Flight route obtained using the Electronic GPS system from Wilkawillina Gorge to Eregunda Creek

The 'Flystat' electronic system captures observation counts every two seconds and stores the counts with a GPS position. While the recorded GPS position is the actual position of the aircraft, this is nevertheless a useful approximation of the position of the sighting. For ease of analysis, the dispersion of animals over time was viewed as univariate data along the linear flight line. Although the electronic system was functional in 1996, the year 1998 was chosen as the start year because this corresponded to the mark-recapture work (Chapter 3). GPS positions and counts from both census days in each year were grouped together. In order to clearly detect changes in dispersion it was necessary to use a univariate density smoothing technique. A normal univariate Kernel density index suggested by Silverman (1985) was used here. This index has no direct biological meaning in this application although it is still useful as an indicator of likely changes in the observed distribution of individuals. Although Silverman (1985) suggests a more rigorous derivation of bandwidth using least squares cross validation, the 'ad hoc' method outlined by Worton (1989) performs comparably and is simpler to calculate. A bandwidth for each year was therefore calculated using the 'ad hoc' technique. In order to compare kernel densities the same

bandwidth must be used for each year (Fotheringham et al, 2000). The annual bandwidths ranged from 386 to 748 metres with a mean of 504 metres. A bandwidth of 500 metres was therefore used for each year. Figure 2.12 shows the smoothed univariate densities for the year 1998 to 2002. Figure 2.13 is an enlargement of Figure 2.12 over the Wilkawillina Gorge only.

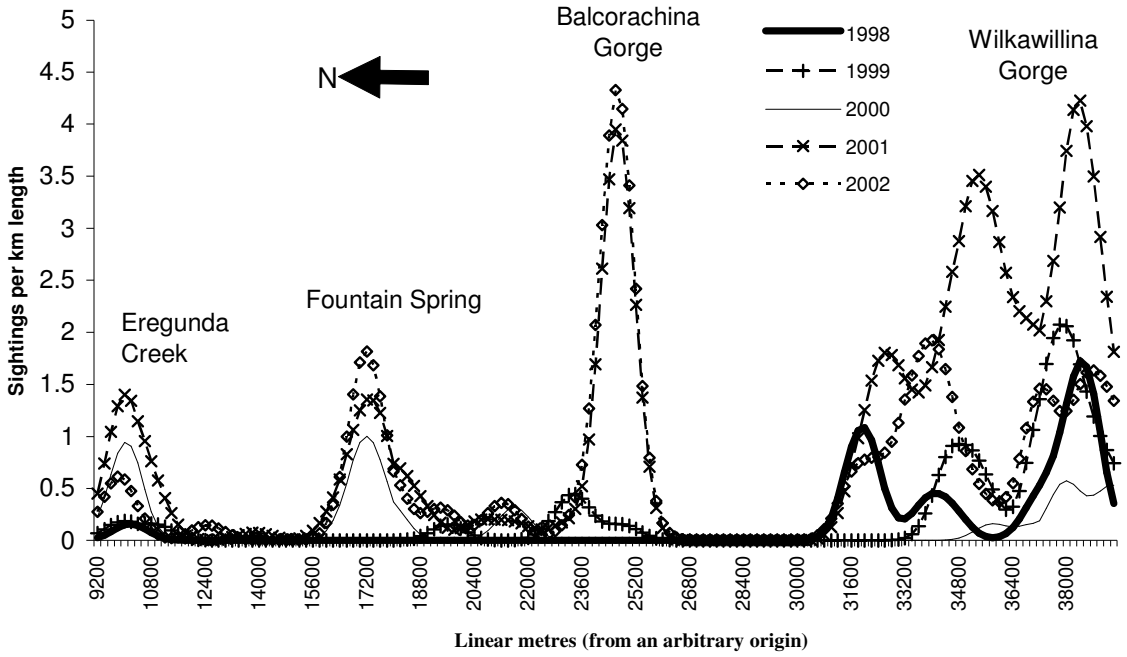


Figure 2.12 Smoothed univariate density estimates from 1998 to 2002.

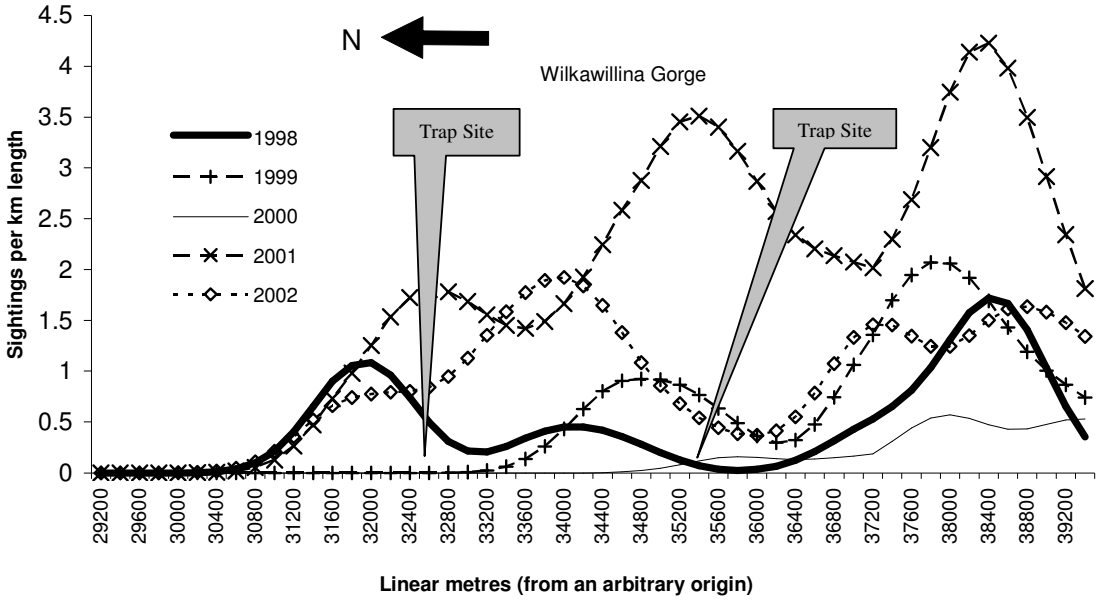


Figure 2.13 An enlargement of the smoothed univariate density estimates from 1998 to 2002 over Wilkawillina Gorge.

The 2000 census is particularly low at Wilkawillina Gorge while the highest counts were obtained across the entire study site in 2001. Unusually high counts are apparent at Balcorachina Creek in 2001 and 2002. Interestingly, the highest fluctuation in counts overall are in Wilkawillina Gorge where the locations of peak densities in each year appear to constantly shift. In Figure 2.12 no sightings were made in the hills between Balcorachina Gorge and the north end of Wilkawillina Gorge while some increases are apparent between Balcorachina Gorge, Fountain Spring and Eregunda Creek.

2.6 Discussion and Summary

2.6.1 Ivlev Parameters

Sharp and Norton (2000) modelled the annual rate of increase derived from aerial counts of *P. x. xanthopus* from 1980 to 1995 in western NSW and using the Ivlev (1961) model linked this to aggregated monthly rainfall data at a nearby rainfall gauge at White Cliffs (average annual rainfall, 245mm). Despite choosing another model for convenience, they found the rate of increase to be most correlated with 9 monthly rainfall intervals, lagged by nine months (R^2=0.35). Conversely in this study the rate of increase is more closely related to three to seven month intervals of rainfall, with no lag. Interestingly, Lapidge (2001) calculated a coarse measure of

survival at Leigh Creek using the number of animals known to be alive and found this to be correlated with the abundance of vegetation at the time of trapping ($F = 10.22, F_{0.05(1)1,9} = 5.12, P > 0.05$) and rainfall immediately three months prior ($F = 6.99, F_{0.05(1)1,9} = 5.12, P > 0.05$). This more closely agrees with the high R^2 values (R^2=0.80) for 3 months interval and no lag found at Wilkawillina Gorge using the Wirrelalpa Station rainfall gauge. Wilkawillina Gorge and Leigh Creek sanctuary have very similar land systems, vegetation and annual rainfalls. Both have permanent water. The Ivlev (1961) parameters only provide summary statistics of a range of underlying environmental and demographic processes and portray the superimposition of these processes.

As previously mentioned, it is expected that rainfall intervals of between seven and ten months would influence the birth pulse contribution to the rate of growth because new-born are not seen for more than six months and an additional few months of rainfall are likely to influence the birth pulses (see Chapter 3). Hence juvenile, sub-adult and adult survival is more likely to have the greatest influence on the rate of growth for rainfall intervals/lags of seven months or lower. Poor R^2 values were obtained for rainfall intervals and lags greater than seven months. However, a seven month interval of rainfall with no lag was chosen not for this reason but because the best overall R^2 values for all zones was obtained for this interval and lag, despite having higher R^2 values at intervals of five months lagged by zero to two months at two sites.

Both r_m and d were found to be more stable than other parameters in the bootstrap tests of the Ivlev (1961) model with lower confidence intervals. Despite these parameters being summary measures of the population, they are likely to be more meaningful than $\bar{r}$. The regression of $\bar{r}$ becomes invalid when populations boom and crash according to environmental fluctuations and in this situation should not be used to determine population responses. All sites, apart from Plumbago Station, have been modeled using the Ivlev (1961) equation up to 2002. Plumbago Station was not censored in 2001, consequently the 2000-2001 annual rate of growth and the 2001-2002 annual rate of growth could not be derived.

In Figure 2.9, the intrinsic rate of growth at Wilkawillina Gorge was lower (r_m=0.24) than all sites and similar to Depot Flat and Hawker (both having r_m=0.26). However, Plumbago Station had a high intrinsic rate of growth (r_m=0.64) with its 5% bias-corrected percentile above the 95% bias-corrected percentiles at Wilkawillina Gorge and Depot Flat.

Moreover, the Plumbago Station estimate of r_m is approximately the maximum attainable biological growth rate this species can possibly achieve (r_m = 0.61 +/- 0.14, Sharp and Norton (2000)). Wilkawillina Gorge and Depot Flat however, are significantly lower. Interestingly, the 95% bias-corrected percentile above the r_m estimate at Hawker also contains the Sharp and Norton (2000) maximum of 0.61. However, the data are too variable for any meaningful conclusions to be drawn about this site. Interestingly, apart from Plumbago Station, all sites are close to the Sharp and Norton (2000) estimates using aerial survey of r_m =0.32.

In contrast, the demographic efficiency (parameter *d* in the Ivlev (1961) equation) was found to be almost identical at both Wilkawillina Gorge and Plumbago Station with *d* equal to 0.048 and 0.050 respectively. Conversely, Depot Flat and Hawker are significantly lower than a value of 0.050. These results indicate that the population's capacity to grow at Wilkawillina Gorge and Plumbago Station is higher than Depot Flat and Hawker.

Wilkawillina Gorge and Plumbago Station have well-established fox and goat control programs in place. However, despite this the Wilkawillina Gorge data does exhibit some limiting factor on r_m. In light of these observations, it is possible that Wilkawillina Gorge may have fewer available resources than Plumbago Station. Conversely, no known integrated pest management is conducted over the Hawker and Depot Flat zones and it is expected that these sites would exhibit lower estimates of both *d* and r_m.

2.6.2 Uncertainty

It is clear from the R^2 estimates that the Ivlev (1961) models have only explained a fraction of the variation in the rates of growth. This unexplained variation is the result a combination of process uncertainty and observation uncertainty (Hilborn and Mangel, 1997).

Process uncertainty is likely to be attributed to several factors. For example, the use of rainfall as a surrogate or indicator of resource availability may be inadequate. This is because resources may respond differently to rainfall in different microclimates, soil types and temperatures, and for different vegetation communities. The nearest rainfall gauges may also not truly indicate the rainfall patterns over the range of the populations being censored. Process variation due to changes in demography, age structure, competition and predation may also account for the unexplained variation.

Observation uncertainty is also likely to contribute to this unexplained variation. A precise sightability index may be achieved from replicate studies over a sufficient and comparable

duration and under a range of habitats and survey conditions (Gibbs, 2000). However, Barnes et al (1986) have cautioned against the uncritical use of aerial correction factors and Kinnear (1994) has been particularly critical of widespread use of the Lim (1987) sightability correction, particularly if this factor is used to estimate absolute abundance. While this analysis has ignored any fixed sightability factors and concentrated on relative abundance, the sightability may still vary due to different observers, prevailing weather conditions, pilot ability and aircraft speeds.

The magnitude of observation uncertainty may also be site specific. For example, sites in open country with less vegetation and less complicated rock formations may have less observation uncertainty than more closed sites. Of equal concern is how sightability varies with total population particularly since most colonies in South Australia consist of small numbers of animals. As previously mentioned, this index may either have a linear or non-linear relationship with the absolute density of a population (Southwell, 1989). However, ascertaining the precision of the aerial sightability correction for *P. x. xanthopus*, and its linear or otherwise relationship the total population, is prohibitively expensive at this time.

The Hawker and Depot Flat sections are flown together and the total length of the flight is particularly long. In the early stages of the flight the conditions may be favorable but towards the end of the flight, the conditions on a few occasions have deteriorated. The rainfall is also higher and more variable in these zones. Consequently the rainfall may be more loosely correlated with the rate of growth. Interestingly, Figure 2.7b, which describes the level temporal autocorrelation present, shows the Depot Flat displaying significant autocorrelation at a one-year lag compared with Hawker displaying no significant autocorrelation. The lack of temporal autocorrelation displayed in the Hawker data is more likely due to this being swamped by observation noise.

2.6.3 The utility of the aerial survey

Originally, the central Flinders Ranges (The Hawker and Depot Flat flight lines) was flown as a control area because it was thought by DEH to have little or no pest control strategies. This was compared with responses to the integrated pest control areas (including Plumbago Station and Wilkawillina Gorge - Alexander, pers comm 1999). However, the noise in the Hawker section, invalidates this as a control site. In hindsight, an area north of Blinman in the Northern Flinders Ranges may have been a better control site. The land systems and rainfall in this northern area are likely to be more comparable with Plumbago Station and Wilkawillina Gorge.

The utility of the aerial census and the parameters derived from it, depends upon the management objectives. For example, is the underpinning objective to maintain a viable metapopulation or to further increase the abundance of the population? These two objectives may not be related and are likely to require different monitoring strategies. Following population trends may fail to indicate the long-term viability of a population.

The use of summary parameters like *d* and r_m is also problematic. In Figures 2.9 and 2.10, due to the structure of the Ivlev (1961) model, the bootstrapped lower percentiles have been truncate to zero if values fall below zero. Caution therefore needs to be exercised when interpreting these lower percentiles. Fortunately this has not discounted comparison of the upper bounds of these estimates. However, as previously mentioned these summary parameters do not clearly distinguish the biological processes that underpin them, and without supporting data it is difficult to ascertain the likely reasons for any differences. For example, why does Wilkawillina Gorge have a lower value for r_m but *d* is almost equal to Plumbago Station when the same integrated pest control is applied in these areas?

As previously mentioned, a useful product of the GPS aerial recording system is the ability to analyse spatial dispersion. Figures 2.12 and 2.13 use a Kernel density smoothing technique to describe the univariate densities recorded along the flight line each year over five years. While these data are likely to be subject to observation noise, there is some evidence to suggest there was significant transient movement, particularly within the Wilkawillina Gorge. The shift in the population density also coincides with a drought when activity from other herbivores around the water holes in the Wilkawillina Gorge may have impacted on the vegetation community.

Figures 2.12 and 2.13 display huge fluctuations within Wilkawillina Gorge but do not appear to indicate an expansion of the colony immediately north of Wilkawillina Gorge. The habitat immediately north of Wilkawillina Gorge is marginal for three to four kilometers until just south of Balcorachina Gorge (see Chapter 4). This may account for the lack of movement of *P. x. xanthopus* into this area. However, Balcorachina Gorge, Fountain Spring and Eregunda Creek all indicate increases in the population. These increases do not appear to directly relate to the fluctuations in Wilkawillina Gorge.

2.6.4 Scale Issues

The design of any survey must be based upon a clear set of objectives and the scale of any monitoring program must be carefully planned to address species management targets. Aerial surveys conducted over a long period are particularly useful in revealling occupancy patterns in the landscape. However, the utility of aerial census sampling on its own, in guiding management strategies, is questionable. There may be little point in continuing to measure regional responses if the threats to local populations are not detectable at the regional scale. Conversely, attempting to understand the detailed ecological processes of a local population may be difficult to extrapolate into other areas and may contribute little to the management of a species as a whole.

Arguably, local populations fluctuate and the timely detection of a net decline in the entire metapopulation may require a multi-scaled suite of monitoring strategies. In Chapter 3, detailed demographic data are presented from mark recapture sampling. At this scale, demographic and behavioural processes are usually revealed. The challenge to conservation biologists is combining or interpreting trends from multiple data sources and scales. In Chapter 4, ground survey data and aerial census data are used to model the habitat preferences of this species. In Chapter 6, a method is presented that combines aerial census data and mark recapture information in a PVA described in Chapter 5, to more effectively guide future management and monitoring strategies.

CHAPTER 3

A mark recapture study of the Yellow-footed Rock-wallaby (*Petrogale xanthopus xanthopus*).

3.0 Introduction

Mark recapture techniques are employed for a variety of reasons including estimating population abundance, gathering vital statistics, sampling tissue for genetic analysis, estimating life history parameters and sampling movement. The experimental design of any mark recapture methodology must therefore be tailored to the questions being asked by the researcher (Hayne, 1978; McCallum, 2000).

In Chapter 2, aerial census data were analysed. This method provided summary statistics related to the relative abundance of *P. x. xanthopus*. However, while population surveys at this level of abstraction may provide useful insights for wildlife managers at the landscape level, they may fail to address many of the processes that underpin the abundance and viability of a species (McCallum, 2000). Conversely, mark recapture techniques that target local populations help reveal the more detailed demographic and behavioural processes that underpin that local population.

Caughley (1977) lists the following information that can be derived from mark recapture techniques:

a) movement,
b) growth rate,
c) age-specific fecundity,
d) age-specifc mortality,
e) size of the population,
f) rate of birth and immigration combined,
g) rate of death and emigration combined,
h) rate of harvesting,
i) rate of increase.

Seber (1986) also provide a rigorous review of mark recapture methods. Approaches a) to d) only require that the subset of marked individuals can be re-identified in subsequent trapping exercises

with the unmarked segment of the population being statistically unimportant when estimating these parameters (Caughley, 1977). Mark recapture methods for estimating fecundity are relatively straightforward. However, the determination of age-specific or stage-specific survival involves the estimation of two parameters: capture probability and survival probability (McCallum, 2000). The estimation of age-specific survival is statistically robust and influenced to a lesser degree by trap-shyness or trap-dependency (McCallum, 2000; Seber, 1986). Unfortunately, survival estimates are often confounded by emigration and non-random transient movement.

The primary aim in this chapter is to compare fecundity, survival and the condition of animals at two sites in the Flinders Ranges, which are each subject to different pest management strategies, namely fox and goat control. These estimates will also be compared with similar work conducted in New South Wales (NSW) by Sharp (2000). In Chapter 5 using a PVA, the difference between Sharp's (2000) findings and the findings in this study will also be tested. Moreover, this chapter attempts to answer the following questions:

1. Does the survival of *P. x. xanthopus* differ between sex, stage and site?
2. Does rainfall as a surrogate of resource availability affect survival?
3. Does fecundity vary with rainfall?
4. Does fecundity vary with site?
5. Does animal condition vary with site?

3.1 Estimating Survival and Fecundity

The Cormack-Jolly-Seber (Cormack, 1979) model for estimating survival from mark recapture data has been adopted in this study using a programme called 'Mark' by Cooch and White (2002). As it is important to understand the structure of any model and the assumptions that underpin it, Sections 3.2 and 3.3, explore the theory and mathematics of the Cormack-Jolly-Seber approach.

The Jolly-Seber model, independently developed by Jolly (1965) and Seber (1965) is used to estimate abundance (Barker and White, 2000). This is a well-known mark recapture technique that applies to open populations. Open populations are subject to immigration and emigration as well as birth and death events. Conversely, closed populations are without immigration and emigration. The Jolly-Seber model is sufficiently general to be able to include different assumptions and specify different constraints. For example, the capture probability for juveniles can be separated from adults by grouping the individuals in the population (Cormack, 1979).

However, the underpinning assumption is that all individuals within a group have an equal probability of being caught (Cormack, 1989). The input data necessary to calculate a Jolly-Seber estimate is a matrix of binary capture histories where 1 denotes captured and 0 denotes not captured (McCallum, 2000).

The general form of the Jolly-Seber model is multinomial and the animals are regarded as N independent multinomial trials with certain probabilities of belonging to different capture probabilities (Seber, 1982). This is in contrast to a classical hypergeometric closed population approach where the data are represented as distributions of random samples and the randomness in sampling is caused by the activity of the experimenter (Seber, 1982).

3.2 The Cormack-Jolly-Seber Model (CJS)

Like the Jolly-Seber model, the rationale behind the Cormack-Jolly-Seber approach is to focus on the individual capture histories and hence the behavior of individual animals. The general form of the model allows the estimation of individual survival probabilities ϕ from time t to time $t+1$ and individual capture probabilities p at time t. This approach incorporates stochasticity by allowing random variation in both the sampling process and the population being studied (Cormack, 1979). Survival in this context refers only to the survival of the sample population. This may or may not be representative of the whole population. Additionally, the fate of an individual first trapped and subsequently not seen will always be unknown in the absence of other information, and the individual may have permanently emigrated, dispersed or died (Bennettes et al, 2001).

The Cormack-Jolly-Seber model involves fitting log-linear models to an incomplete contingency table (Seber, 1982). Consider an example of a five capture occasions where there are 2^5 different combinations of trap histories that any individual animal is likely to encounter (eg 11111, 10000, 11000, 11100, etc). A corresponding five dimensional incomplete contingency table can be constructed to solve for survival (ϕ) and capture probability (p). This table contains a combination of these capture history categories arranged in a standard hierarchy (Cormack, 1989). This hierarchy contains parameters that describe the main, first order, second order etc. effects of the trap histories. More generally, a contingency table contains count data of cohorts in mutually exclusive classes with which structural models can be fitted to the expected counts (Bishop et al, 1975; Cormack, 1989). In mark recapture experiments these structural models use stipulated census dependencies to solve unknown entries (Fienberg, 1972).

The Cormack-Jolly-Seber approach has been adapted from Fienberg (1972). Fienberg (1972) describes the use of an incomplete 2^s contingency table to calculate the total population size in a

closed population, where *s* is the number of capture occasions. For example, Table 3.1 is a simple two-dimensional incomplete contingency table that describes two capture occasions where the individuals are sampled with replacement.

Table 3.1 Incomplete contingency table for two captures.

	Second capture		
First capture	**Present**	**Absent**	
Present	n_{11}	n_{12}	n_{1+}
Absent	n_{21}	$\boldsymbol{(n_{22})}$	
	n_{+1}		**(N)**

In Table 3.1, a subscript of 1 represents presence and a subscript of 2 represents absence. Thus n_{11} represents the number of animals caught on the first and second occasions, n_{12} represents the number of animals caught on the first occasion but absent on the second occasion and n_{21} represents the number of animals absent on the first occasion but caught on the second occasion. In Table 3.1, n_{+1} and n_{1+} are column sums and row sums respectively.

The table is incomplete because $\boldsymbol{n_{22}}$, the number animals absent on the first and second occasion, is unknown and hence N, the total population is unknown. Using log-linear models, Fienberg (1972) describes a method of projecting the observed data (n_{11}, n_{12}, n_{21}) to derive $\boldsymbol{n_{22}}$ and hence N. The expected values of the observed counts m_{ij}= E(n_{ij}) = Np_{ij}, where p_{ij} is the probability of an individual occurring in that element.

Bishop et al (1975, p13) describe a number of conditions that can be met but suggest the more useful cross-product (or odds ratio) condition (Equation 3.1a).

$$\frac{m_{11}m_{22}}{m_{12}m_{21}} = \alpha \qquad \textbf{Equation 3.1a}$$

This can also be written as:

$$\log m_{11} + \log m_{22} - \log m_{12} - \log m_{21} = \log \alpha \qquad \textbf{Equation 3.1b}$$

If the two samples were independent, $\alpha = 1$ and $\log \alpha = 0$. Since the conditional maximum likelihood estimates of the expected values of m_{ij} are simply n_{ij}, an estimate can be made of the total population size using Equation 3.3 (Bishop et al, 1975; Fienberg, 1972). This relationship is equivalent the traditional two-sample Peterson estimate (Equation 3.2). See Caughley (1977) for a practical description of the Peterson estimate.

$$N = n_{11} + n_{12} + n_{21} + \frac{n_{12}n_{21}}{n_{11}} = \frac{n_{1+}n_{+1}}{n_{11}} \qquad \textbf{Equation 3.2}$$

When there are a large number of sample occasions it is useful to construct a log linear model for each m_{ij} in the form of main, first and second order interactive effects (denoted as $u\ldots$) because these interactions or interdependencies are quite often known. The number of parameters $u_{\ldots}$ in the log-linear model therefore depends upon the dimension (or number of capture events) and the interdependencies between the dimensions (Bishop et al, 1975). Providing biologically meaningful interdependencies can be found, the log-linear model can be constrained by setting some of the parameters $u_{\ldots}$ to zero. This is called an unsaturated model. This also reduces the model's variance.

Now consider an experiment with s capture occasions. There will exist 2^s - 1 known elements with n and m now having s subscripts, $n_{i1\ldots is}$ and $m_{i1\ldots is}$ for i_j where j = 1 to s. Here $n_{22\ldots2}$ is unknown because it is the number of animals absent on all occasions. If the total sample size is n and the total population is N then N – n individuals will be absent from all samples (Bishop et al, 1975).

The most general form of log-linear model is:

$$\log m_{i_1\ldots i_s} = u + u_{1(i_1)} + \ldots + u_{s(i_s)} + \sum u_{\alpha\beta(i_\alpha i_\beta)} + \ldots + u_{1\ldots s(i_1\ldots i_s)} \qquad \textbf{Equation 3.3}$$

The subscript brackets $(i_1)\ldots(i_s)$ refers to a function for which u depends. This contains all $m_{i_1\ldots i_s}$ that are all either 1 (present) or 2 (absent) at that capture occurrence (1 to s).

The term $\sum u_{\alpha\beta(i_\alpha i_\beta)}$ refers to the second order interactive effects, which is all of the other possible combinations between every $m_{i1\ldots is}$ except $u_{1\ldots s(i_1\ldots i_s)}$, which is a function of diagonal elements of $m_{i1\ldots is}$. In this model the sum of any individual over any of its subscripts i_1, i_2, .. i_s are zero (Bishop et al, 1975).

Fienberg (1972) used hierachical models, that is, models where the higher order u parameters are set to zero when their lower order counterparts are set to zero. For example if u_{12} = 0, u_{123} = 0 and if u_1 = 0 , u_{12} = 0. By way of example, Table 3.1 is a two dimensional contingency table including Bishop et al's (1975) log-linear model where the parameters $u\ldots$ represent the means of the logarithms of $m_{i1\ldots is}$.

$$\log m_{i_1 i_2} = u + u_{1(i_1)} + u_{2(i_2)} + u_{12(i_1 i_2)} \qquad \textbf{Equation 3.4}$$

Quasi-independence can be defined as "a form of independence, conditional on the restriction of our attention to an incomplete proportion of a table" (Bishop et al, 1975, p181). Assuming quasi-independence, $u_{12(i_1 i_2)}$ is zero because $m_{22\ldots2}$, the incomplete portion of the table is unknown. Equation 3.4 therefore reduces to Equation 3.5.

$$\log m_{i_1 i_2} = u + u_{1(i_1)} + u_{2(i_2)} \qquad \textbf{Equation 3.5}$$

Fienberg (1972) derived the parameters *u* from averaging techniques over all levels. Here the *u* is the overall mean of all $m_{i1\ldots is}$. This is given by Equation 3.6.

$$u = \tfrac{1}{4}\left(\log m_{11} + \log m_{12} + \log m_{21} + \log m_{22}\right). \qquad \textbf{Equation 3.6}$$

The main effects can be denoted by,

$$u + u_{1i_1} = \tfrac{1}{2}\left(\log m_{i_1 1} + \log m_{i_1 2}\right) \qquad \textbf{Equation 3.7}$$

and

$$u + u_{2i_2} = \tfrac{1}{2}\left(\log m_{1i_2} + \log m_{2i_2}\right). \qquad \textbf{Equation 3.8}$$

Equation 3.7 can be more specifically stated as Equations 3.8a and 3.8b.

$$u + u_{11} = \tfrac{1}{2}\left(\log m_{11} + \log m_{12}\right) \quad \text{and,} \qquad \textbf{Equation 3.9a}$$

$$u + u_{12} = \tfrac{1}{2}\left(\log m_{21} + \log m_{22}\right). \qquad \textbf{Equation 3.9b}$$

Alternatively, if we assumed equal trapability and independence in the samples, the main effects are equal (i.e. $u_1 = u_2 = \ldots u_s$, - Bishop et al, 1975).

3.2.1 Cormack-Jolly-Seber Model for Closed Populations

Cormack (1989) proposed an alternative approach to Fienberg in which $u = \log(m_{111..1})$ and the log of an expected absence event on a sample occasion is a function of the main effect of that subscript and u. For example, $\log m_{2111...1} = u + u_1$ and log $\log m_{1211...1} = u + u_2$, however when two capture occasion in succession have missed animals, the first order interactive effects are included, $\log m_{1221...1} = u + u_2 + u_3 + u_{23}$. In this approach Cormack (1989) does not introduce second order interactive effects, meaning non-successive sample occasions are not directly interdependent. Again the $\log m_{222...2}$ model is not defined.

In terms of biological parameters in a closed population, Cormack (1989) shows that $m_{111...1} = Np_1p_2p_3..p_s$, and $m_{211...1} = N(1-p_1)p_2p_3...p_s$, $m_{121...1} = Np_1(1-p_2)p_3...p_s$ etc. Where p_i is the probability of an individual being captured on occasion i. Hence the parameters u can be solved as:

$$u = \log(Np_1p_2p_3..p_s) \qquad \textbf{Equation 3.10a}$$

$$u_{i_1} = \log(1-p_{i_1})/p_{i_1} \qquad \textbf{Equation 3.10b}$$

$$u_{i_1i_2} = 0 \qquad \textbf{Equation 3.10c}$$

After substituting Equations 3.10a, 3.10b and 3.10c into Equation 3.3, maximum likelihood estimates are calculated for $\log m_{i1...is}$.

3.2.2 Cormack-Jolly-Seber Model for Open Populations

Open populations are subject to birth and death events. In practice it is often difficult to separate birth events from immigration and death events from emigration. Cormack (1989) introduces the following terms; ϕ_{i_1} is the probability an individual survives from the i^{th} to $(i+1)^{th}$ capture occasions, γ_i is the probability that an individual is not seen after the i^{th} capture occasion and ψ_i is a multiplicative factor where ψ_i multiplied by the number of unmarked individuals surviving from the i^{th} occasion equals the total number of unmarked individuals at the $(i+1)^{th}$ occasion (Cormack, 1989). If there is no immigration the number of births at the $(i+1)^{th}$ capture occasion equals $N_i(1-p_i)\phi_i(\psi_i - 1)$.

A similar multiplicative parameter, λ_i is introduced by Cormack for animals departing from the population. Assuming no emigration, $\lambda_i = \gamma_i /(\phi_i(1-p_{i+1})\gamma_{i+1})$. Using these relationships, Cormack derived equations for $m_{i1\ldots is}$. The terms *u* are then derived by Cormack from the various ratios of $m_{i1\ldots is}$ in Table 3.2.

Table 3.2 Relationship between *u* and biological parameters.

Overall Mean	u	$\log(Np_1\phi_1 p_2\phi_2..p_{s-1}(1-\gamma_{s-1}))$
Main Effects	u_1, u_i, u_s	$\log(1-p_1)\gamma_1 / p_1, (1-p_i)/p_i, \gamma_{s-1}/(1-\gamma_{s-1}))$
Interactions	$u_{12}, u_{123}, u_{1234}, \ldots$	$\psi_2, \psi_3, \psi_4, ..$
	$u_{(s-1)s}, u_{(s-2)(s-1)s}, \ldots$	$\lambda_{s-2}, \lambda_{s-3}, \lambda_{s-4}, ..$

(adapted from Cormack, 1989)

The strength in the Cormack-Jolly-Seber approach is its ability to constrain parameters to be fixed, made to vary with time and/or between cohorts. A cohort is a group of animals that share their first trap occasion together and by model design share equal survival and capture probabilities throughout the experiment. The following three examples illustrate the flexibility of these parameter constraints. Tables 3.3a and 3.3b below illustrate a simple capture scenario over five occasions where the survival and capture probabilities are specified to vary over time but not between cohorts.

Table 3.3a Time varying capture probabilities.

	Capture Occasion				
Cohort *I*	**1**	**2**	**3**	**4**	**5**
1		p_2	p_3	p_4	p_5
2			p_3	p_4	p_5
3				p_4	p_5
4					p_5

Table 3.3b Time varying survival parameters.

	Capture Occasion				
Cohort *i*	**1**	**2**	**3**	**4**	**5**
1	ϕ_1	ϕ_2	ϕ_3	ϕ_4	
2		ϕ_2	ϕ_3	ϕ_4	
3			ϕ_3	ϕ_4	
4				ϕ_4	

Here the survival parameters represent the probability of surviving from one capture occasion to the next and the capture probabilities represent the probability of becoming captured on a particular capture occasion. Tables 3.4a and 3.4b below illustrate a scenario where the survival probabilities are specified to vary over time and not between cohorts but the capture probabilities are fixed. Conversely, the capture probabilities have been fixed over the entire period and for all cohorts.

Table 3.4a Constant capture probabilities.

	Capture Occasion				
Cohort *i*	**1**	**2**	**3**	**4**	**5**
1		p_2	p_2	p_2	p_2
2			p_2	p_2	p_2
3				p_2	p_2
4					p_2

Table 3.4b Time varying survival parameters.

	Capture Occasion				
Cohort *i*	**1**	**2**	**3**	**4**	**5**
1	ϕ_1	ϕ_2	ϕ_3	ϕ_4	
2		ϕ_2	ϕ_3	ϕ_4	
3			ϕ_3	ϕ_4	
4				ϕ_4	

Table 3.5 describes a situation where survival in the first interval is different to survival between any subsequent occasions and different to other cohort survivals. Subsequent to a cohort's first two captures, its survival varies with time but not between cohorts. Allowing new cohorts to have different survival probabilities to existing cohorts is indicative of an age-specific survival model. Here the cohorts may be grouped such that juveniles or sub-adults are separated from the adults (McCallum, 2000). In this scenario it is preferable to time the trap occasions seasonally or, where possible, in synchronisation with breeding and development patterns.

Table 3.5 Time and cohort varying survival parameters.

	Capture Occasion				
Cohort *i*	**1**	**2**	**3**	**4**	**5**
1	ϕ_1	ϕ_5	ϕ_6	ϕ_7	
2		ϕ_2	ϕ_6	ϕ_7	
3			ϕ_3	ϕ_7	
4				ϕ_4	

Conversely, in Table 3.6 the survival probabilities are specified such that every cohort has the same probability of survival on the first trap interval but different fixed probability of survival thereafter.

Table 3.6 Time and cohort varying survival parameters.

	Capture Occasion				
Cohort *i*	**1**	**2**	**3**	**4**	**5**
1	ϕ_1	ϕ_2	ϕ_2	ϕ_2	
2		ϕ_1	ϕ_2	ϕ_2	
3			ϕ_1	ϕ_2	
4				ϕ_1	

3.3 Constrained Linear Models

Further developments in mark recapture modelling in the last 20 years have led to a more unified approach to capture-recapture theory (Lebreton et al, 1992) and extensions to the Cormack-Jolly-Seber approach now allow both the survival and capture probability parameters to be constrained as functions of external covariate variables such weight, size, condition and rainfall (Burnham et al, 1987; Lebreton et al, 1992; McCallum, 2000).

The parameter estimates in the Cormack-Jolly-Seber model are able to be specified as fixed or made to vary with time and/or between cohorts. However, this assumes independence of fates and identities of the individuals (Lebreton et al, 1992). In other words, the fate of each individual should be independent of one another but the average rates of survival and trapability should follow an identifiable distribution across the population. These assumptions seldom hold true and survival probability and capture probability often depend upon a range of other factors. The confounding numerical problem associated with separating estimates of survival probability and capture probability and a failure of these assumptions has led to the development of linear link equations which allow covariates to be included in the model. Covariates are facilitated in the general form of the linear additive models (see Equations 3.11a or 3.11b) for the estimation of capture probability (p) and survival (ϕ).

As previously mentioned, the fate of an individual first trapped and subsequently not seen will always be unknown in the absence of other information and an individual may have dispersed or died (Bennettes et al, 2001). As such the term ϕ referring to survival has been replaced by the term χ in this study from here on, referring to the probability that an animal remains in the population.

The use of covariates is particularly useful given the negative bias in the estimation of χ when capture probabilities are low (Lebreton et al, 1992; Pradel et al, 1997). This bias is present in time specific or constant parameter models (Pradel et al, 1997).

The estimates *p* and χ can be constrained on a 0 to 1 scale (Cormack, 1989). In order to achieve this a log-odds (or logit) transformation is applied to Equations 3.11a and 3.11b giving Equations 3.12a and 3.12b. These functions are constructed in a design matrix in the programme 'Mark' (Cooch and White, 2002).

$$p = \beta_0 + \beta_1 x \qquad \textbf{Equation 3.11a}$$

$$\chi = \beta_0 + \beta_1 x \qquad \textbf{Equation 3.11b}$$

$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 x \qquad \textbf{Equation 3.12a}$$

$$\ln\left(\frac{\chi}{1-\chi}\right) = \beta_0 + \beta_1 x \qquad \textbf{Equation 3.12b}$$

Here the variable *x* in Equations 3.12a and 3.12b may be a lagged interval of rainfall (as a surrogate variable representing resource availability), temperature (perhaps associated with trappability) or any other environmental conditions thought to affect *p* or χ. These equations can also be multivariate and include more than one environmental state x_i. The variable x_i can also be binary or categorical, representing two (or more) different known states of a group of individuals or catch effort. For example, these groups might be sex, site or stage of development. These effects may also be interactive. The categorical variables are also known as 'dummy' variables.

Equation 3.13 represents an unconstrained logistic model relating survival to two categorical variables, *sex* and *stage*. The categorical variables, *sex* and *stage* represent the first order effects and *sex.stage* is an interactive effect.

$$\ln\left(\frac{\chi}{1-\chi}\right) = \beta_0 + \beta_1 sex + \beta_2 stage + \beta_3 sex.stage \qquad \textbf{Equation 3.13}$$

Lebreton (1992) suggest first testing the goodness-of-fit of a global (more complex) model with the data using bootstrapping. Parametric bootstrapping involves simulating the encounter histories from the parameter estimates *p* and χ, and repeating this a large number of times using a random number generator. This approach allows the observed deviance of the data to be

compared with the distribution of simulated deviances to see if it adequately falls within the distribution (Cooch and White, 2002).

Unfortunately, the programme 'Mark' does not facilitate parametric bootstrapping of complex linear models. Instead, parametric bootstrapping of these more complex models was carried out by manipulating the input data in the database using a separate C++ programme. A lack of fit of the model to the data using parametric bootstrapping suggests that the heterogeneity between animals (i.e. capture rate and survival) cannot be adequately explained. The identity of rates assumption is therefore violated. After finding an adequate fit of the global model, Akaike's Information Criterion (AIC) scores (Akaike, 1973) are used in 'Mark' (Cooch and White, 2002) to compare the relative fit of other simpler candidate models such as Equations 3.14a, 3.14b and 3.14c (Lebreton et al, 1992).

$$\ln\left(\frac{\chi}{1-\chi}\right) = \beta_0 + \beta_1 sex + \beta_2 stage \qquad \textbf{Equation 3.14a}$$

$$\ln\left(\frac{\chi}{1-\chi}\right) = \beta_0 + \beta_1 sex \qquad \textbf{Equation 3.14b}$$

$$\ln\left(\frac{\chi}{1-\chi}\right) = \beta_0 \qquad \textbf{Equation 3.14c}$$

Equations 3.14a, 3.14b and 3.14c are nested models. Equation 3.14a is a more complex model with two covariates. At the other extreme, Equation 3.14c has dropped both covariate terms and assumed χ is constant and independent of *sex* and *stage*. AIC scores are advocated by Lebreton (1992) to be a useful tool for selecting the most parsimonious mark recapture model (i.e. the model that accounts for most of the variation in the data with the fewest parameters). AIC scores, unlike likelihood ratio tests, also allow non-nested models to be tested (Akaike, 1973; Hilborn and Mangel, 1997). The AIC for a model is given by:

$$AIC = -2\ln(L) + 2K \qquad \textbf{Equation 3.15}$$

Here, $\ln(L)$ is the log-likelihood of the data given a particular model and K is the number of parameters in the model. A modified version of AIC is the bias-corrected AIC (called AICc). This is used in the programme 'Mark' (Cooch and White, 2002). This accounts for differences in effective sample size.

$$AIC_c = -2\ln(L) + 2K + \frac{2K(K+1)}{M-K-1} \qquad \textbf{Equation 3.16}$$

A further modification of this called quasi-AIC score ($QAIC_c$) is used during parametric bootstrapping (Cooch and White 2002). Here the –2ln(L) term in Equation 3.16 is divided by $\hat{c}$ where $\hat{c} = \frac{\chi^2}{df}$ (a chi-square distribution), is a measure of the magnitude of 'binomial' noise or over-dispersion in the model. If $\hat{c} > 1$, the data is over-dispersed. If $\hat{c} = 1$, a given simulated model fits the data perfectly. Although when $\hat{c} < 1$, it is also not a perfect fit, Cooch and White (2002) recommend setting $\hat{c} = 1$ in this instance.

In programme 'Mark', normalised Akaike weights are also provided (Cooch and White, 2002).

$$w_i = \frac{e^{(\frac{-\Delta AIC}{2})}}{\sum e^{\frac{-\Delta AIC}{2}}} \qquad \textbf{Equation 3.17}$$

Here, ΔAIC is the change in AIC from the next highest AIC scoring model to the current model having a smaller (and better) AIC score. The denominator in Equation 3.17 is the sum of the all of the exponentially transformed ΔAIC values.

Time dependent models don't use temporal covariates such as rainfall. In this situation, χ and p vary independently with time rather than vary with an identifiable covariate such as rainfall. However, simple models incorporating only one or two categorical variables such as site (or colony) and sex are best built as 'group' models. Group models are more appropriate when 'parallelism' is not present. In other words each sex or colony group exhibit different patterns in χ and p over time. Parallelism can be best explained using Equation 3.18. This is a constrained model where rainfall has been used as a covariate combined with the sex categorical variable.

$$\ln\left(\frac{\chi}{1-\chi}\right) = \beta_0 + \beta_1 sex + \beta_2 rain \qquad \textbf{Equation 3.18}$$

Before the logit transformation, these effects are additive and termed 'parallel' (Lebreton et al, 1992).

3.3.1 Open Populations: Estimating Survival

As previously mentioned, the fate of an individual first trapped and subsequently not seen will always be unknown in the absence of other information. The individual may have permanently emigrated, dispersed or died and the presence of transient animals in a population invalidates the estimate of survival in traditional mark recapture models unless emigration is random (Bennettes et al, 2001; Barker and White, 2000; Pradel et al, 1997). Under a random emigration scenario, the probability of capture is confounded by movement rather than survival (Barker and White, 2000).

Bennettes et al (2001) discuss four classes of re-observation data:

1. recovery data where the individuals are recovered dead,
2. recapture/resighting data, where the animals are subsequently recaptured or sighted alive,
3. known status data, where the animals are reobserved dead or alive with a probability of 1.0, and
4. combined data, where data of more than one type are collected.

However, dispersal cannot be estimated from data at a single site (Bennettes et al, 2001). Pradel (1997) developed a technique to estimate the proportion of transients at a single site under the assumption of equal capture probabilities, providing a two-age class model is used. However, this approach does not deal with permanently dispersing individuals. While multi-site models do permit age-specific probabilities of movement between pairs of sites (Bennettes et al, 2001), this requires a large amount of field sites in complex landscapes. This is not practical in the complex rocky and often inaccessible landscape in the Flinders Ranges.

Known status data can be collected using radio-telemetry providing the animal can safely carry a radio collar and the radio collar can potentially endure for the lifetime of the study. If a mortality indicator is fitted to the collar the status of the individual can be instantly collected. In the absence of a mortality collar each individual would have to be tracked to visibility on a regular basis. If the status of individual can be assured, a 100% detection probability can be incorporated into the model (Bennettes et al, 2001). However, due to financial constraints, radio tracking was not employed for the purpose of this study.

3.4 Materials and Methods

3.4.1 Study Sites

The aim of this study was to compare the fecundity, condition and survival (here on called vital rates) at two sites in the Flinders Ranges. However, a third site was also trapped for the collection of genetic data. Figure 3.1 shows the locations of the three trap sites in the Bunker Range of the Flinders Ranges. Trap sites one and three (named Wilkawillina South and Wilkawillina North respectively) were located in the Flinders Ranges National Park. Populations at these sites have been subject to integrated pest control programme since the early 1990's. These two trap sites are approximately 3km apart. Trap site two (Eregunda Creek) is located approximately 24km north of trap site three in pastoral property. This property has only limited goat control. Fox and rabbit control extend north of the Flinders Ranges National Park approximately to the Balcorachina Gorge.

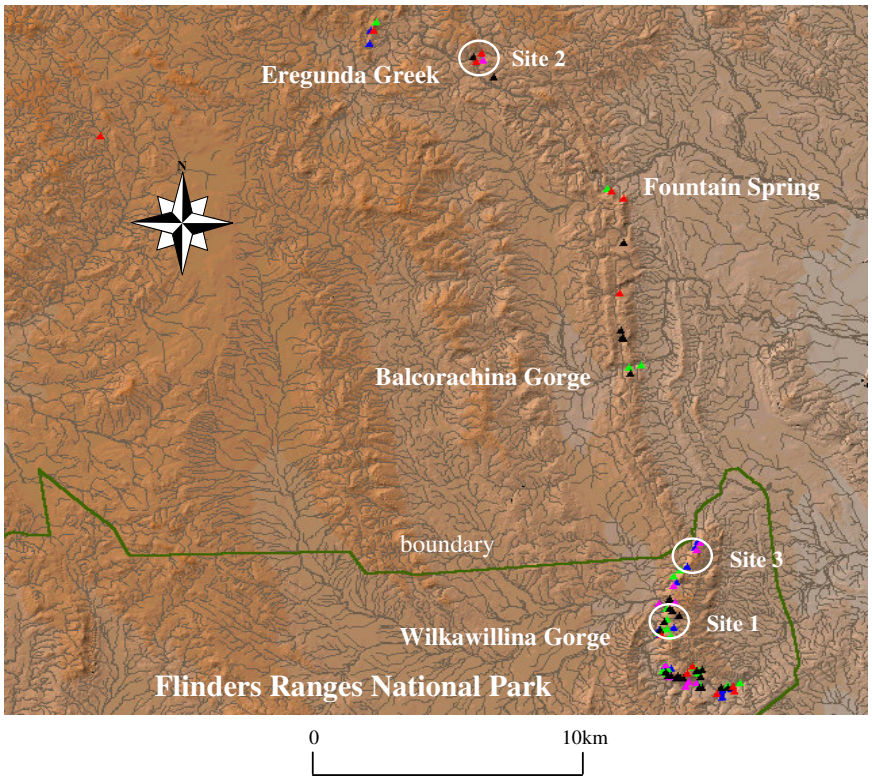


Figure 3.1 Trap Sites

3.4.2 Trap Methodology

A mark recapture programme commenced in March 1998 at site one (Wilkawillina South) and site two (Eregunda Creek). The mark recapture of the third site (Wilkawillina North) began in February 1999. The frequency of trap sampling was six-monthly. If all pouched young ages are estimated, a six-monthly capture interval is able to sample most birth events because breeding mothers cannot successfully produced offspring at an interval smaller than approximately 200 days (Poole et al, 1985). Each trap session consisted of three trap nights.

Ten traps were located at each site. An adapted fox treadle 'soft' trap design with shade-cloth on the top and two sides was used to minimise injury (see Plate 3.1). This design was recommended by Sharp (*pers com*, 1997).



Plate 3.1 Soft treadle trap

3.4.3 Measurements

All animals were weighed and foot, leg and tail measurements taken. Vitamin-E-Selen (*DL-Alpha-tocopheryl Acertate* and *Sodium Selenite Pentahydrate*) was also administered to all animals over 2.5kg according to the recommended dosages in order to minimise the likelihood of trap myopathy. All animals over 2.5kg animals were also ear marked with Allflex® 28 millimetre coloured button tags (see Plate 3.2). This was recommended by Sharp (*pers com*, 1997). Smaller animals and pouched young were notched in the ears with a small punch hole according to a recognisable coding system. Where possible all animals more than 150 days old had biopsy notches removed from the ears for subsequent genetic analysis.

Radio tracking is part of a continuing programme at the trap site 2, and is collected as part of a separate study by the author. The results of radio tracking are incomplete and are not presented in this study. Selected adults are radio collared and tracked using an automated radio tracking system (see Plate 3.3).



Plate 3.2 Ear Tagging



Plate 3.3 Radio Collar

A common response by macropods to a threatening situation such as a trapping event is to throw their pouched young as a diversionary tactic. In order to prevent this from occurring, it is common practice to tape the pouch opening to hold the young inside. However, taping has not been found to work for *P. x. xanthopus*. Instead, females with larger pouched young were secured in the pouch by suturing the opening using dissolvable Ethicon 6 metric chromic gut suture. This method involved securing four or five anchor points around the rim of the pouch, sewn parallel with the pouch rim and pulled together in a 'purse string' action leaving a small breathing hole for the young inside. The technique has been perfected by Royal Adelaide Zoological Society vetinary surgeons, Dr Sue Conaughty and Dr David Shultz. This technique was also used by Lapidge (1997; 2001) and has been adopted in this study. See Plate 3.4.



Plate 3.4 Pouch suturing

Approximate age estimates were derived from tail measurements combined with estimations of molar eruption stages. These age-growth models were derived from Poole et al (1985) using captive animals (see Figures 3.2 and 3.3). While these figures show that tail, leg, foot and molar growth tend to cease at about four years of age, they are nevertheless useful age-class approximations.

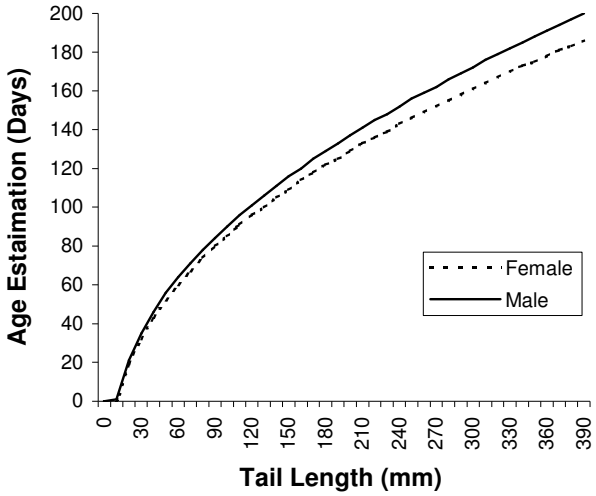


Figure 3.2 Age estimates from tail (adapted from Poole et al, 1985)

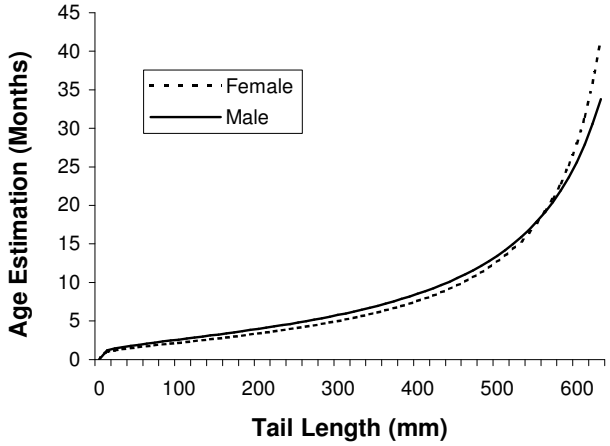


Figure 3.3 Age estimates from tail (adapted from Poole et al, 1985)

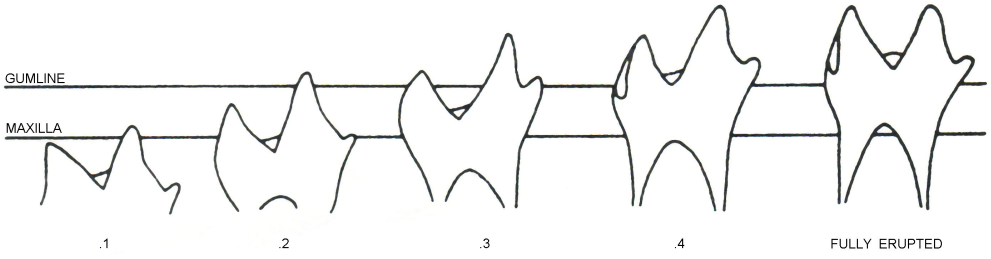


Figure 3.4 Molar Eruptions (from Sharman 1964)

Poole et al (1985) quantified the forward progression of the molar tooth row and the eruption of the posterior molars in relation to age for captive *P. x. xanthopus*. They used four methods for scoring the stages of molar teeth with age including three techniques for measuring molar progression. Of these methods the molar eruption technique was found to be more useful in this study when using live animals. The five-stage system for measuring molar eruption developed by Sharman (1964) and shown in Figure 3.4 had been adapted by Poole et al (1980) for grey kangaroos on a 10 to 44 scale for all molars and later on a 1 to 21 scale by Poole et al (1985) to enable regression equations to be fitted with the age in days as the dependant variable. In the study by Poole et al (1985) the data available for analysis was from 150 days to 2100 days after which all molars have fully erupted. Poole et al (1985) suggest that because the change in molar eruption index on this scale takes approximately 100 days, this technique should be used to estimate the age in years or at very best, the age in seasons.

The molar eruption technique employed in this study was approximated from Poole et al (1985) involving a qualitative inspection of the third and fourth molar eruptions in relation to the gum line. Care was taken not to mistake the third molar for the second molar in the presence of the deciduous premolar. Without tail measurements as a secondary estimate of age, the deciduous premolar may be mistaken for the premolar. The following four-stage eruption schedule for the third or fourth molars was devised (Table 3.7) where Stage 1 is when the molar first appears above the gum line and Stage 4 is when the molar appears fully erupted. Molar inspections were carried out on fully conscious animals using an illuminated lyringoscope.

Table 3.7 Approximate age estimations using molar eruptions (*adapted from Poole et al, 1985)*

Eruption:	***Stage 1***	***Stage 2***	***Stage 3***	***Stage 4***
Molar III	>2 years	>2.4 years	>2.7 years	> 3.1 years
Molar IV	>4.0 years	>4.7 years		

3.4.4 Modelling Survival/Emigration

As previously mentioned, trapping at site 3 (Wilkawillina North) commenced sometime after trapping commenced at sites 1 and 2. The Wilkawillina North was excluded from the analysis of survival and emigration data mainly because trapping at this site had started at a later date.

While this study did not aim to ascertain movement between the trap sites, some insights about movement were obtained from genetic information. Genetic analysis can offer an indirect approach of ascertaining isolation and movement between populations. Mitochondrial DNA (mtDNA) and microsatellite analysis of genetic samples at all three sites was conducted by Dr Mark Eldridge (unpublished) at Macquarie University. Hence the primary purpose of trapping the Wilkawillina North site, in addition to the two other sites, was to obtain genetic data. This will be discussed in Section 3.5.9.

It is important to reiterate that the fate of an individual first trapped and subsequently not seen will always be unknown and that the symbol χ, represents the probability of an individual remaining in the population and not survival. Lebreton (1992) suggest the following steps when selecting an appropriate model for mark recapture:

1. start from a global model compatible with the biology of the species studies and with the design of the study, and assess its fit using parametric bootstrapping,
2. select a more parsimonious model using Akaike's Information Criterion to limit the number of formal tests;
3. test for the most important biological questions by comparing this model with neighboring models using likelihood ratio tests;
4. obtain maximum likelihood estimates of model parameters with estimates of precision.

Several approaches were first tested in relation to animal size, age, rainfall and site. A global model was first tested where the ages of all animals were grouped into two age classes (or stages). Adults were in the first group and sub-adults and juveniles were in the second group. Adults were assumed to be two or more years of age. By way of contrast, a model was also tested where stage, sex and site were separated using binary 'dummy variables' as covariates. The probability of an individual remaining in the population models was also tested with wide range of different rainfall intervals and lags.

3.4.5 Fecundity

The most common definition of fecundity is "the number of live female offspring produced per adult female per unit of time" (McCallum, 2000, p102). McCallum (2000) also suggests that this definition usually includes some juvenile mortality. However, Caughley (1977) defines fecundity as the number of live births a female produces over a period of time, usually one year. Lebreton et al (1990) on the other hand define fecundity as the number of young per litter. For the purpose of

the PVA modelling in Chapter 5, this study defines fecundity as the number of live offspring produced per adult female over a year. This definition does not include any subsequent juvenile mortality. However, an attempt is made here to account for premature terminations of pouched young caused by the mother due to environmental stress, as these terminations will bias the estimate of fecundity. Age-specific fecundity is not explored here because there are too few birth events for this to have any statistical power.

3.4.6 Birth Frequency

The trends in birth pulses within a year are also explored in this study. These data are also compared with rainfall. *P. x. xanthopus* has a similar gestation period to its oestrous cycle and is known to have post-partum oestrus followed by mating within a few days (Poole et al, 1985). If conception occurs, the embryo develops to a 100 cell unilaminar blastocyst with the suckling stimulus of the pouched young serving to inhibit subsequent embryonic development (Hinds and Loudon, 1997; Poole et al, 1985; Sharman et al, 1966). This is known as embryonic diapause. Loss of the pouched young induces the reactivation of the quiescent blastocyst, hence continuing the cycle (Hinds and Loudon, 1997). Unfortunately, Poole et al (1985) did not observe the time between the natural vacation of a pouched young and the birth of the quiescent blastocyst. On one occasion they removed a pouched young (aged 81 days) and observed the birth of a quiescent blastocyst 31.5 days later.

The interval from birth to final pouch vacation is reported as being 190 to 201 days (Poole et al, 1985). Hence, six-month intervals between capture events were thought to be sufficient to estimate birth dates by aging the pouched young. Each pouched young was aged using the tail length graph in Figure 3.2 adapted from Poole et al (1985). Using this information, the month in which a pouched young was born could be determined. In Chapter 5, the PVA model uses annual fecundity estimates. This has been calculated by estimating the pouch young prevalence. This is the ratio of pouched young to trapped sexually mature females. Corrections were therefore applied to these figures for known terminations. These data have been modelled with annual rainfall using a logit link function.

3.5 Results

3.5.1 Preliminary Investigations of Rainfall

Before testing more complex models, it was deemed necessary to test a broader range of possible rainfall intervals and lags and their influence on χ and *p*. Rainfall data were supplied by the Australian Bureau of Meteorology on the 'Climate Data Australia' version 2.2 database (2002). These data were aggregated into more convenient monthly rainfall intervals and lags using a complied Borland C++ programme. For convenience these lags were selected prior to January and July of each year despite not every capture event falling exactly in January and July. The Blinman (Angorichina Station) rainfall gauge was found to be the best indicator of rainfall in this area. This gauge was 12 kilometers from the Eregunda site and approximately 27 kilometers from the Wilkawillina site. This gauge was compared with the slightly closer Wirrealpa Station rainfall data however, the Blinman (Angorichina Station) data indicated a better fit of the data overall.

The preliminary model used to explore the influence of rainfall on χ and *p* use the logistic Equations 3.19 and 3.20. Initially, χ and *p* were assumed to be equal between each site, stage and sex but vary according to two different rainfall intervals and lags respectively. Qualitative observations suggested that fewer animals might be caught when resources leading up to a capture event were more favourable. So it was expected that higher rainfall events closer to the trap event would have a negative effect on *p* because the presence of new succulent plants might lure the animals away from the food in the traps. Conversely it was expected that a more sustained interval of rainfall might have a positive effect on survival.

$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 rain1 \qquad \textbf{Equation 3.19}$$

$$\ln\left(\frac{\chi}{1-\chi}\right) = \beta_2 + \beta_3 rain2 \qquad \textbf{Equation 3.20}$$

Here β_0 and β_2 are constants, and β_1 and β_3 are the rainfall parameters for *rain1* and *rain2* respectively. The variables *rain1* and *rain2* are different lagged rainfall intervals related to *p* and χ respectively.

A wide combination of rainfall lags and intervals for χ and *p* were first tested using AIC scores. Using a range of one to 12 month intervals and zero to 18 month lags there are 228 combinations of rainfall intervals and lags possible for the *rain1* and *rain2* variables in Equation 3.19 and 3.20 respectively. This means 51,984 candidate models were possible using both *rain1* and *rain2*. For

this reason a nested approach was adopted where the variable p was first held fixed and χ was tested with a range of rainfall interval and lags (in *rain2*), then the variable χ was held fixed and p was tested with a range of rainfall interval and lags (in *rain1*). A window of rainfall intervals and lags around the peak AIC scores for each of these sub-models were subsequently explored to find a best fit model where both p and χ were allowed to vary with *rain1* and *rain2* respectively. The AIC score results of this test are found in Table 3.8.

Table 3.8 AIC scores using a combination of rainfall intervals and lags

From Equations 3.17 and 3.18. The brackets indicate (rainfall interval in months followed by the lag in months). The rainfall lag refers to the period (in months) before the capture event. The 'X' entries indicate a solution convergence could not be reached.

Rainfall intervals/lags tested for χ (x_2 in equation 3.18)	Rainfall intervals/lags tested for p (x_1 in equation 3.17)								
	(4, 6)	(4, 7)	(4, 8)	(5, 6)	(5, 7)	(5, 8)	(6, 6)	(6, 7)	(6, 8)
(11, 11)	337.7	338.2	340.4	X	340.6	337.7	X	339.2	306.6
(11, 12)	337.7	302.9	303.9	303.6	X	303.6	338.0	339.2	307.6
(11, 13)	308.5	304.8	305.2	318.6	X	306.6	338.0	X	305.4
(12, 11)	337.7	300.7	322.7	330.8	X	302.3	338.0	339.2	305.4
(12, 12)	X	X	X	X	X	X	X	X	X
(12, 13)	308.4	304.7	300.9	305.1	X	306.5	338.0	325.5	310.4

The model with the lowest AIC score has a combination of four months interval of rainfall lagged by seven months for *rain1* (Equation 3.19) and 12 months interval of rainfall, lagged by 11 months for the *rain2* (Equation 3.19). Table 3.9 shows the design matrix used for this model. Rainfall combinations of (5, 8), (12 ,11) and (4,7), (11,12) are also close candidates. Figure 3.4 uses the parameters β_0 and β_1 in Equation 3.19 calculated by the programme 'Mark' to show the relationship between *rain1* four monthly rainfall interval lagged by seven months and p. Figure 3.5 uses the parameters β_2 and β_3 in Equation 3.20 calculated by the programme 'Mark' to show the relationship between a 12 month rainfall interval lagged by eleven months and χ. Figure 3.6 shows the 95% confidence intervals for rainfall parameters β_1 and β_3.

Table 3.9 Example design matrix.

This shows candidate rainfall readings in mm for β_1 and β_3, and constants β_0 and β_2 from Equations 3.17 and 3.18.

	β_0:	β_1:	β_2:	β_3:
χ_1:	0	0	1	277.2
χ_2:	0	0	1	267
χ_3:	0	0	1	261.1
χ_4:	0	0	1	226.9
χ_5:	0	0	1	187
χ_6:	0	0	1	130
χ_7:	0	0	1	186.6
χ_8:	0	0	1	377.2
p_1:	1	114.8	0	0
p_2:	1	27.2	0	0
p_3:	1	125	0	0
p_4:	1	47.8	0	0
p_5:	1	65.8	0	0
p_6:	1	93.2	0	0
p_7:	1	195.8	0	0
p_8:	1	21.2	0	0

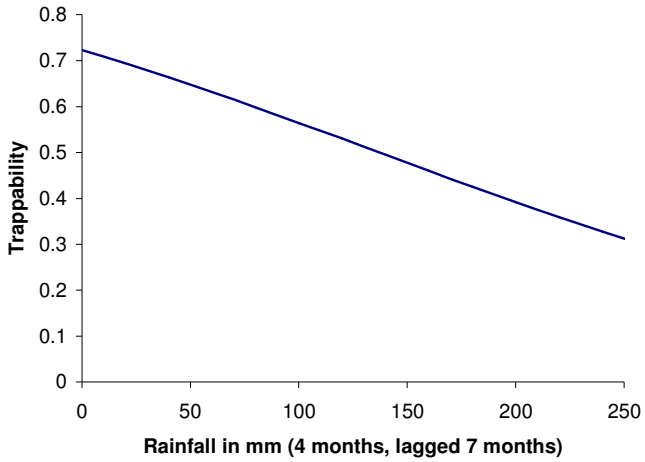


Figure 3.4 Trappability with a 4 month interval rainfall, 7 months lagged, $\ln\left(\frac{p}{1-p}\right) = 0.968 - 0.007 rain1$.

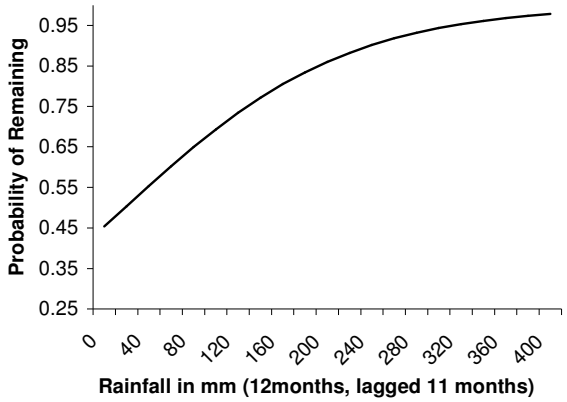


Figure 3.5 The Probability of remaining in the population for 12 months interval rainfall, 11 months lagged, $\ln\left(\frac{\chi}{1-\chi}\right) = -0.489 + 0.011 rain2$.

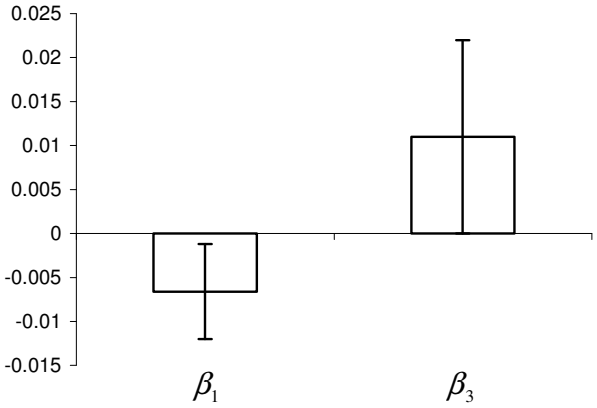


Figure 3.6 The rainfall parameters associated with p (β_1) and χ (β_3) with 95% confidences intervals.

This preliminary investigation is not intended to find the precise combination of rainfall intervals and lags related to χ and p. The intention is to narrow the range of candidate rainfall combinations that best fit the data, so that there are fewer rainfall combinations when testing more complex models having additional parameters.

3.5.2 Stage/Sex/Site Global Model

Here a global model was tested where the individuals were grouped into two ages classes. Adults above two years of age were in one age class. Juveniles and subadults under two years of age were grouped in the second age class. In addition to these two groups, individuals were also grouped according to site (Eregunda Creek or Wilkawillina South) and sex. This amounts to eight distinct groups. Table 3.10 is the input file for programme 'Mark' used to test this global model.

Table 3.10 Data input file for stage/site/sex grouped model.

MAE – Male Adults at Eregunda Site; MAW – Male Adults at Wilkawillina South site; MSE – Male sub-adults & juveniles at Eregunda; MSW - Male sub-adults & juveniles at Wilkawillina South; FAE – Female Adults at Eregunda Site; FAW – Female Adults at Wilkawillina South site; FSE – Female sub-adults & juveniles at Eregunda; FSW - Female sub-adults & juveniles at Wilkawillina South.

Capture History	MAE	MAW	MSE	MSW	FAE	FAW	FSE	FSW
110000000	0	0	0	1	0	0	0	0
111111001	0	0	0	0	0	1	0	0
010000100	0	0	0	0	0	0	0	1
010011101	0	1	0	0	0	0	0	0
011110101	0	1	0	0	0	0	0	0
011100000	0	0	0	0	0	1	0	0
001011001	0	1	0	0	0	0	0	0
000100000	0	1	0	0	0	0	0	0
000100000	0	0	0	1	0	0	0	0
000100000	0	1	0	0	0	0	0	0
001010011	0	1	0	0	0	0	0	0
000100000	0	0	0	0	0	1	0	0
000010000	0	1	0	0	0	0	0	0
000010010	0	0	0	1	0	0	0	0
000010000	0	1	0	0	0	0	0	0
000011101	0	0	0	0	0	0	0	1
000010000	0	1	0	0	0	0	0	0
000010000	0	1	0	0	0	0	0	0
000011111	0	0	0	0	0	0	0	1
000011000	0	0	0	0	0	0	0	1
000010000	0	0	0	0	0	1	0	0
000010000	0	0	0	0	0	0	0	1
000001000	0	0	0	0	0	1	0	0
000001111	0	0	0	0	0	1	0	0
000001000	0	0	0	0	0	1	0	0
000001000	0	0	0	1	0	0	0	0
000000100	0	1	0	0	0	0	0	0
000000100	0	0	0	0	0	0	0	1
000000001	0	0	0	0	0	1	0	0
000000001	0	0	0	1	0	0	0	0
000000001	0	1	0	0	0	0	0	0
000000001	0	1	0	0	0	0	0	0
000000001	0	1	0	0	0	0	0	0
000000001	0	0	0	0	0	1	0	0
000000001	0	0	0	0	0	1	0	0
111011111	1	0	0	0	0	0	0	0
100110001	1	0	0	0	0	0	0	0
111111111	0	0	0	0	1	0	0	0
111010100	1	0	0	0	0	0	0	0
011111001	0	0	0	0	1	0	0	0
011011111	0	0	0	0	1	0	0	0
011111100	0	0	0	0	1	0	0	0
011100001	0	0	0	0	1	0	0	0
010000000	0	0	0	0	1	0	0	0
010000100	0	0	0	0	1	0	0	0
011100000	0	0	0	0	1	0	0	0
001111011	0	0	0	0	0	0	1	0
000011000	0	0	0	0	1	0	0	0
000011001	0	0	1	0	0	0	0	0
000010000	0	0	0	0	1	0	0	0
000100000	0	0	1	0	0	0	0	0
000110000	1	0	0	0	0	0	0	0
000001000	1	0	0	0	0	0	0	0
000001111	0	0	0	0	1	0	0	0
000001111	1	0	0	0	0	0	0	0
000000100	0	0	1	0	0	0	0	0
000000010	1	0	0	0	0	0	0	0
000000001	0	0	0	0	0	0	1	0
000000001	1	0	0	0	0	0	0	0
000000001	0	0	1	0	0	0	0	0

An additive model was constructed using Equations 3.21 and 3.22.

$$\ln\left(\frac{\chi}{1-\chi}\right) = \beta_0 + \beta_1 sex + \beta_2 stage + \beta_3 site + \beta_4 rain1 \qquad \textbf{Equation 3.21}$$

$$\ln\left(\frac{p}{1-p}\right) = \beta_5 + \beta_6 sex + \beta_7 stage + \beta_8 site + \beta_9 rain2 \qquad \textbf{Equation 3.22}$$

The preferred abbreviated notation used here on for Equations 3.21 and 3.22 is $\chi(sex + stage + site + rain1), p(sex + stage + site + rain2)$. The limited range of rainfall intervals and lags shown in Table 3.8 were AIC scored. However, unlike Table 3.8 on this occasion the lowest AIC score of 304.16 was obtained for the combination of *rain1* (for χ in Equation 3.21) having an interval of 11 months, lagged by 13 months and *rain2* (for *p* in Equation 3.22) having an interval of 4 months, lagged by 7 months. The observed deviance was 222.4. Parametric bootstrapping was used to test the goodness of fit of the model to the data. Figure 3.8 summarises the results of 220 parametric bootstrap simulations. More than 28% of the simulated bootstrap deviances are greater than the observed deviance of 222.4. This indicates that the model does fit the data well at a 5 or 10% acceptance level.

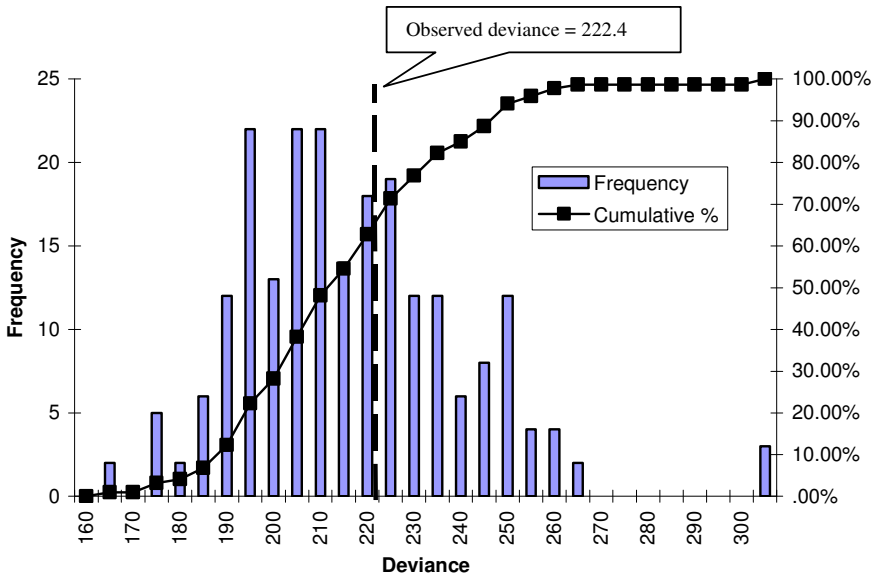


Figure 3.7 Histogram of parametric bootstrap results from 220 simulations.

For the grouped version of the model $\chi(sex + stage + site + rain1), p(sex + stage + site + rain2)$. The dashed line shows the observed deviance. The solid line with squares shows the cumulative percentage of the results verses deviance.

By way of comparison, a covariate version of the same model (Equations 3.21 and 3.22) was tested rather grouping the individuals into eight distinct groups. Here each individual was given a binary number (or 'dummy' variable) for its respective membership to a particular group. The first column in Table 3.11 has the binary capture history data. The remaining columns show the appropriate covariate variables (0 or 1) depending upon an individual's membership to different groups or states. The variable *sex* has two states 1 (males) and 0 (females). The variable *site* is 1 (Eregunda) and 0 (Wilkawillina South). The variable *stage* is 1 (adults) and 0 (sub-adults/juveniles).

Table 3.11 Data input file for stage/site/sex covariate model.

Capture History	Stage	Site	Sex
110000000	0	0	1
111111001	1	0	0
010000100	0	0	0
010011101	1	0	1
011110101	1	0	1
011100000	1	0	0
001011001	1	0	1
000100000	1	0	1
000100000	0	0	1
000100000	1	0	1
001010011	1	0	1
000100000	1	0	0
000010000	1	0	1
000010010	0	0	1
000010000	1	0	1
000011101	0	0	0
000010000	1	0	1
000010000	1	0	1
000011111	0	0	0
000011000	0	0	0
000010000	1	0	0
000010000	0	0	0
000001000	1	0	0
000001111	1	0	0
000001000	1	0	0
000001000	0	0	1
000000100	1	0	1
000000100	0	0	0
000000001	1	0	0
000000001	0	0	1
000000001	1	0	1
000000001	1	0	1
000000001	1	0	1
000000001	1	0	0
000000001	1	0	0
111011111	1	1	1
100110001	1	1	1
111111111	1	1	0
111010100	1	1	1
011111001	1	1	0
011011111	1	1	0
011111100	1	1	0
011100001	1	1	0
010000000	1	1	0
010000100	1	1	0
011100000	1	1	0
001111011	0	1	0
000011000	1	1	0
000011001	0	1	1
000010000	1	1	0
000100000	0	1	1
000110000	1	1	1
000001000	1	1	1
000001111	1	1	0
000001111	1	1	1
000000100	0	1	1
000000010	1	1	1
000000001	0	1	0
000000001	1	1	1
000000001	0	1	1

After a standardisation correction, the parameters derived for Equations 3.21 and 3.22 using the covariate approach were found to be identical to the 'eight groups' approach. The lowest AIC score of 304.16 is identical to the score obtained previously. However, a deviance of 282.3 was obtained this time. The best model again had a rainfall interval of 11 months, lagged 13 months for *rain1* and an interval of 4 months, lagged 7 months for *rain2*.

However, the programme 'Mark' is unable to carry out parametric bootstrapping of covariate models. Instead, parametric bootstrapping had to be carried out by randomising the input data in the database in the same way suggested by Cooch and White (Cooch and White, 2002) using a C++ programme and measuring the distributional properties if the deviances after repeated randomisations and model re-runs. Figure 3.8 is a cumulative frequency distribution curve of the results of these bootstrap simulations. Here, more than 75% of the simulated bootstrap deviances are greater than the observed deviance of 282.3. While this goodness of fit test is a substantially different to the 'eight group' model it still confirms the model fits the data well at a 5 or 10% acceptance level. Unfortunately, this approach was very time consuming and only 100 randomisations were possible.

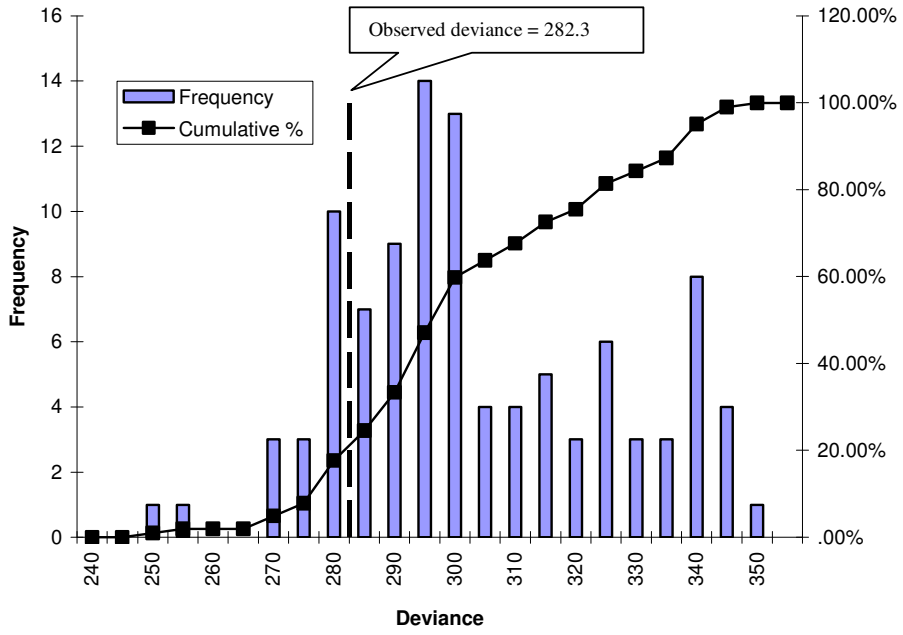


Figure 3.8 Histogram of parametric bootstrap results from 100 simulations.

For the covariate version of the model $\chi(sex + stage + site + rain1), p(sex + stage + site + rain2)$. The dashed line shows the observed deviance. The solid line with squares shows the cumulative percentage of the results verses deviance.

3.5.3 Nested Stage/Sex/Site Models

Having obtained a good fit of the data using the 'eight group' model in Section 3.5.2, AIC scores were then used to test the fit of a series of models where successive terms were removed from the global model. These sub-models are not necessarily nested. AIC scores test which model is the most parsimonious.

No over-dispersion was found with parametric bootstrapping as the observed deviance was 222.4 and the average deviance using bootstrapping was 226.4. Using the method suggested by Cooch and White (2002), $\hat{c} = \frac{222.4}{226.4} = 0.98$. When less than 1.0, the data is considered to be slightly under-dispersed. Cooch and White (2002) therefore recommend leaving $\hat{c} = 1$ in this case when comparing nested models.

Table 2.3 shows the AIC scores for these sub-models. Like the global model, all of these models were additive and no interactive effects were tested. Not all combinations of parameters have been tested as some of the parameters were found to be insignificant and did not account for the variation in the data. The model with the lowest AIC score (298.5), having seven parameters was $\chi(site + rain(i:11, l:13)), p(sex, stage, rain(i:4, l:7))$. The abbreviations i and l refer to the rainfall intervals and lags respectively. The parameters derived here are shown in Equations 3.21 and 3.22. Figures 3.9 and 3.10 are graphs of Equations 3.23 and 3.24 respectively.

$$\ln\left(\frac{\chi}{1-\chi}\right) = 0.503 + 1.013 site + 0.004 rain_{11,13} \qquad \textbf{Equation 3.23}$$

$$\ln\left(\frac{p}{1-p}\right) = 0.867 - 1.044 sex + 0.801 stage - 0.007 rain_{4,7} \qquad \textbf{Equation 3.24}$$

Figures 3.11 and 3.12 show graphs of the 95% confidence intervals and 90% confidence intervals respectively around selected parameters of interest. Figure 3.13 shows the 95% confidence intervals around the two parameters associated with rainfall.

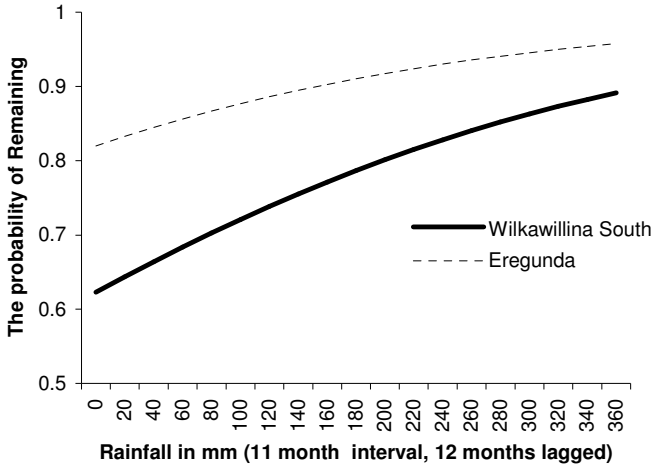


Figure 3.9 The probability of remaining, χ with rainfall using Equation 3.23.

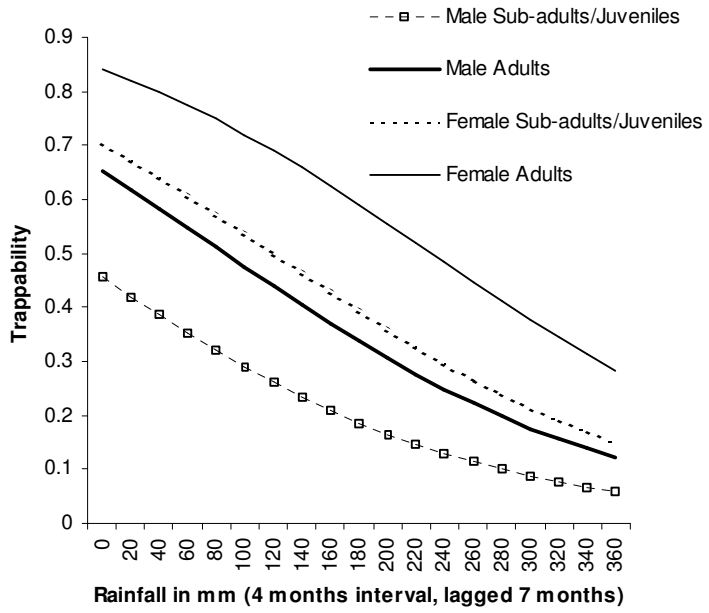


Figure 3.10 The trappability, *p* with rainfall using Equation 3.24.

Table 3.12 AIC scores for models nested under the stage/sex/site model

AICc	Model	Parameters	Deviance
298.5	*χ (site+rain(i:11,l:13)),p(sex+stage+rain(i:4,l:7))*	7	223.8
299.6	*χ (site),p(stage)*	4	231.5
300.0	*χ (site+rain(i:11,l:13)),p(sex+site+rain(i:4,l:7))*	7	225.3
300.0	*χ (rain(i:11,l:13)),p(sex+stage+rain(i:4,l:7))*	6	227.5
300.2	*χ (rain(i:11,l:13)),p(sex+site+rain(i:4,l:7))*	6	227.7
300.2	*χ (site+rain(i:11,l:13)),p(sex+stage+site+rain(i:4,l:7))*	8	223.1
300.3	*χ (rain(i:11,l:13)),p(sex+stage+site+rain(i:4,l:7))*	7	225.5
301.6	*χ (site),p(sex+stage)*	5	231.3
302.0	*χ (site+rain(i:11,l:13)),p(sex+stage)*	6	229.4
302.1	*χ (site+rain(i:11,l:13)),p(rain(i:4,l:7))*	5	231.8
302.2	*χ (stage+site+rain(i:11,l:13)),p(sex+site+rain(i:4,l:7))*	8	225.1
302.2	*χ (sex+site+rain(i:11,l:13)),p(sex+site+rain(i:4,l:7))*	8	225.2
302.4	*χ (stage+site+rain(i:11,l:13)),p(sex+stage+site+rain(i:4,l:7))*	9	223.0
302.5	*χ (sex+stage+site+rain(i:11,l:13)),p(sex+stage+rain(i:4,l:7))*	9	223.1
302.5	*χ (stage+rain(i:11,l:13)),p(sex+stage+site+rain(i:4,l:7))*	8	225.5
302.6	*χ (site),p(sex)*	4	234.4
303.2	*χ (rain(i:11,l:13)),p(sex+stage+site)*	6	230.7
303.2	*χ (rain(i:11,l:13)),p(sex+stage)*	5	232.9
303.4	*χ (site+rain(i:11,l:13)),p(sex+stage+site)*	7	228.6
303.4	*χ (.),p(sex+stage)*	4	235.2
303.5	*χ (sex+stage+site+rain(i:11,l:13)),p(sex+rain(i:4,l:7))*	8	226.4
303.9	*χ (sex+site+rain(i:11,l:13)),p(sex+stage)*	7	229.1
304.0	*χ (stage+site+rain(i:11,l:13)),p(sex+stage))*	7	229.2
304.1	*χ (stage+site+rain(i:11,l:13)),p(rain(i:4,l:7))*	6	231.6
304.2	*χ (sex+site+rain(i:11,l:13)),p(rain(i:4,l:7*	6	231.6
304.2	***χ (sex+stage+site+r(i:11,l:13)),p(sex+stage+site+r(i:4,l:7))***	**10**	**222.4**
304.7	*χ (sex+stage+rain(i:11,l:13)),p(sex+stage+site+rain(i:4,l:7))*	9	225.4
304.8	*χ (rain(i:11,l:13)),p(rain(i:4,l:7))*	4	236.6
305.3	*χ (.),p(sex)*	3	239.3
305.4	*χ (sex+site+rain(i:11,l:13)),p(sex+stage+site)*	8	228.3
305.4	*χ (site),p(site)*	4	237.3
305.4	*χ (stage+site+rain(i:11,l:13)),p(sex+stage+site))*	8	228.4
305.5	*χ (.),p(site)*	3	239.5
305.6	*χ (site),p(.)*	3	239.5
305.6	*χ (sex+stage+site+rain(i:11,l:13)),p(sex+stage))*	8	228.6
306.0	*χ (sex+stage+site+rain(i:11,l:13)),p(rain(i:4,l:7))*	7	231.3
306.1	*χ (sex+stage+site+rain(i:11,l:13)),p(site+rain(i:4,l:7))*	8	229.1
307.1	*χ (sex+stage+site+rain(i:11,l:13)),p(sex+stage+site))*	9	227.7
307.1	*χ (sex+stage+site+rain(i:11,l:13)),p(sex))*	7	232.4
307.4	*χ (sex+stage+site+rain(i:11,l:13)),p(stage+rain(i:4,l:7))*	8	230.4
307.8	*χ (sex+stage+site+rain(i:11,l:13)),p(sex+site))*	8	230.8
308.1	*χ (sex+stage+site+rain(i:11,l:13)),p(stage+site+rain(i:4,l:7))*	9	228.7
308.3	*χ (.),p(stage)*	3	242.3
308.5	*χ (.),p(.)*	2	244.6
309.9	*χ (sex+stage+site+rain(i:11,l:13)),p(site))*	7	235.2
310.4	*χ (sex+stage+site+rain(i:11,l:13)),p(.))*	6	237.8
311.3	*χ (sex+stage+site+rain(i:11,l:13)),p(stage))*	7	236.5
764.5	*χ (sex+stage+site),p(sex+stage+site+rain(i:4,l:7)*	9	685.2
768.3	*χ (sex+site),p(sex+stage+rain(i:4,l:7))*	7	693.6
780.8	*χ (sex+site),p(sex,site,rain(i:4,l:7)*	7	706.0
784.3	*χ (site),p(sex+rain(i:4,l:7))*	5	714.0
786.9	*χ (site),p(sex+stage+rain(i:4,l:7))*	6	714.3
787.9	*χ (stage+site),p(sex+stage+rain(i:4,l:7))*	7	713.2
788.9	*χ (sex),p(sex+stage+site+rain(i:4,l:7)*	7	714.2
794.9	*χ (sex+stage),p(sex+stage+site+rain(i:4,l:7)*	8	717.8
797.7	*χ (.),p(sex+stage+site+rain(i:4,l:7)*	6	725.2

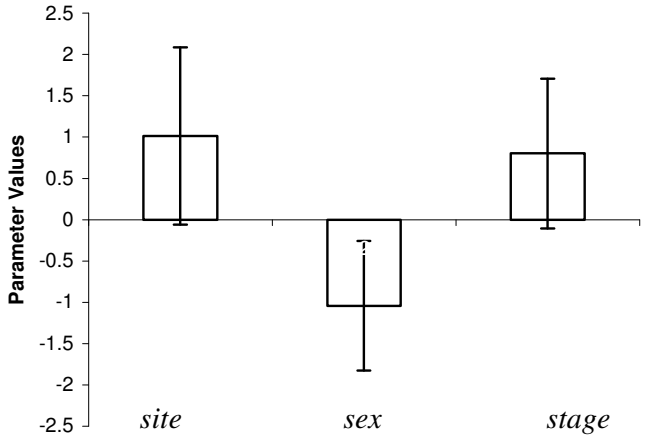


Figure 3.11 Graph of 95% confidence intervals around parameters related to *site*, *sex* and *stage* in Equations 3.23 and 3.24.

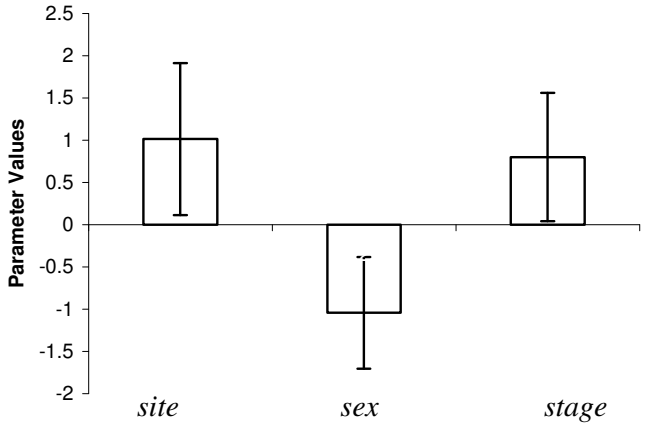


Figure 3.12 Graph of 90% confidence intervals around parameters related to *site*, *sex* and *stage* in Equations 3.23 and 3.24.

In Figures 3.11 and 3.12, using a 95% confidence interval, only sex is significantly different from zero. Using a 90% confidence interval all three parameters are significantly different from zero.

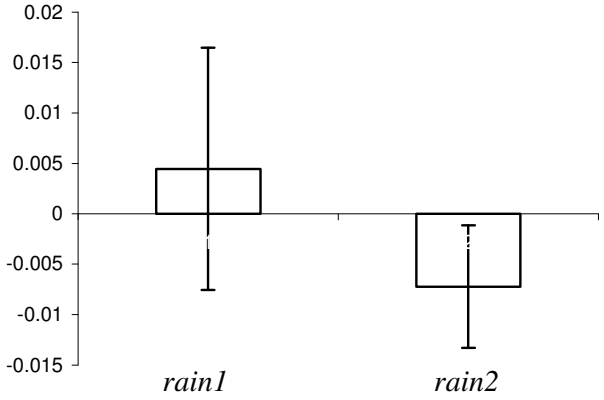


Figure 3.13 Graph of 95% confidence intervals around parameters related to *rain1* and *rain2* in Equations 3.23 and 3.24.

Interestingly, the simplified $\chi(site), p(sex)$ model, which ranked 16th having an AIC 302.6 has all of its parameters (including the constants), significantly different from zero ($\alpha = 0.05$). See Equations 3.25, 3.26 and Figure 3.14.

$$\ln\left(\frac{\chi}{1-\chi}\right) = 1.380 + 1.134 site \qquad \textbf{Equation 3.25}$$

$$\ln\left(\frac{p}{1-p}\right) = 0.764 - 0.865 sex \qquad \textbf{Equation 3.26}$$

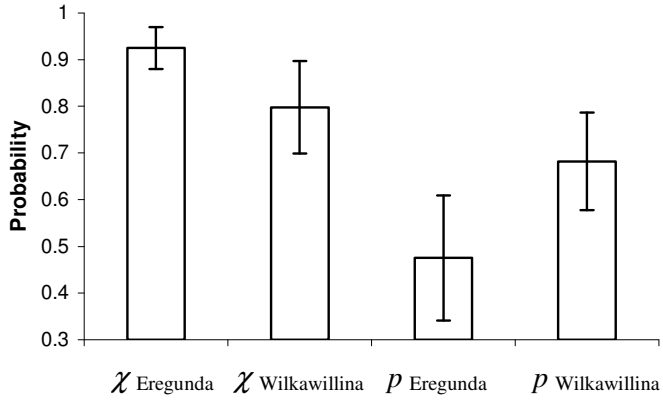


Figure 3.14 Final estimates of p and χ for the model $\chi(site), p(sex)$ in Equations 3.25 and 3.26

3.5.4 An adapted Stage/Sex/Site Global Model with Stage dependent on the first survival interval.

A similar model to the covariate stage/sex/site model was tested. However, here the 'dummy' variables *stage* and *site* were separately related to χ over the interval after an individual's first release. This notation for this model given by:

$\chi(stage(1st) + site(1st) + sex + site + rain(i:11,l:13)), p(stage + sex + rain(i:4,l:7))$. Using AIC scoring (Table 3.13), the most parsimonious model nested under this had an AIC score of 287.8. The parameter estimates from the model:

$\chi(site(1st) + rain(i:11,l:13)), p(stage + sex + rain(i:4,l:7))$ are graphed in Figures 3.15 and with 95% confidence intervals to show their significance with respect to zero. Figure 3.16 shows 90% confidence intervals.

Table 3.13 AICc scores for models nested under the adapted stage/sex/site model

AICc	Model	Parameters	Deviance
287.8	**χ(site(interval1)+rain(I:11,I:13)), p(stage+sex+rain(I:4,I:7))**	**7**	**272.8**
288.7	χ(site(interval1)+rain(I:11,I:13)), p(sex+rain(I:4,I:7))	6	276.0
290.0	χ(site(interval1)+rain(I:11,I:13)), p(stage+sex+site+rain(I:4,I:7))	8	272.8
291.8	χ(site(interval1)+rain(I:11,I:13)), p(stage+sex)	6	279.1
293.9	χ(site(interval1)+sex+site+rain(I:11,I:13)), p(stage+sex+site+rain(I:4,I:7))	10	272.0
294.2	χ(stage(interval1)+site(interval1)+sex+site+rain(I:11,I:13)), p(stage+sex+site+rain(I:4,I:7))	11	269.9
297.6	χ(stage(interval1)+sex+site+rain(I:11,I:13)), p(stage+sex+site+rain(I:4,I:7))	10	275.7

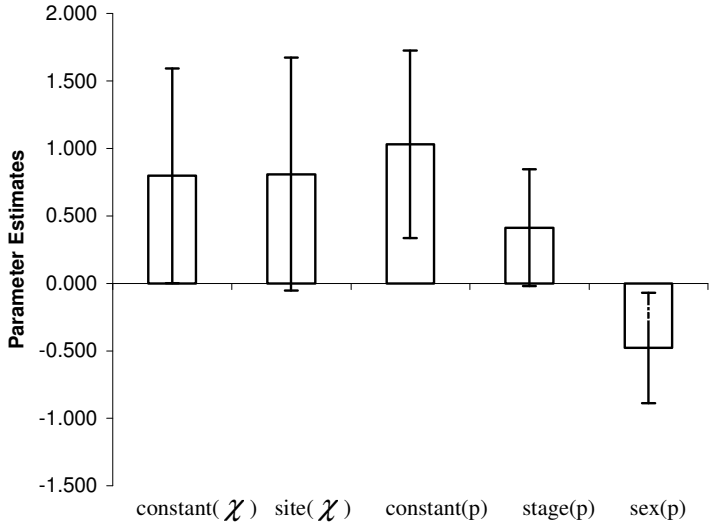


Figure 3.15 Graph of selected parameters with 95% confidence intervals for the model:

$$\chi(site(1st) + rain(i:11, l:13)),\ p(stage + sex + rain(i:4, l:7))$$

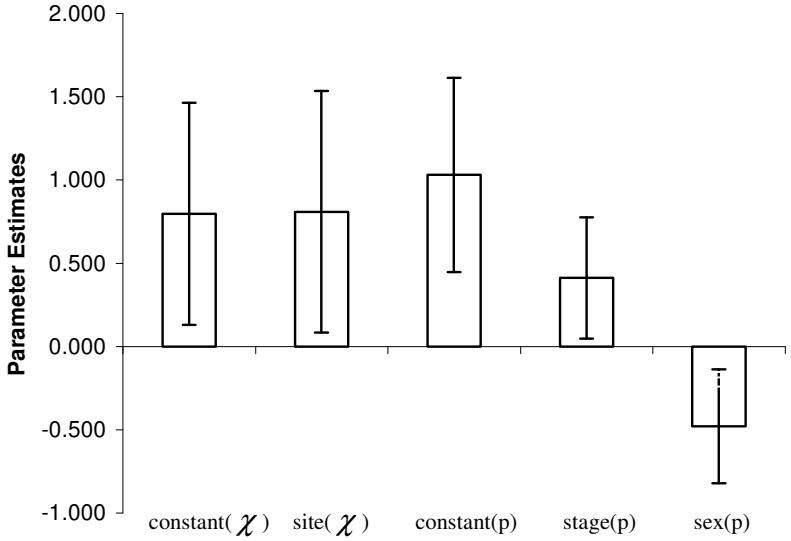


Figure 3.16 Graph of selected parameters with 90% confidence intervals for the model:

$$\chi(site(1st) + rain(i:11, l:13)),\ p(stage + sex + rain(i:4, l:7))$$

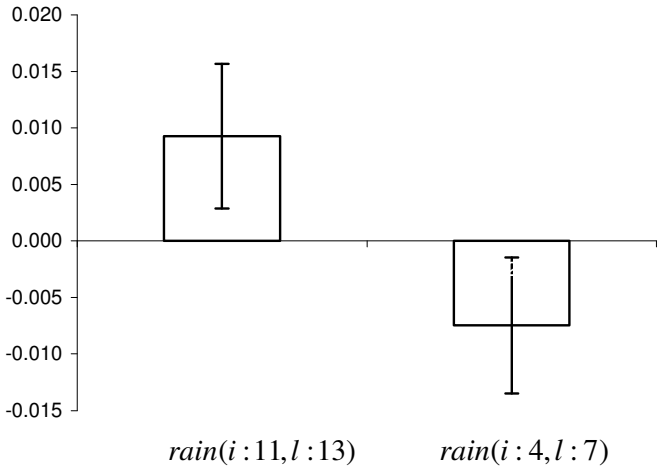


Figure 3.17 Graph of rainfall parameters associated $rain(i:11,l:13)$ and $rain(i:4,l:7)$ with 90% confidence intervals for the model:

$$\chi(site(1st)+rain(i:11,l:13)),\ p(stage+sex+rain(i:4,l:7))$$

3.5.5 Time varying models

The global time varying model, $\chi(stage+site+sex+time),\ p(stage+site+sex+time)$ was tested for goodness of fit using parametric bootstrapping.

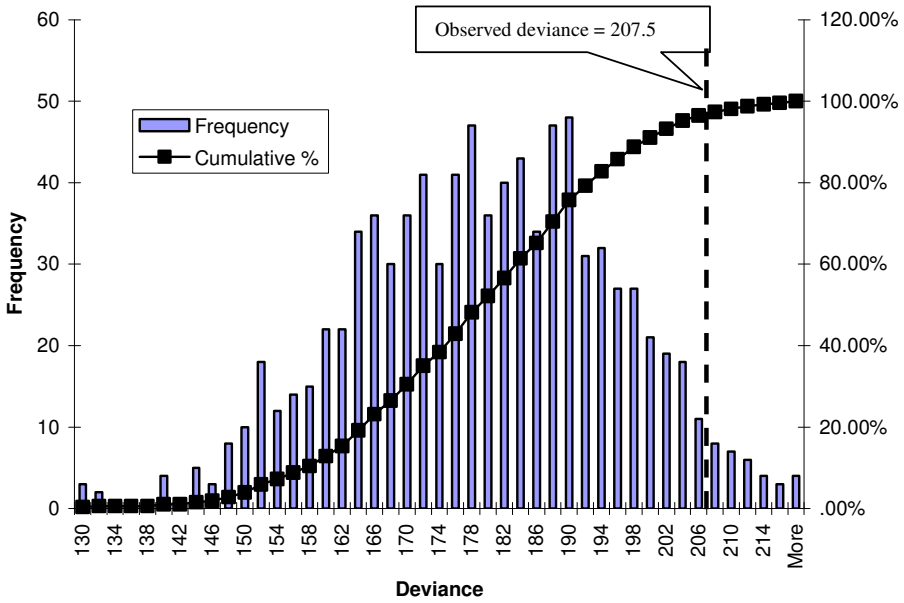


Figure 3.18 Histogram of parametric bootstrap results from 1000 simulations of the covariate version of the model: $\chi(stage+site+sex+time),\ p(stage+site+sex+time)$.

The addition signs between the variables indicate that this is an additive model and each group is not allowed to separately vary with time (Lebreton et al, 1992). Interactive effects were not explored here as there were insufficient data for the model to calculate standard errors for every parameter. One thousand simulations were necessary here because of the close proximity of the observed deviance to the tail of the distribution of simulated deviances (Cooch and White, 2002). A mere 2.7% of the simulated deviances were found to be greater than the observed deviance indicating that the global model is a not a good fit of the data. Nested models were therefore not explored (Cooch and White, 2002; Lebreton et al, 1992).

3.5.6 Interactive Effects

As the number of possible interactive effects between the parameters in models that include rainfall or time is unwieldy, interactive effects were explored for a selection of constant models that ignore rainfall and time. A goodness-of-fit test was not carried here, hence these models are considered to be exploratory only. Interestingly, these AIC scores are well above the rainfall models described earlier.

Table 3.14 AIC scores exploring interactive effects

Model	AIC	Parameters	Deviance
*p(site+sex+sex*stage)+ (.)*	301.6	5	291.1
*p(stage+sex+sex*site)+ χ (.)*	303.3	5	292.8
*p(stage+site+sex+sex*stage)+ χ (.)*	303.8	6	291.1
*p(stage+site+sex+sex*site)+ χ (.)*	305.3	6	292.6
*p(site+sex+sex*site)+ χ (site+sex+sex*stage)*	305.4	8	288.2
*p(stage+site+sex+sex*stage+sex*site*stage)+ χ (.)*	306.0	7	291.0
*p(stage+site+sex+sex*site+sex*stage)+ χ (.)*	306.0	7	291.0
*p(.)+χ (site+sex+sex*stage)*	306.9	5	296.4
*p(site+sex*site)+ χ (.)*	307.2	4	298.8
*p(site+sex+sex*stage)+ χ (stage+sex+sex*site)*	307.5	8	290.3
*p(site+sex+sex*stage+ χ (stage+site+sex+t)*	309.7	15	275.4

3.5.7 Fecundity

The histogram in Figure 3.19 shows the observed births grouped into monthly bins over the entire year. Using tail length to estimate age, the month in which a pouched young was born was determined. These data have been pooled across all three sites, Eregunda Creek, Wilkawillina North and Wilkawillina South, as there is insufficient data to compare the data between sites. The first two capture events (March 1998 and June 1998) were excluded because pouched young were not aged and there were too few captures. The last capture event (June 2002) only includes captures at Eregunda Creek.

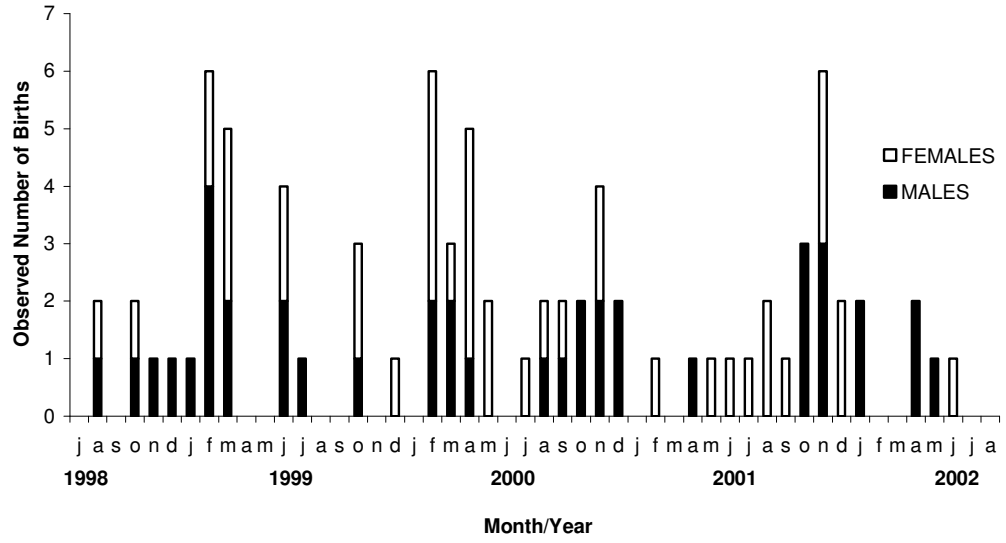


Figure 3.19 Observed birth pulses binned monthly and pooled across the three sites

Figure 3.20 is a histogram of the days between births for each mother at the three sites in 10 day bins. The data at Wilkawillina South and Wilkawillina North have been grouped. The mean difference between successive birth dates was found to be 190.3 +/-20.4 (+/-SE) days at Wilkawillina Gorge (n=14) and 192.7+/-17.0 (+/-SE) days at Eregunda Creek (n=18). These data also agree with the findings of Poole (1985) who found cycles in captive animals of 190 to 201 days (n=7).

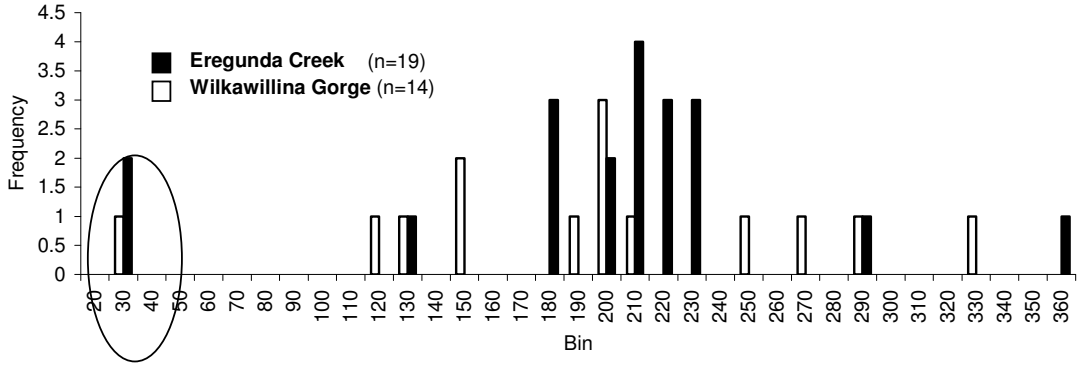


Figure 3.20 Days between births for individual mothers. Eregunda Creek - black bars (n=18), Wilkawillina Gorge – white bars (n=14).

The circle indicates possible outliers cause by measurement error.

Of particular interest are the outliers below the main group from 160 days to 240 days. The 160 to 240 day range has been selected because of the likely age estimation error of up to 30 days and uncertainty associated with the period of pouch duration. The three 30 day intervals circled in Figure 3.20 are likely to be pouched young measurement errors and have also been omitted. It is possible that some terminations have occurred between captures that were missed, accounting for intervals greater than 240 days. However, regardless of whether intervals of greater than 240 days are the result of further terminations or embryonic diapause, births after this delay were usually associated with a high rainfall event. Intervals between births under 160 days indicate a termination. In the following analysis, births after 240 days have been assigned a positive number for comparison with rainfall events (indicating a positive correlation) and due to the gestation period of approximately 30 days, 30 days have been subtracted from these events. The actual termination date of a pouch young is unknown. For birth intervals of under 160 days the termination date was therefore approximated as the date of capture when the young was last seen. Terminations here were given a negative number for comparison with rainfall events. A range of rainfall patterns (intervals and lags) were compared with these events and it was found that rainfall two months immediately prior to these events best indicated the trends. Figure 3.21 shows the estimated termination times (as downward bars) and estimated times of the onset of gestation (as upward bars) compared with rainfall immediately 2 months prior to the events.

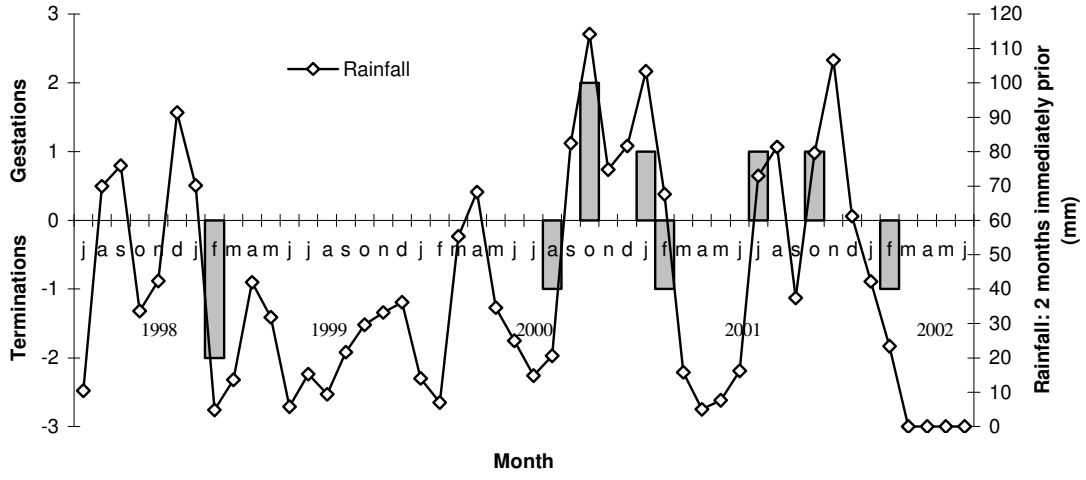


Figure 3.21 The estimated termination times (down) and estimated times of the onset of gestation (up) compared with rainfall (using Angorichina Station) immediately two months prior to the events.

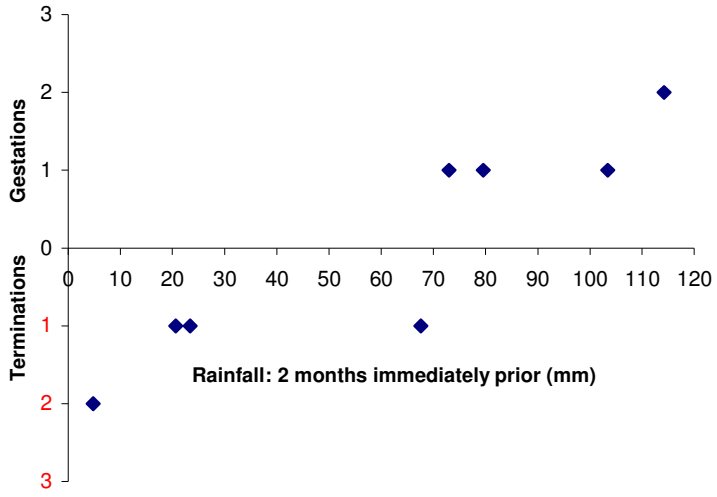


Figure 3.22 The estimated termination times (down) and estimated times of the onset of gestation (up) plotted against rainfall (using Angorichina Station) immediately 2 months prior to the events.

In Figure 3.22, the terminations would presumably asymptote at zero and the number of gestations encountered after high rainfall events have followed low rainfall events would presumably asymptote according to the number of females in the population that have not already given birth. The prevalence of births in each year was calculated by dividing the number of females carrying pouched young into the number of sexually mature females trapped that year. Table 3.15 shows the rainfall from July to June compared with the prevalence of births. Known terminations have not been counted. The 12 months of rainfall from July in one year to June in the following year was considered more appropriate than the rainfall interval over the calendar year. Figure 3.23 shows the prevalence at each site plotted against rainfall with a logistic curve fitted over the Eregunda Creek data only.

Table 3.15 Twelve months rainfall from July to June compared with prevalence of births

Uses Angorichina Station gauge. Any known terminations are not counted.

Period	Rainfall (mm)	Eregunda Creek	Wilkawillina Gorge
July 1998 – June 1999	257	1.00	0.67
July 1999 – June 2000	183	0.71	0.79
July 2000 – June 2001	365	1.00	0.90
July 2001 – June 2002	246	0.83	0.80

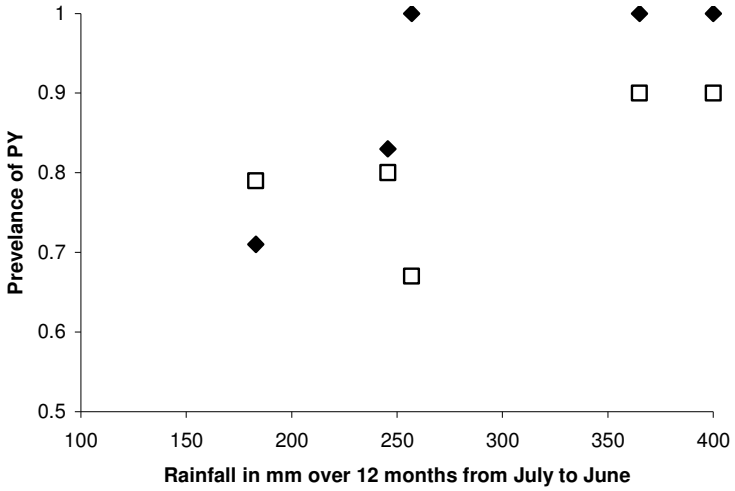


Figure 3.23 Prevalence of Pouched young versus rainfall in mm over 12 months from July to June.

Diamond symbols representing Eregunda Creek birth prevalence and squares representing Wilkawillina Gorge prevalence (both sites pooled).

In Figure 3.23, the squares, representing the Wilkawillina Gorge sites, are lower at higher rainfalls than Eregunda Creek. This has not been significance tested and there are too few data here to be able to draw meaningful conclusions.

3.5.8 Condition

Unfortunately scores of body condition (fat scores) have only been carried out more recently in the continuing mark recapture work. Sharp (2002) used the residuals of a regression through the log of weight divided by the log of body measurements for the sample population as an estimate of condition. Here I have instead used an age-corrected estimate of condition. Equations 3.27 and 3.28 have been derived from sex and age-specific weight and leg formulae for captive *P. x. xanthopus* calculated by Poole et al (1985).

$$male\ condition = \frac{\log(weight) + 26.1}{5.9\log(leg)} \qquad \textbf{Equation 3.27}$$

$$female\ condition = \frac{\log(weight) + 13.8}{3.3\log(leg)} \qquad \textbf{Equation 3.28}$$

The length of the leg is thought to be the most precise measurement although it may not be a good indication of age. Condition scores were averaged across each sex for each site. Juveniles having weights of under 3 kilograms were excluded. However, the Tukey boxplots revealed ten other

outliers primarily attributed to animals weighing less than 5 kilograms. These outliers were removed before attempting to fit candidate models of condition indices to rainfall and site.

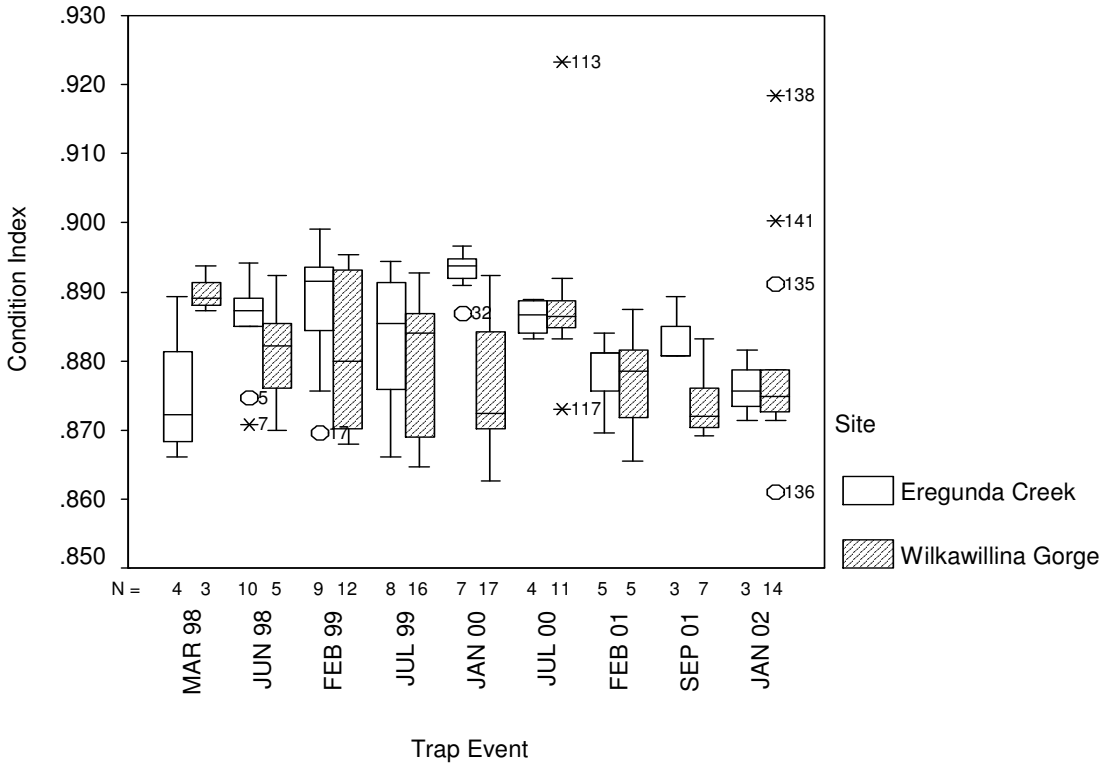


Figure 3.24 Tukey boxplots of age and sex-corrected condition estimates for Eregunda Creek and the pooled Wilkawillina Gorge sites.

The Tukey boxplots show the median horizontal line at the center of each box, the interquartile range as boxes and 95% confidence intervals as error bars. Outliers further than 1.5 times the interquartile range are show as a circle and outliers further than 3 times the interquartile range are show as an asterix. The number of samples N for each box are shown at the foot of the graph.

To test the significance and the relationship of rainfall and site location to condition, outliers were removed and a range of candidate rainfall intervals and lags were fitted to the condition data for each site. The ranges of different monthly rainfall intervals from zero to twelve months and lags from zero to twelve months were regressed using Equation 3.29.

$$condition = \beta_0 + \beta_1 rain + \beta_2 site \qquad \text{Equation 3.29}$$

The *site* and *rainfall* contributions to condition were assumed to be linear and additive. The value for *site* is a dummy variable where 0 represents the Eregunda Creek site and 1 represents the pooled Wilkawilina Gorge sites. The *rainfall* value represents a candidate rainfall interval/lag.

Parameters $\beta_0, \beta_1, \beta_2$ were derived using linear regression. Table 3.16 shows four rainfall interval and lag combinations having the lowest AIC scores.

Table 3.16 AIC Scores for the best rainfall interval fits of Equation 3.29.

Rainfall Interval/lag (months)	AIC Score
12/3	**948.3**
12/2	948.9
11/3	950.2
11/4	950.3

Table 3.17 shows the coefficients estimates for 12 months interval rainfall, lagged by three months. All conditions scores were multiplied by 1000 before regressing the data for simplicity.

Table 3.17 Estimates of coefficients using Equation 3.29

For 12 months interval, lagged by 3 months ($t_{0.05(2),130} = 1.987$) , AIC = 948.3.

	Estimate	Std. Error	*t*-value	Probability	
(Intercept)	898.1	3.370	266.5	P <0.01	Reject $H_0: \beta = 0$
rain	-0.055	0.014	-4.077	P <0.01	Reject $H_0: \beta = 0$
site	-5.990	1.510	-3.967	P <0.01	Reject $H_0: \beta = 0$

In Table 3.17, all parameters appear to be significant for $\alpha = 0.01$, although the R^2=0.20 indicates a large amount of variation between individuals in the population. Hence there does appear to be significant differences in condition indexes between sites with Eregunda Creek having higher condition indexes overall. The magnitudes of the standardised parameters are also useful indicators of parameter contribution. The standardised coefficients (*t*-values) for rainfall and site are very similar indicating an equal contribution to the variation in the data. However, the negative correlation between rainfall and condition (-0.055 in Table 3.17) is counterintuitive to the presumption that condition increases with rainfall.

3.5.9 Genetic Analysis

Biopsy samples were obtained from all three sites, Wilkawillina South (n=22), Wilkawillina North (n=12), Eregunda Creek (n=19). In a separate study, biopsy samples were also removed at Plumbago Station (n=12), 150km East of these sites in the Olary Hills, South Australia. Mitochondrial DNA (mtDNA) and microsatellite analysis of these samples was conducted by Dr Mark Eldridge (unpublished) at Macquarie University. The following is a brief summary of the results of analysis carried out by Dr Eldridge.

Using two mtDNA haplotypes, Eregunda Creek was found to be uniquely different to both of the Wilkawillina sites. As previously mentioned, Eregunda Creek is approximately 24 km from Wilkawillina North and Wilkawillina North is approximately 4km north of Wilkawillina South. However, the two haplotypes at Wilkawillina South and Wilkawillina North were found to have very different frequencies (WN: haplotype 1, 0.71; haplotype 2, 0.29; WS: haplotype 1, 0.09; haplotype 2, 0.91). These results indicate limited gene flow, mainly between Wilkawillina North and Wilkawillina South although it should be remembered that mtDNA describes maternal gene flow.

Using microsatellite data, Eregunda Creek (and Plumbago Station) are both genetically well differentiated from the Wilkawillina sites (Average Fst = 0.16) whereas Wilkawillina North and Wilkawillina South are much closer (Average Fst = 0.06). An assignment test was then conducted using the programme Geneclass. Assignment tests involve classifying each individual to its site of origin using microsatellite data from selected loci.

Eldridge tested two assignment assumptions using both Bayesian and Frequency methods. These included leaving in or keeping out the assigned animals. Using the Bayesian method and leaving out the individuals to be assigned, two individuals found at Wilkawillina South were assigned to Wilkawillina North. Leaving in the individual to be assigned, only one individual found at Wilkawillina South was assigned to Wilkawillina North. Using the Frequency method and leaving out the individuals to be assigned, one individual found at Wilkawillina South was assigned to Wilkawillina North and one individual found at Wilkawillina North was assigned to Wilkawillina South. Leaving in the individuals to be assigned, two individuals found at Wilkawillina South were assigned to Wilkawillina North and two individuals found at Wilkawillina North were assigned to Wilkawillina South. In all cases the same subset of animals are being assigned to other sites. Most of these animals were males. Up to 50% of the animals at Wilkawillina South could not be assigned to either site. This result was expected since Wilkawillina South is nearer to the centre of Wilkawillina Gorge and aerial sightings indicate *P. x.*

xanthopus is scattered all along the gorge. Conversely, Wilkawillina North is found nearer to the northern edge of the gorge.

No assignments were revealed between Eregunda Creek and the Wilkawillina sites. An attempt was also made to trap individuals at a fourth site, Fountain Spring, approximately 8 km south of the Eregunda Creek site. However, despite several attempts, none of the animals observed at this site were able to be captured.

3.6 Discussion and Summary

3.6.1 Survival differences between sex, stage and site

The primary question raised in this study relates to how survival differs between sex, stage and site. Furthermore, survival at Eregunda Creek was compared with Wilkawillina South. Although not quantified in this study, foxes and goats are known to be present at Eregunda Creek with fox control and limited goat control undertaken by the property owner. Conversely, Wilkawillina South is in the Flinders Ranges National Park where there is extensive fox and goat control. It should be also remembered that survival could not be directly measured in this study. Instead, the notation χ was used to denote the probability that an individual remains in the population.

Using 220 parametric bootstrap simulations of the global eight-group model, $\chi(sex + stage + site + rain1), p(sex + stage + site + rain2)$, more than 28% of the simulated bootstrap deviances were greater than the observed deviance of 222.4 (see Figure 3.7). The alternative parametric bootstrap approach using covariate version of this model also indicated more than 75% of the simulated bootstrap deviances were found to be greater than the observed deviance of 282.3 (see Figure 3.8). The differences in these two percentages have been attributed to the difference in assumptions that underpin the parametric bootstrapping embedded in the programme 'Mark' with the assumptions in the C++ bootstrap programme written by the author. However, both of these approaches indicate there is a good fit of the data.

The most parsimonious model, $\chi(site + rain(i:11, l:13)), p(sex, stage, rain(i:4, l:7))$, having an AIC score of 304.16 indicates that the Eregunda Creek site has a significantly higher survival than Wilkawillina South when $\alpha = 0.10$ but not significantly different at $\alpha = 0.05$. This appears to be contrary to the expected values of χ at these sites. Although interactive effects were not fully explored, the variations in χ were not adequately explained by the sex or stage of the population. The variations in *p* were adequately explained by sex when $\alpha = 0.05$ and when $\alpha = 0.10$, sex and stage adequately explained the variation in *p*.

The model $\chi(stage(1st) + site(1st) + sex + site + rain(i:11, l:13)), p(stage + sex + rain(i:4, l:7))$ was also tested. Here stage and site were separately related to χ for the first capture interval of each individual. The model $\chi(site(1st) + rain(i:11, l:13)), p(stage + sex + rain(i:4, l:7))$, was the most parsimonious model (AIC score of 287.2). Here the term $site(1_{st})$ was found to significantly explain the variation in χ for the first capture interval when $\alpha = 0.10$ but not when $\alpha = 0.05$. Again χ was found to be higher at Eregunda Creek. Unfortunately the most

parsimonious model dropped the *stage(1st)* parameter as an indirect measure of sub-adult and juvenile survival over the first capture interval. Sex also did not influence χ.

In summary, these modelling approaches showed no signs that χ varies between stage (age) and sex. Furthermore, χ was found to be significantly higher at Eregunda Creek at $\alpha = 0.10$ but not $\alpha = 0.05$.

3.6.2 Rainfall Correlations

Another question raised in this study relates to how rainfall as a surrogate of resource availability affects survival. Interestingly, the most parsimonious models using both approaches indicate that rainfall does affect χ, despite the rainfall parameter in the model, $\chi(site + rain(i:11, l:13)), p(sex, stage, rain(i:4, l:7))$ not being significantly different from zero ($\alpha = 0.10$), and the rainfall parameter in the model,

$\chi(site(1st) + rain(i:11, l:13)), p(stage + sex + rain(i:4, l:7))$ not being significantly different from zero ($\alpha = 0.05$). These conflicting results could be due to a combination of factors. Firstly, the 'Frequentist' approach (significance testing parameters) compared with the likelihood approach (here AIC scoring) will sometimes disagree in these circumstances (Hilborn and Mangel, 1997) leaving the research often stuck between two opposing philosophies. The lack of significance in these parameters does not discount their importance but does question how tightly coupled rainfall is with χ. Secondly, as so many rainfall combinations were tested, by chance the right combination of rainfalls could have converged with the model, and unfortunately in this study there has been no other biological evidence collected that confirms these rainfall lags and intervals. In the absence of resource (vegetation) and rainfall studies, the loosely coupled relationship between rainfall and χ should be treated with caution. The fact that χ does not directly measure survival could also account for this loose relationship. This is discussed further in Section 3.6.3. Finally, these additive models combine the Eregunda Creek data with the Wilkawillina Gorge data with a single binary variable distinguishing the two sites. An obvious limitation of this additive approach is that Eregunda Creek may have an entirely different relationship (or no relationship) with rainfall when compared with Wilkawillina Gorge.

Relating rainfall to *p* trappability may also be tenuous. While the best fit of *p* is 4 months interval of rain, 7 months prior to a capture event, there is no behavioral evidence that suggests rainfall is negatively correlated with *p*. This relationship was also negatively correlated, which contradicted *a priori* the observations of animal trap behaviour (see Section 3.5.1). There also remains some doubt about the validity of this relationship given the close interdependency between *p* and χ.

Significantly, Sharp (2002) found no evidence to support a relationship between rainfall and survival and found the lowest AIC score supported a model where p and χ were constant. Nor did his best model distinguish any differences between stage or sex. However, there were some differences in methodology. Firstly, he trapped four times per annum as opposed to twice per annum in this study. Secondly, the length of his study was over 48 months as opposed to 54 months in this study. Thirdly, he grouped sub-adults with adults as opposed to juveniles with sub-adults in his study.

3.6.3 Survival (ϕ) verses χ

A more precise definition of χ is the probability that any one individual, randomly drawn from the sample of individuals, remains in the population. Hence, if one were to assume equal dispersal rates at the two sites and no emigration, the Eregunda Creek colony would have a higher survival rate across all age classes. Testing for dispersal is difficult at these sites because the complexity of the landscape forbids the adequate re-observation of individuals around each site. This problem has been highlighted by Bennettes (2001). In addition, radio telemetry equipment could not be fitted to juveniles, for fear of them outgrowing the collars and choking. A number of ear tag transmitters and expandable collar transmitters were tested during the period of this research, however none were deemed to be satisfactory.

As an experiment, a simple single sex Leslie matrix (Caswell, 2001) was constructed using only three stages. This does not consider stochasticity and assumes a stable age distribution has been reached (Caswell, 2001). An average birth rate of 0.8 was estimated from Figure 3.23. Assuming the sex ratio is 1:1, the single sex fecundity equivalent is half of this (i.e. 0.4). A value $\bar{r} = 0.17$ was calculated for Wilkawillina Gorge, using the aerial data and Monte Carlo simulations in Chapter 2. This equates to $\lambda = 1.27$. Using the Leslie matrix (Table 3.18), survival was calculated to be 0.925 for all stages. In the absence of stage-specific survival parameters from the mark recapture analysis, an equal survival for all stages has been assumed for this exercise. The Leslie matrix also assumed a stable age distribution has been reached. Given this is a deterministic model, a survival estimate of 0.925 is conservative. Stage 1 represents juveniles (aged 0 to 1 years), stage 2 represents sub-adult (aged 1 to 2 years) and stage 3 represents adults aged above 2. Given that these animals reach sexual maturity at about 18 months, the annual fecundity figure of 0.4 adjusts to 0.1 for stage 2 animals. The fecundity estimate of 0.4 here also assumes that no pouch young terminations have been missed.

Table 3.18 Three stage Leslie Matrix

	Stage 1	Stage 2	Stage 3
Stage 1	0.0	0.1	0.4
Stage 2	0.925	0.0	0.0
Stage 3	0.0	0.925	0.925

Using the model $\chi(site), p(.)$, a constant 6-monthy survival of 0.92 (95% CI = 0.82 to 0.97) is obtained for Eregunda Creek, and a constant 6-monthy survival of 0.79 (95% CI = 0.68 to 0.87) is obtained for Wilkawillina South. The annual survival of 0.925 in Table 3.18 equates to a 6-monthy survival estimate of 0.962. This is higher and outside of the expected 95% bounds (0.68 to 0.87) of constant survival at Wilkawillina South. It is unlikely that juvenile survival is the same as adult survival hence the disparity between these figures is likely to be one of the following:

1. Fecundity is higher than estimated here.
2. The sex ratio is not 1:1
3. The aerial data is too coarse.
4. The animals are moving out of the trap site.

Interestingly, in Figure 2.13, the univariate density dropped markedly in 2002 around the Wilkawillina South trap site. This is close to one of the largest permanent water sites and one of the last remaining available water points in this area in severe drought (the other being 2km south). Cursory observations in 2002 (at the peak of a drought period) indicated that there is a higher grazing pressure around these water points and that this grazing pressure drops off away from the water points.

The genetic assignment tests conducted by Eldridge (unpublished) suggest that there is limited movement between Wilkawillina North and Wilkawillina South, and although these are low sample sizes, more animals at the time appeared to move south. On the other hand, no movement was found between Eregunda Creek and Wilkawillina North or South. Similar results were obtained by Sharp (1997) (see Section 3.6.4). This tends to suggest that there is no movement northward out of Wilkawillina Gorge. Thus a feasible explanation for the difference between

aerial data and trapping data estimates is the probability that individuals remaining in the population (x) could be significantly influenced by movement within Wilkawillina Gorge. Only by trapping further sites in Wilkawillina Gorge and immediately outside of the gorge, could this be ascertained.

Through intensive radio tracking, Lapidge (2001) calculated a coarse estimate of survival of 12 individuals released from captivity at the Leigh Creek Sanctuary in South Australia. For the purpose of comparison, it will be assumed that the value x obtained at Wilkawillina Gorge and

Eregunda Creek does represent survival rather than the probability of remaining in the population. Wilkawillina Gorge and Leigh Creek Sanctuary have permanent water and rainfalls of around 200mm and both have had integrated pest control programmemes for many years. Conversely, Eregunda Creek has no integrated pest control although there is permanent water within three kilometers. In Table 3.19, an annual survival value has been added in the third column, calculated from Lapidge's (2001) coarse survival data.

Table 3.19 Results from Lapidge (2001) at Leigh Creek Sanctuary Using a coarse calculation of annual survival.

Fraction of Period Annual Survival Cohort (years) Rate

This image is included in the print thesis available from the University of South Australia Library.

The average annual survival calculated from Table 3.19 is approximately 0.70. This equates to an average six-monthly survival of approximately 0.82. As previously mentioned, the model x (*site*), $p(.)$, a constant six-monthly survival of 0.92 (95% CI = 0.82 to 0.97) is obtained

for Eregunda Creek, and a constant six-monthly survival of 0.79 (95% CI = 0.68 to 0.87) is obtained for Wilkawillina South. The coarse figure of 0.82 at Leigh Creek is therefore not significantly different to either Wilkawillina South or Eregunda Creek although it may be closer to Wilkawillina South.

Sharp (2002) also trapped animals on a site where there was little or no integrated pest control. However, in his study aerial fox baiting was applied on one occasion. He calculated a constant survival probability over three months of 0.93 (95% CI = 0.91 to 0.95). This equates to a 6 monthly survival of 0.86. Interestingly, Sharp (2002) found that while survival did increase after

a single aerial fox bait, the difference was not statistically significance. However, this figure again falls inside the confidence intervals of both Eregunda Creek and Wilkawillina South.

On the assumption that the value χ is survival in all of these studies, (i.e. no movement, immigration equals emigration or transient movement is random) these comparisons show no significant difference at sites with pest control and sites without pest control. While the differences may be close, if monitoring was to continue at Wilkawillina Gorge and Eregunda Creek over say another few years, these confidence intervals may narrow. Another cautionary note is that the figures derived from Lapidge (2001) are coarse and as yet no formal approach to the estimation of survival parameters has been conducted at Leigh Creek Sanctuary.

Sharp (2002) calculated that the population at the Hill of Knowledge (HoK - in the Idalia National Park in Queensland) was decreasing (r = -0.041 to -0.052). Using a matrix population model (Caswell, 2001), Sharp (2002) conducted elasticity tests and suggested that λ was more sensitive to adult survival followed by pouch young survival, juvenile survival and fertility. If Sharp's (2002) survival data is not significantly different to Wilkawillina South or Eregunda Creek, there begs an important question: how sensitive is the population's long term viability to small changes in age-specific survival? I will attempt to answer this question in Chapter 5.

3.6.4 Genetic Analysis

The assignment test carried out by Eldridge (unpublished) revealed that despite many years of threat abatement work carried out by DEH in Wilkawillina Gorge, there was little movement in ecological time evident over the four kilometre distance between Wilkawillina North and Wilkawillina South. The individuals that were likely to have moved were primarily males. This tends to support the general findings of Johnson (1989) who reports bias in sub-adult males across most macropods.

A study of this species was carried out at Sharp (1997) at three sites including HoK. One of the other sites was 600 metres from HoK and the second was 2.5km from HoK. Fifty-two wallabies were radio tracked from HoK during this study between October and November 1994 (four weeks) he trapped all three sites. Sharp (1997) did not radio collar animals under 4kg. Only at the site 600 metres from HoK did he catch a male, which had dispersed as a juvenile male from HoK. The results of Sharp's (1997) analyses tend to agree with the findings of Pope (1993) and Pope et al (1996) where an examination of the distribution and frequencies of microsatellite alleles also indicated infrequent dispersal between colonies at the Idalia National Park sites.

Both Sharp's (1997) results as well as the results in this study, suffer from small sample size. Nevertheless, the limited dispersal between Wilkawillina North and Wilkawillina South does tend

to agree with Sharp (1997). Interestingly, Sharp (1997) found intra-colony movement, particularly transient movement, and the single dispersal event of 600 metres corresponded with periods of low resource availability. He also found that intra-colony movement was evident mainly among males.

Wilkawillina Gorge consists of apparently continuous habitat for *P. x. xanthopus* and consequently it is difficult (and probably meaningless) to attempt to distinguish one colony from the next. Furthermore, the number of different social groups in the gorge is obviously unknown but likely to be quite high. Given the condition of animals at Wilkawillina Gorge were lower that Eregunda Creek it is conceivable that the movement in Wilkawillina Gorge is transient (temporary) and that juveniles are remaining primarily in or near their natal patch. As previously mentioned, in Chapter 2 there is some support for transient movement in Wilkawillina Gorge, particularly as environmental conditions and grazing pressure varies, although this could be clouded by observation noise. Higher short distance transient movement and lower dispersal is likely to be due to the cost of dispersal being much higher than transient movement where the animals are already familiar with the conditions and patches (Sharp, 1997). This is also known as the "fence" effect (Krebs, 1992).

3.6.5 Carrying Capacity

Another question raised in this study relates to the comparison of the condition of individuals between sites. Most of the mark recapture models in this study indicate the probability of individuals remaining in the population (χ) at Eregunda Creek is higher than Wilkawillina South by approximately 15%. The condition of sub-adults and adults at Wilkawillina South was also found to be significantly lower than Eregunda Creek.

This evidence tends to suggest that the available resources and carrying capacity at Wilkawillina Gorge could be lower than Eregunda Creek. This is partly supported by the Ivlev (1961) parameters calculated using the aerial data in Chapter 2. Here it was found that the population at Plumbago Station, which has also been threat abated using the same methodology for many years by DEH, had an almost equal demographic efficiency to Wilkawillina Gorge but had a significantly higher intrinsic rate of growth r_m=0.64 (0.49-1.88, 5-95 bootstrap percentiles) compared with r_m=0.24 (0.08-0.36, 5-95 bootstrap percentiles). Unfortunately vegetation surveys in these hills have not been conducted to support this evidence. It is also not known whether the carrying capacity has always been lower at Wilkawillina Gorge (including pre-European occupation). However, higher numbers of *Macropus robustus* observed in Wilkawillina Gorge competing for resources in this area as well as transient goats could be likely causes (De

Preu, pers comm., 2002). Another possibility suggested by Sharp (pers comm., 2003) is that predators are regulating the population at Eregunda Creek at a level of equilibrium such that the population is maintaining below carrying capacity.

3.6.6 Fecundity

While there may be too few data, the birth patterns in this study tend to agreed with the findings of Robinson et al (1994), Lapidge (2001) and Sharp (2002), contending that *P. x. xanthopus* is a continuous breeder. However, unlike Sharp (2002) in this study there did appear to be a correlation between apparent terminations and low rainfall events, and the onset of gestation with high rainfall events (Figure 3.21). These findings tend to agree with Robinson et al (1994) where periods of low rainfall trigger embryonic diapause. In this study, terminations were deemed to have taken place when the pouch young was thought to have prematurely vacated the pouch under 160 days between successive traps. This finding suggests that not only will *P. x. xanthopus* utilise embryonic diapause but females will also displace their pouch young when stressed by environmental conditions.

When the data at Wilkawillina South and Wilkawillina North were grouped, the mean difference in birth dates was found to be 190.3 +/-20.4 (+/-SE) at Wilkawillina Gorge (n=14) and 192.7+/-17.0 (+/-SE) at Eregunda Creek (n=18). Capture events in 1998 were excluded because of the lack of data and the second capture event in 2002 (exclusive to Eregunda Creek) was excluded. Lapidge (2001) found continual breeding cycles of 189 to 203 days for 22 *P. x. celeries* caught at Lambert Station. Hornsby (1978) also noted 181 days between two successive permanent pouch vacations from a captive female. Superficially, these data would seem to agree with the findings of Poole et al (1985) who found intervals from birth to pouch vacation in captive animals of 190 to 201 days (n=7). However Poole et al (1985) did not observe the time between the natural vacation of a pouched young and the birth of the blastocyst. On one occasion they removed a pouched young (aged 81 days) and observed the birth of a blastocyst 31.5 days later. This delay is because the 100 cell blastocyst (Hinds and Loudon, 1997) needs to continue gestation for this period before parturition. Hinds and Loudon (1997) describe two control mechanisms for the inhibitory regulation of the quiescent blastocyst. These are photoperiod relays from the pineal gland in the brain that detect day length and are found in seasonal breeders, and the suckling stimulus of the pouch young. *P. x. xanthopus* is not recognised as a seasonal breeder (Lim, 1987; Sharp, 2002) and thus a curious anomaly in these findings is that the blastocyst appears to have been reactivated (i.e. gestation) in these animals possibly up to 30 days before final pouch vacation. In this study, the anomaly may be due to the low number of samples, and the average

period between births may, with more sample data, converge closer to Poole et al's (1985) estimates of 190 to 201 days added to the 31.5 days to parturition.

Interestingly, the prevalence of births at Eregunda Creek appear to be higher that Wilkawillina Gorge. Unfortunately, there were too few data to test the significance of this difference.

A curious anomaly that requires further investigation was the negative correlation between condition and rainfall. While rainfall variability (i.e rainfall variance over the lagged period) was not tested, this might shed some light on this counterintuitive relationship. Nevertheless, the evidence of lower fecundity at Wilkawillina Gorge tends to be supported by the difference in condition of the animals between these sites and the differences in probability of remaining in the population. Furthermore, the parameter r_m derived from in the Ivlev (1961) equation from aerial data comparisons between Plumbago Station and Wilkawillina Gorge, also suggest there may be limited resources in Wilkawillina Gorge.

CHAPTER 4

The habitat of the Yellow-footed Rock-wallaby (*Petrogale xanthopus xanthopus*).

4.0 Introduction

The analysis of the relationship between species and the environment is a central issue in ecology (Guisan and Zimmermann, 2000) and increasingly ecologists are being required to produce estimates of these species distributions for conservation and biodiversity programmes (Lehmann et al, 2002). Spatially explicit habitat models are also important tools for highlighting areas that could support a species and may need protecting. However, ecosystems are not constant or static environments but dynamic and because these systems are constantly in flux, the notion of defining a habitat with static variables is inherently flawed (Hirzel et al, 2001). Consequently, relating a dynamic system to ecological variables and classifications is usually vague and at times contradictory (Peters, 1991). At best these relationships can only be made at one particular time and over a limited geographical range (Guisan and Zimmermann, 2000; Pople, 1989).

In this chapter, a range of habitat modelling approaches will be reviewed. Following this, two distinctly different habitat modelling approaches at two different scales are presented. The first approach is an aspatial approach based upon presence-absence data of this species and habitat characteristics observed at 150 sites from 2000 to 2002 in the Flinders Ranges South Australia. The second approach is a spatially explicit habitat model constructed using a GIS. A range of candidate modelling algorithms will be tested and using the approach that best fits the data, prediction surfaces will be generated. This will use presence and absence data based upon 5 years of aerial survey data, ground survey data and biophysical data including climate, vegetation community and topographical data.

The primary aim of this chapter is to gain an understanding of the current habitat preferences of *P. x. xanthopus* populations and, with this information, spatially define the potential range of *P. x. xanthopus* in the Flinders Ranges. In Chapter 5, the spatial habitat model will be used as a spatial framework that underpins the spatially explicit Population Viability Analysis (PVA) of this species. A second aim of this chapter is to determine any change of status of *P. x. xanthopus* at the sites visited by Copley in 1981.

4.1 Distribution in South Australia

As mentioned in Chapter 2, the first extensive research and regional field survey of *P. x. xanthopus* in South Australia was conducted in 1980 and 1981 by Peter Copley for the Nature Conservation Society of South Australia (Copley, 1981). The aim of this survey was to establish the range of *P. x. xanthopus*. However, comparing this work with historical data suggested that the species had declined since early European records despite maintaining its former range in South Australia (Copley, 1981).

4.1.1 Aerial Surveys

The field survey conducted by Copley also established a framework for aerial survey monitoring conducted by the Department for Environment and Heritage (DEH), South Australia (Copley and Alexander, 1997). Of eleven key areas identified, the Olary Hills and Gawler Ranges were identified as 'most at risk' with some colonies in the Flinders Ranges identified as threatened (Alexander, 1994). These aerial surveys were designed to measure the relative abundance of these colonies and their response to threat abatement management strategies in government investment areas (Alexander et al, 1993; Copley, 1983; Copley and Alexander, 1997).

As mentioned in Chapter 3, the aerial surveys first commenced in 1981 at the Olary Hills and the Southern Flinders Ranges between Quorn and Hawker. They recommenced for the period from 1989 to present except 1994 and in the Olary Hills up until 2000 (Copley and Alexander, 1997; De Preu, 2000). Aerial surveys also commenced in 1993 in the Flinders Ranges National Park and surrounds. In 2000 this was extended to the Gammon Ranges National Park. Intermittent surveys have also been conducted in 1995, 1999 and 2000 in the Gawler Ranges with some work in the Mt Remarkable National Park more recently. In 1996, a GPS electronic census system was trialled and then fully

implemented in 1997 by DEH. The significance of the implementation of a GPS methodology in 1996 is that positions of the aircraft were now possible to within approximately 150 metres along the aircraft track (considering GPS 'selective availability' satellite clock errors, acquisition delays and movement), and within approximately 100 metres cross-track (primarily 'selective availability' satellite clock errors). Prior to the trial in 1996, sightings of *P. x. xanthopus* were only approximated by manually marking clusters of *P. x. xanthopus* colonies on a map.

After March 2000, when GPS 'selective availability' clock errors were removed by the US government, these positions improved significantly and cross-track errors are now likely to be as low as 20 metres with along-track errors as low as 70 metres. Given that the animals are usually seen up to 200 metres from the aircraft (horizontal distance), the accuracy of a recording of an individual animal is most likely to be within 250 metres of its true position. The mass GPS sampling of individual locations of a species at this scale using this type of electronic system is still unprecedented in Australia and given that the aerial survey of *P. x. xanthopus* still continues annually, many years of these data provide a comprehensive spatial sample of *P. x. xanthopus*.

4.1.2 Ground Surveys since 1981

Financial constraints have precluded the annual aerial survey of *P. x. xanthopus* in most other areas of the state and particularly the area of the Flinders Ranges north of the Flinders Ranges National Park and south of the Gammon Ranges National Park. Little was known about the fate of *P. x. xanthopus* in these areas apart from a few opportunistic sightings and property specific surveys. In a survey conducted in July and October 1999 on the Warraweena pastoral lease by the Nature Conservation Society of South Australia, three colonies were found to still be extant. There are also confirmed sightings at Red Gorge by Lapidge (1997) and Arkaroola (Sprigg, 2000 pers comm). In May 2000, the author conducted a preliminary survey in the Narrina & Oratunga (Angorichina) pastoral leases at Anne Hill and Mt Brook where, in 1981 Copley had reported a presence. This last survey indicated that of the three colonies visited, *P. x. xanthopus* was found to be absent at all sites. Further anecdotal evidence from Mr. A. Ireland of Narrina Station indicated that other colonies were still persisting but a few had not been visible for some time.

4.2 Habitat Modelling Review

A wide variety of habitat modelling and species distribution modelling techniques have been employed over the last two decades including Principle Component Analysis, Canonical Correlation Analysis, Discriminant Function Analysis, Hyper-envelope (or Hyper-volume) approaches (see BIOCLIM (Busby, 1991)) and Generalised Linear Models, Classification and Regression Trees, Artificial Neural Networks (Brito et al, 1999), non-parametric Classification approaches (Skidmore and Gauld, 1996), Genetic Algorithms, Generalised Additive Models (Austin, 2002) and Multivariate Adaptive Regression Splines (Friedman, 1991).

Each of these approaches have important advantages and disadvantages and the appropriate model employed depends upon the objective of the study, and importantly, the nature of the data. For this reason, a range of habitat models have been reviewed in order to be able to choose an appropriate strategy (or strategies).

Most habitat models are deterministic and probabilistic, relating species distributions to their present environment (Guisan and Zimmermann, 2000; Skidmore and Gauld, 1996). Consequently, a variety of habitat modelling approaches have been developed for various uses and over a wide range of spatial, and to a lesser degree, temporal scales. Guisan & Zimmermann (2000) provide a very thorough summary of the application of predictive distribution models. They suggest that some habitat models are analytical in their design and strike a compromise between generality and precision (after Levins (1966) and Sharpe (1990)). According to Levins (1966), models deliver a compromise in a triangle of precision, generalisation, and realism. For example, Fausch et al (1988) suggest that models developed for specific areas may have relatively few explanatory variables and that while they may be precise, they lack the generality to be applied more broadly.

However, Guisan and Zimmermann (2000) argue that some predictive models can also be mechanistic, enabling the researcher to better understand biologically meaningful causal relationships. These may be biotic and abiotic parameters. These may include climatic data including rainfall, solar radiation and temperature; landform variables including soil, slope, aspect and wetness indicators; and land cover variables such as vegetation data (Overton et al, 2002; Skidmore and Gauld, 1996). Lehmann et al (2002) argue that models should not only be precise, but should also be based upon ecologically sound theory that can be applied more generally.

There are essentially two categories of habitat models. These are abundance models and presence-absence models. Presence-absence models have the distinct advantage that they do not rely on abundance estimates, which are usually more difficult to estimate. However, a disadvantage of

presence-absence models, is that synergistic effects among the habitat parameters may be ignored and the model may either underestimate or overestimate the presence of a species (van Horne, 1983). Presence-absence models may also fail to indicate the quality of biotic and abiotic components of the landscape that support a viable population (van Horne, 1983). Hirzel et al (2001) point out that relying on absence data is both a strength and a weakness, and notwithstanding observation errors associated with false absences, absence data can be intrinsically biased, particularly if a species has declined historically. These biases might include disturbance, barriers to movement or ecological influences such as competition and predation (Hirzel et al, 2001).

The assumption that the density of a species is proportional to the habitat quality is also flawed for similar reasons. Hutchinson (1957) differentiates the 'realised' niche of a species from its 'fundamental' niche. He defines fundamental niche as that abstract hyper volume in n-dimensional environmental variable space in which a species can potentially survive and produce. Conversely the realized niche is the actual range of the species (Hutchinson, 1957). In highly variable environments, such as semi-arid environments, this is particularly problematic (van Horne, 1983). Van Horne (1983) also challenges the notion of habitat quality and offers an alternative definition. He suggests that habitat quality should be defined as (or related to) a measure of fitness of the population at a location, where the level of fitness is the product of density, survival probability and a measure of fecundity.

4.2.1 Scale, Space and Uncertainty

The problem of spatial and temporal scale confounds our scientific construct of the real world. At one level the system may be apparently chaotic, at another level it may be partly explained by one domain of variables and at another level again a different domain of variables may partly explain the system. These problems are widely discussed in the literature but have rarely been resolved (Norton and Williams, 1992). Ultimately, the scale of the study will also depend upon the question being asked by the researcher (Pople, 1989) and the level of uncertainty that is acceptable. Spatially explicit habitat models are therefore scale-dependent. Unfortunately spatially-explicit explanatory variables are expensive and those data that are available through government agencies are usually constrained by the resolution and level of aggregation for which they were originally intended. Furthermore, these spatial data rarely hold accurate biological information for microhabitat studies (Guisan and Zimmermann, 2000), despite their dangerous impression of being accurate representations of the landscape (or the biota) (Elith et al, 2002). This uncertainty can be either

spatial and/or aspatial. Uncertainty propagates through the model to the final prediction (Burrough, 1986). The combined uncertainty from several explanatory variables is not always additive and will vary with the interaction of these variables (Lehmann et al, 2003). These problems will affect the accuracy, scale dependence and utility of the model.

One advantage with spatially-explicit habitat models is that the patterns of the estimated uncertainty in the prediction (the dependent variable) can also be analysed spatially. Lehmann (2002) and Elith et al (2002) suggest that mapping both the prediction and the estimated uncertainty of the prediction are necessary in conservation planning. This is so that conservation efforts are not unrealistically founded on weak assumptions and misdirected in the wrong areas (Elith et al, 2002). Estimating uncertainty is important in risk management. This also provides a formal indication of where further sampling efforts should be directed (Guisan and Zimmermann, 2000).

Uncertainty in predictions is from two main sources, model uncertainty and data uncertainty (Burrough, 1986). Data uncertainty consists of process uncertainty and observation error (Hilborn and Mangel, 1997; White, 2000). In addition to these uncertainties are the spatial and temporal uncertainties associated with scale and resolution (Burrough, 1986). Model uncertainty is usually associated with the level of generalisation of a model and the assumptions upon which it is specified.

4.2.2 Model Validation and Calibration

Guisan & Zimmermann (2000) suggest there should be a clear distinction between model formulation, calibration and evaluation. Predictive model validation methods can include independent data validation (dubbed 'extrinsic validation' (Anderson et al, 2003)); bootstrap re-sampling and cross-validation techniques (dubbed 'intrinsic validation' (Anderson et al, 2003)) and threshold –independent techniques such as Receiver Operating Characteristics (ROC) plots (Guisan and Zimmermann, 2000) which is also an intrinsic measure of model performance at the sample points. As an alternative to ROC plots, Anderson et al (2003) carried out model validation of presence and absence data using a confusion matrix showing the correct and incorrect predicted presences and absences compared with actual presence and absence data.

4.2.3 Envelope and Classification Techniques

The BIOCLIM approach by Busby et al (1991) is a biogeographical approach that overlays presence-only data on environmental gradient surfaces. The environmental data are superimposed over species

presence data from which environmental hyper envelopes (the maximum and minimum values from each environmental surface) can be derived for the species (Skidmore and Gauld, 1996). This follows Hutchinson's (1957) idea of a fundamental niche being that hyper volume of environmental gradients in which the species falls. The environmental data may include climate data such as solar radiation, rainfall and temperature information. Other environmental data may include biotic data such as vegetation data and abiotic data including soil and geology and topography (e.g. slope and aspect). This hyper volume of environmental variables can be superimposed back in geographical space providing the environmental data are spatially explicit.

A major limitation of this approach is that the envelopes are rectangular and this could potentially misclassify multi-dimensional frequency distributions that take another shape (Walker and Cocks, 1991). For example in Figure 4.1, the frequency (or density) of presence data across the environmental gradients of two variables appears to be disjointed and the envelope overlaid on this includes an area where there is no presence data.

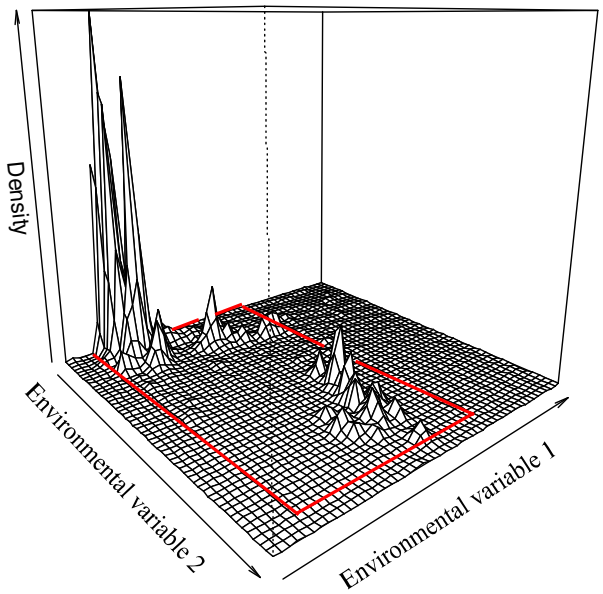


Figure 4.1 Example of presence data across the gradient of two environmental variables.

Walker and Cocks (1991) offer an alternative solution. In an application called HABITAT, the procedure begins by using convex polygon envelopes (rather than rectangular envelopes). The

convex polygons enclose the presence data more tightly. The data is then partitioned into smaller rectangular sub-envelopes to maximize homogeneity. A classification tree (see 4.3.7) is also used to partition the sub-envelopes.

Using data from Caughley at el (1987), Skidmore et al (1996) tested three approaches for predicting kangaroo distributions at a broad biographical scale. These included the BIOCLIM approach, a Classification and Regression Tree approach (see 4.3.7) and a non-parametric classification approach adapted from remote sensing. The non-parametric classification approach was originally derived by Skidmore and Turner (1988) for classifying SPOT remote sensing data. When applied to climate and environmental data, the approach begins in the same way as the envelope approach where presence-only data is overlaid on multiple gridded surfaces to extract a multi-dimensional domain of parameters. Each of 'n' environmental variables becomes a new axis in 'n' dimensions of parameter space. The number of species presences falling over these dimensions forms a multidimensional frequency histogram.

If more than one species were overlaid in parameter space, more than one class of histogram can be analysed. Using Bayes theory and the areal extents of each species in relation to the total area, *a priori* probabilities are used to weight the posterior probability of each species for a given combination (or vector) of parameters (Skidmore and Turner, 1988).

Curiously, no studies appear to have pursued the non-parametric kernel density estimator (Silverman, 1985) as a classification technique. The advantage with the kernel density estimator is its ability to optimally fit a surface to the frequency distribution of the species presence (and absence) data in parameter space. Irregularly shaped frequency responses of a species across environmental gradients can be easily discriminated with adaptive and anisotropic Kernel smoothing techniques (see figure 4.1). Kernel-smoothing techniques and their application with multivariate data are discussed in detail by Silverman (1985) and Wand and Jones (1995). More recently these techniques have been confined to density mapping, movement and species activity (including human activity) in two-dimensional geographical space. However these techniques can also be used to calculate densities and probabilities in multivariate (parameter) space.

4.2.4 Generalised Linear Models

Generalized Linear Models (GLMs) facilitate the modelling of responses that are not normally distributed (Smyth, 1989). This is more useful in the study of ecology than Ordinary Least Squares (OLS) because many ecology processes are non-linear, exhibit non-normal error structures (McCallum, 2000) and have non-homoscedastic distributions where the variance alters with the mean (Guisan and Zimmermann, 2000). The GLM approach involves using a Maximum Likelihood (ML) approach to fitting models to data. ML can also be used to test a group of competing hypotheses (a suite of models) (Hilborn and Mangel, 1997). The general form of a GLM equation is shown in equation 4.1.

$$g(y) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + ... + \beta_n x_n + \varepsilon \qquad \textbf{Equation 4.1}$$

Here $g(y)$ is a link function (for example a log, exponential or logit transformation, or simply $g(y) = y$). β_0, β_1, .. β_n are the parameters being estimated and ε is the stochastic term. Simple product interactive effects can be specified. For example in equation 4.2 the product interaction between x_1 and x_2 have been explicitly specified.

$$g(y) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 + \varepsilon \qquad \textbf{Equation 4.2}$$

The ML approach requires the user to specify the distribution of the data. This is a hypothesis about the way in which randomness enters into the model (Hilborn and Mangel, 1997). For example, the variance in the data may change with the mean such that the randomness is log-normal, poisson, binomial or negative-binomial, gamma or multinomial (Guisan and Zimmermann, 2000; Hilborn and Mangel, 1997). In a logistic model, randomness is likely to enter the system in a binomial distribution. Unfortunately the GLM approach does not deal with data distributions that are non-homogenous or non-parametric (Smyth, 1989).

4.2.5 Generalized Additive Models

Generalised Additive Models (GAMs) are a non-parametric extension of GLMs that deal with non-parametric responses to predictors (Lehmann et al, 2002, p2087). The approach uses non-parametric

splines to smooth each predictor's response independently before combining the spline functions (called basis functions) in an additive multiple regression equation (Guisan and Zimmermann, 2000). GAMs are very popular in the medical sciences (Wahba, 1990) but can also be very useful in habitat modelling (Lehmann et al, 2002). Unlike GLMs, GAMs allow the species responses to different environmental gradients to be any distribution. The general form of a GAM equation is shown in equation 4.3.

$$g(y) = \beta_0 + s_1(x_1) + s_2(x_2) + ... + s_n(x_n) + \varepsilon \qquad \textbf{Equation 4.3}$$

Here, $g(y)$ is a link function (as in equations 4.1 and 4.2) and apart from the constant β_0, the parameters in the GLM equation 4.1 have now been replaced with the univariate basis functions (spline functions s_1, s_2, .. s_n) for each explanatory variable x_1, x_2, .. x_n (Hastie and Tibshirani, 1990). Wood (2002) describes three spline fitting approaches. The first is a univariate cubic spline that is fitted through all of the ($g(y), x_i$) data points using a smoothing parameter λ (Wahba, 1990). Unfortunately this approach can potentially lead to as many parameters as there are data points (Wood, 2002). The second approach involves the fitting of local piecewise polynomial equations using regression between distinctive data points called knots (Friedman, 1991). While the cubic spline approach is technically similar to a cubic piecewise polynomial fit, there are fewer constraints in the latter approach (Wood, 2002). However, the polynomial approach becomes complicated by the choice of knot locations and the number of knots (Friedman, 1991; Hastie and Tibshirani, 1990; Wood, 2002). To reduce the number of parameter estimates and avoid knot placement problems, several authors discuss a third method known as penalized regression splines (see Marx and Eilers (1998), Ruppert and Carroll (2000) and Wood (2000)). The addition of knots has the tendency to over-fit the data thereby creating a 'wriggly' effect (Hastie and Tibshirani, 1990). In this approach, a large number of knots penalizes the goodness of fit of the piecewise regression polynomials (Wood, 2002). This is analogous to an AIC score in a parametric model being increasingly penalized with an increasing number of parameters. The approach proposed by Wood (2002) uses cubic splines and the optimal smoothing parameter λ is computed by a Generalized Cross Validation (GCV). Not all terms in the GAM must be non-parametric and GAMs can facilitate a mixture of parametric and non-parametric terms (Hastie and Tibshirani, 1990).

Unfortunately, GAMs do not adequately deal with complex parameter interactions because they employ additive models of univariate splines rather than multivariate splines (called interaction splines) (Wahba, 1990). As with GLMs, the user is required to explore these interactions manually and specify these interactions explicitly in the model at best by their products. This is almost impossible with high dimensional datasets. For this reason Artificial Neural Networks (ANN), Classification and Regression Trees (CART) and Multivariate and Adaptive Regression Splines (MARS) (see 4.2.6, 4.2.7 and 4.2.8) may be better suited when interactive effects are present (Friedman, 1991; Lehmann et al, 2003). GAMS also attempt to fit continuous splines to the distributions and consequently don't deal well with classified or discontinuous data. However, to overcome this problem GAMs do have the potential of being able to be hybridised with a Classification and Regression Tree (see 4.3.6).

4.2.6 Classification and Regression Trees

Classification and Regression Trees (CARTs) are able handle complex non-linear and non-additive data structures and interactions (Miller and Franklin, 2002). The term CART here is generic and should not be confused with the CART software by Breiman et al (1984). CARTs often contain a combination of categorical and continuous explanatory variables. Classification trees consist of a non-parametric set of hierarchical decision rules that deal with categorical and continuous explanatory variables. Their counterpart regression trees, consist of a tree of decision rules that terminate at regression equations. Classification trees are used when there is a class response variable whereas regression trees are used when there is a continuous response variable. In each case the tree begins its growth using recursive partitioning (Moisen and Frescino, 2002). Rules are split according to whatever classification reduces the impurity in the data (Walker and Cocks, 1991). These splits are repeated until the data are finally divided into homogenous subsets (Skidmore and Gauld, 1996). The degree of homogeneity is defined by the user (for example a standard error tolerance). Classification trees can grow with binary splits or multiway splits (Kim and Loh, 2001), although the former approach is generally more popular. Several approaches are used in tree binary recursive partitioning. Each approach has a different philosophy and grows a different style of tree. The growth of the tree will also depend upon the sample size, number and type of variables in the data (Kim and Loh, 2001). This can also create biases if the wrong selection method is chosen to split the tree. Hence alternative methods such as bootstrap bias correction have been proposed by Kim and Loh (2001). While the accuracy of tree algorithms is important, Kim et al (2000) also suggest tree

comprehensibility is important. This again draws on Levins' (1966) observation that analytical models are often a compromise between generality and precision.

CARTs usually require 'pruning' to prevent over-fitting of the data (Moisen and Frescino, 2002). A popular method of tree pruning is the cross-validation technique. This method involves a 'n' fold test of the tree using a $1/n^{th}$ of the data at a time to make initial estimates of the error rates in the tree. A total of 'n' separate tests are therefore carried out.

There are several limitations of CARTs. Firstly, they suffer from the problem of discontinuity between tree nodes (Friedman, 1991). This will give rise to a lack of smoothness in the predictions. A bootstrap method known as 'bagging' helps overcome this problem by averaging multiple tree structures (Hastie et al, 2001). CARTs also become unstable with small changes in the data which may change the structure of the tree splits (Miller and Franklin, 2002; Hastie et al, 2001).

CARTs can also be used as a preliminary data exploration tool. This allows the researcher to gain early insights about the sample data that later guides the selection of a more appropriate modelling strategy (Kim and Loh, 2001). Given that regression trees involve the use of simple regression polynomials or GLMs they assume the terminal node data have a linear relationship with the response (or transformed response) variable. This is not always the case (see Section 4.3.6). In this situation a hybrid model involving the use of a GAM and a classification or regression trees could be employed.

4.2.7 Multivariate Adaptive Regression Splines

Friedman (1991) developed a non-parametric regression method to deal with the complex shape of the response variable in relation to a suite of explanatory variables. This method is called Multivariate Adaptive Regression Splines (MARS). Unlike GAMs, the elegance with this technique lies firstly in its ability to model categorical as well as non-linear, and non-normal responses of a species to an environmental gradient, and secondly its ability to find the contribution of high dimensional interactive effects in the explanatory variables. The MARS approach is therefore very useful when dealing with high dimensional datasets (Hastie et al, 2001).

MARS uses an approach called "recursive partitioning" regression (Friedman, 1991). The MARS approach involves first dividing the explanatory variables into regions, then fitting piecewise linear functions to each of these regions, and finally exploring region specific interactions (Abraham and Steinberg, 2001).

$$y = \beta_0 + s_1(x_1) + s_2(x_2) + .s_{ij..}(x_i, x_j, ..). + s_n(x_n) + \varepsilon \quad \textbf{Equation 4.4}$$

Here $s_{ij..}(x_i, x_j, ..)$ is the general form of a basis function where the *ij*.. or *ijk*.. etc subscripts denote two to n dimensional interactions for $x_i, x_j, \ldots$ Single subscripts, for example $s_1(x_1)$, denote univariate piecewise linear segments. Like their univariate counterparts, the boundaries dividing the piecewise interactive basis functions are called knots. The algorithm proposed by Friedman (1991) uses judicious selection methods of defining the regions, the number of regions required and the order of the basis functions (Abraham and Steinberg, 2001). The process first begins by over-fitting the data with a large number of knots and regression functions in a forward stepwise fashion building a decision tree of the process history. The knots are then pruned (and the associated regression functions) systematically back by removing knots which contribute least to the overall fit (Abraham and Steinberg, 2001; Friedman, 1991). In conjunction with this, a brute force search of candidate basis functions, starting at a lower order and progressively increasing in order, are tested for Mean Square Errors (MSE) (Friedman, 1991). An optimal number of knots and selection of the orders of basis functions will determine the final fit (Abraham and Steinberg, 2001). The final model is the sum of single variable basis functions, first order interactive basis functions (involving two variables), and up to n degree interactive basis functions for each region (Moisen and Frescino, 2002).

Unlike other spline fitting GAM approaches, MARS effectively fits piecewise linear functions to the data, divided by knots. Chaudhuri et al (1994) also offer an alternative approach called Smoothed and Unsmoothed Piecewise-Polynomial Regression Trees (SUPPORT). The SUPPORT approach splits a node into two from the positive and negative residuals after fitting a linear polynomial to the data. These linear polynomials can potentially be discontinuous constants or they can smoothed between splits.

MARS deals with multiple categories in the explanatory variables by dividing them into binary dummy variables. Unfortunately MARS does not regress using a logit transformation to properly deal with binary responses. Alternatively, Stone et al (1997) developed a hybrid of MARS called PolyMARS, which uses a maximum likelihood approach that is more robust for logistic responses (Hastie et al, 2001). PolyMARS, unlike MARS also uses a log-likelihood approach and can regress binary predictions such as presence-absence data.

Wood (2002) highlights one drawback of multi-dimensional smoothing. This relates to how the explanatory variables should be scaled and smoothed in multi-dimensional space. The effect of different explanatory variable scales and dependent variable responses in multidimensional space is anisotropic. Consequently the level of smoothing should be different for each explanatory variable in multidimensional polynomial splines. As such, correctly modelling anisotropic effects is likely to be a future challenge in habitat modelling (Wood, 2002).

4.2.8 Artificial Intelligence Systems

Artificial Neural Networks (ANNs) are a more recent advance in data mining based upon a machine learning paradigm analogous to the function of neurons in the human brain (Fotheringham et al, 2000; Jørgensen and Bendoricchio, 2001). Any number of interactions and variable types can be accommodated in an ANN. Typical applications include image recognition, speech processing, planning and predictive modelling (Kasabov, 1996). ANNs are useful when there are no easy formulae that can be derived for the data (i.e. parametric modelling) or there is high dimensionality in the data with the potential for complex interactive effects.

An artificial neuron consists of a simple linear equation used to combine all of the input data x_1, x_2, x_3 using weights w_1, w_2, w_3 respectively (see Figure 4.2). The term $g(y)$ is a threshold link function. This may logit, logarithmic, exponential or simply $g(y) = y$. The threshold link function is labeled thus because it has the added capacity of not outputting any data if the weighted input data do not sum to a certain threshold. The output can be binary [0,1], bivalent [-1,1], continuous [0→1] or discrete (Kasabov, 1996).

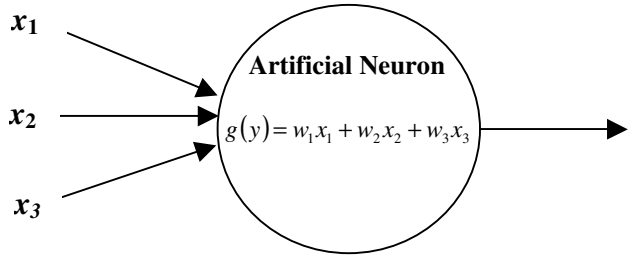


Figure 4.2 Artificial Neuron

In an ANN system there are usually several neurons. For example in Figure 4.3, there are seven neurons (depicted as circles). Figure 4.3 is typical of a network of neurons consisting of an input layer, one or more hidden layers and an output layer (Jørgensen and Bendoricchio, 2001).

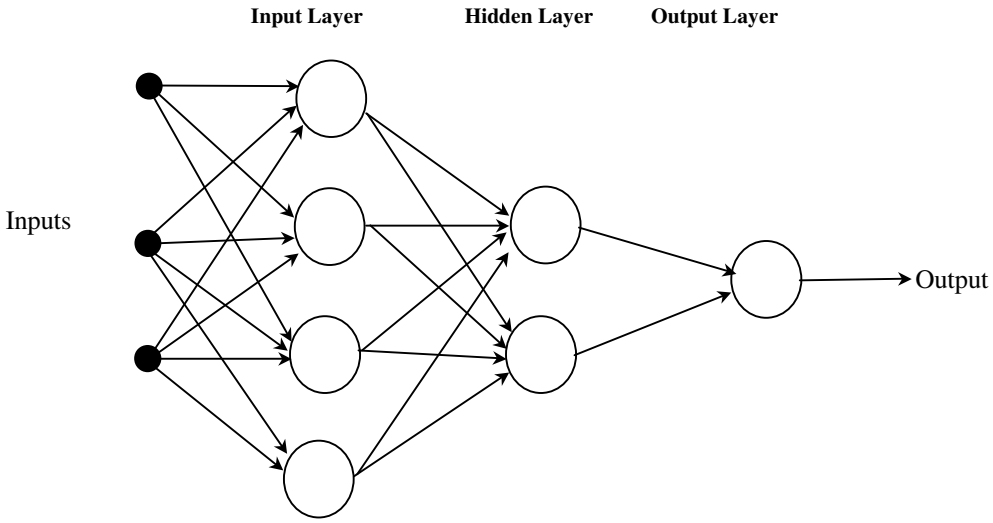


Figure 4.3 Example of a three-layered feed-forward ANN Structure

In Figure 4.3, the inputs into each layer cross to more than one neuron. This is how ANNs are able to deal with complex interactive effects. The most beneficial characteristic of neural networks is their ability to learn. The process of supervised learning involves the user providing training data including explanatory variables and response variables (Fotheringham et al, 2000). Following this, the network is optimized and the software finds suitable threshold weights. An alternative approach is unsupervised learning where no set desired responses are required (Fotheringham et al, 2000). Once the network has been trained, it is then used to predict the responses from a new set of inputs.

There are three disadvantages with ANNs. Firstly, they usually require a large quantity of data to train and validate the network. Secondly, on their own they do not indicate the relative contribution of explanatory variables or classes, nor do they indicate the interaction of these variables (Pearson et al, 2002). As a result, ANNs have often been dubbed the 'black box' approach as they do not provide the researcher with any indication of causal relationships. Causal relationships may be just as important and at times more important than the final prediction. A third problem with neural networks is specifying the number of neurons required. Like an over-parameterised parametric model, a large number of neurons will precisely describe the training data but may have less utility when other explanatory data is entered into the model (Kasabov, 1996). This occurs when the

training data contains outliers (Fotheringham et al, 2000). While fewer neurons may smooth out or remove these spurious effects, there is less robust theory about how to optimise for the correct number of neurons (Fotheringham et al, 2000). Hence ANNs are often precise but may have little capacity for the user to generalise from the model and apply it in other circumstances.

Fuzzy Inference systems have shown some promise in helping to open the ANN 'black box' because they begin to provide the researcher with insights about the causations in the system (Kasabov, 1996). For example Abraham and Steinberg (2001) provide a comparison of Adaptive Network Based Fuzzy Inference Systems and the MARS approach. Alternatively, Olden and Jackson (2002) have attempted to gain an understanding of causations and variable contributions in ANNs using an input randomisation approach.

4.2.9 Summary of Habitat Models

Hilborn and Mangel (1997) advocate a philosophy where the researcher confronts a range of models with the data. This is a 'data driven' approach. The most appropriate model employed therefore depends upon the objective of the study and importantly, the nature of the data.

The distinct advantage of non-parametric approaches such as GAMs, MARS and PolyMARS, is their ability to facilitate non-linear and non-normal species responses to environmental gradients. The elegance of MARS and GAMs lies in their ability to clearly describe the level of importance and the shape of the response of the species to each environmental gradient. These approaches can fit relatively precise models to the data while also allowing the researcher to gain insights about the distributional response of the species to environmental gradients and make generalizations about these responses. An understanding of these responses can be equally, if not more, important than the overall precision of the model. MARS fits piecewise linear functions to the data whereas GAMs and PolyMARS fit a series of interconnected splines or polynomial functions to the response. The advantage with PolyMARS and MARS over GAMs is their ability to deal interactive effects in the explanatory variables. Unlike MARS, PolyMARS supports a more robust logistical framework and deals better with categorical variables (Hastie et al, 2001). This also allows binary predictions such as presence-absences data to be regressed.

CARTs are also well equipped to deal with both presence absence data and complex interactions (Hastie et al, 2001). Unfortunately, CARTS are very clumsy when attempting to gain insights about the distributional responses of a species to one or more environmental gradients. They are nevertheless useful tools for exploring likely interactive effects in the responses.

4.3 Modelling with spatial autocorrelation

Spatial autocorrelation reduces the number of independent observations (Brito et al, 1999) and therefore violates the assumptions in many modelling approaches, particularly GLMs and GAMs. This has the effect of reducing the power of the model (Anselin, 1988). Spatial autocorrelation can be tested with a technique known as Moran's Index (Cliff and Ord, 1973), using an experimental semi-variogram (Burrough, 1986; Wood, 2002) or a covariogram. Moran's Index can be calculated globally (i.e. for all data) or locally at various distance lags (or distance bins). The latter is called Moran's correlogram. The other two approaches display either a semi-variance or covariance for each lag (or distance bin).

There are several methods for removing autocorrelation, for example Brito et al (1999) attempted to remove its effects by using non-adjacent data with up to 10 kilometre separations. Here they used a Moran's correlogram to determine the critical distance at which the effects of autocorrelation were reduced. Another approach is to remove a sub-set of the points randomly. Alternatively, Bivand (1998) describes two formal approaches that deal with spatial autocorrelation. These are also found under the guise of spatial econometrics (Anselin, 1993). The first approach called the spatial error modelling assumes there is a shared spatial process affecting all of the variables and that a systematic bias due to spatial autocorrelation is present in the stochastic term ε. The second approach is called a spatial lag model. This assumes a more structurally complex autoregressive relationship exists in the data Anselin (1993).

Regression approaches including GAMs, MARS and PolyMARS are able to facilitate autoregressive responses using the spatial error model approach. Autoregressive response models of this type were originally proposed by Besag (1972) for logistic data and more recently described by Augustin et al (1996). This approach adds an autocovariance term to the regression equation (Guisan and Zimmermann, 2000). Augustin et al (1996) describe a parametric logistic model where they added an autocovariance error term to the general logistic form (Equation 4.1). This is shown in Equation 4.5.

$$g(y) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + ..\beta_i x_i .. + \beta_n x_n + \beta_{n+1} \left(\frac{\sum_{k=1}^{m_j} w_{jk} y_k}{\sum_{k=1}^{m_j} w_{jk}} \right) + \varepsilon \qquad \textbf{Equation 4.5}$$

Assuming the model is spatially explicit and each term (including the response) is depicted as a separate raster grid, the bracketed term in Equation 4.5 is the error model where w_{jk} is a weight function that is applied to raster cells surrounding cell *j*. This is meant to absorb the spatial

autocorrelative bias from the stochastic term ε. Augustin et al (1996) used an inverse distance weight function for w_{jk}, where $w_{jk} = 1/d_{jk}$ and d_{jk} is the distance between the data point *j* and a neighboring grid cell *k*. The variables y_k represent the values of the neighboring grid cells. This includes non-contiguous grid cells. The idea behind this approach is to estimate how much of the value y_j is contributed by the values from surrounding cells as distinct from causal effects within cell *j*. Unfortunately, the prevalence of 'no data' in the surrounding grid cells confounds the use of this weight function. To overcome this lack of data, Augustin et al (1996) used a Gibbs sampler methodology and estimated the predicted presence or absence at un-sampled grid squares using a logistic equation first without the autocovariance term.

The autocovariance term approach assumes the effect of spatial autocorrelation is additive. This may not always be the case. Anselin (1988) and on the other hand uses a more formal approach that deals with autocovariance interactions. This is called mixed regressive spatial autoregression modelling.

4.4 Habitat Associations of Rock-wallabies

Macropod habitat models cover a wide range of scales from fine scale to biogeographic. At a local scale, food, shelter, water and predation appear to effect the distribution and abundance of most macropods (Pople, 1989). At a broader scale, although distributed patchily, Caughley et al (1987) found that climate, particularly rainfall and temperature patterns, determined the range of the larger and more mobile macropods such as *Macropus rufus*, *M. giganteus* and *M. fuliginosus*. The effect of rain on pasture also affects kangaroo distribution and movement at a finer scale (Priddel, 1986; Priddel, 1987).

At the other extreme, Short (1982) devised a 15 parameter aspatial habitat model for the Brush-tailed Rock-wallaby, *Petrogale penicillata,* in New South Wales. These parameters were quite detailed and intended as a predictive model for assessing specific sites for translocation strategies. These parameters included cliff height; aspect; slope; the size, number and location of ledges; the number of caves; possible routes or runs; the density and type of vegetation above and below the cliffs; and the distance of the site from water.

Lim and Giles (1987) conducted an extensive ground and aerial habitat survey of *P. x. xanthopus* covering approximately 70,000 km^2 in north-western NSW. They used geological data to stratify the survey. The large-scale aerial census was used to further prioritise follow-up ground surveys. They established a habitat rating methodology that included the presence of the following factors:

- steep cliffs
- rocky outcrops
- gullies
- terraces
- caves
- rock piles
- water
- boulders
- rock surface texture

A score of 0 or 1 was assigned to the absence or presence of each of these factors except rock surface and boulder size, which were each assigned a 0-3 range. The final habitat scores were therefore on a 0 to 13 scale. These scores were related separately to the presence of *P. x. xanthopus*, the abundance of *P. x. xanthopus* (where recorded) and historical sightings. Table 4.1 summarises the findings of their large-scale survey.

Table 4.1 Summary of landscape-scale Habitat Survey Results from Lim and Giles (1987).

This image is included in the print thesis available from the University of South Australia Library.

Lim and Giles (1987) concluded that the species appeared to have become extinct in areas where there was a lack of appropriate rock type (i.e. sandstone or quartzite). A more detailed habitat and faecal survey was also conducted by Lim and Giles (1987) at two sites where *P. x. xanthopus* was known to be present. Here, an identical habitat scoring system to the large-sale survey was adopted only over more discernible sections of these sites. Old faecal pellets were also distinguished from fresh faecal pellets. A total of 33 sections were surveyed with the results summarised in Table 4.2.

Table 4.2 Summary of detailed Habitat Survey Results at the Gap and Coturaundee Ranges, from Lim and Giles (1987)

This image is included in the print thesis available from the University of South Australia Library.

These findings confirmed that at both microhabitat scale and landscape scale, *P. x. xanthopus* preferred habitat scores of ten and above, where nearly all factors are present. The presence of windblown caves was reported to have not been a critical factor and instead gullies, gorges, shelter, boulders, smooth rock surfaces and access to water were found to be more important. Lim and Giles (1987) also concluded that while the species may use a wider range of habitat, possibly for dispersal, they appeared to maintain core areas where habitat scores were higher than nine.

However, there were several limitations with their approach. Firstly, Lim and Giles (1987) did not consider the available food resources at these sites. Secondly, due to the scale of their survey, they were unable to search for faecal pellets over the wider area. This may have provided better insights about habitat utilisation of *P. x. xanthopus*. Thirdly, the number of sites surveyed was relatively small and hence not statistically powerful enough to pick up low numbers of *P. x. xanthopus* at low habitat scores. Finally, these data provide little understanding of the role of shelter sites and extent to which *P. x. xanthopus* uses these sites (Sharp, 1997).

Gordon et al (1993) also conducted a ground survey of *P. x. celeris* at 44 sites in Queensland from 1984 to 1987 using animal sightings and three levels of faecal pellet densities. They did not attempt to distinguish old and fresh faecal pellets. They established a habitat rating methodology that included the presence of the following factors:

- cliffs or gorges
- boulders
- rocky terraces
- fissures in the cliff face
- caves or overhangs

They assigned a score of 0 or 1 to the absence or presence of each of these factors. The final habitat scores were therefore on a 0 to 5 scale.

Table 4.3 Summary of Habitat Survey Results in Queensland, from Gordon et al (1993).

This image is included in the print thesis available from the University of South Australia Library.

Like Lim and Giles (1987), the number of sites surveys was relatively small and hence not statistically powerful enough to detect low numbers of *P. x. celeries* at low habitat scores. Again, these data provide little understanding of the role of shelter sites and extent to which the subspecies uses these sites (Sharp, 1997).

Sharp (1997) examined the use of shelter sites of *P. x. celeris* at a colony in central-western Queensland. This survey was undertaken over four days for four seasons between summer 1992 and winter 1994. While there appeared to be a distinctive seasonal trend between shelter sites, overall Sharp (1997) found that tree shade was used more extensively than any other shade types and that adult *P. x. celeris*, particularly males, relied much less on high quality shade sites such as rockpiles and caves. Furthermore, this study revealed that there may be an avoidance of caves by adult *P. x. celeris*. Sharp (1997) suggests that this may be due to a lesser need by adults to thermo regulate and that caves may present a higher predation risk if the animals are cornered. While these findings disagree with the findings of Lim et al (1987) and Lim (1987), where there has tended to be more of a reliance on caves, Sharp (1997) contends that this may be a function of the higher summer rainfalls experienced at the Queensland site rather than behavioral difference between the sub-species.

While Sharp's (1997) study provides more insights about the relative importance of shelter sites, the utility of this data is limited to the particular land system and climate of that region. The aim of the current study is pitched primarily at a landscape scale. Consequently a hybrid approach between the landscape level studies undertaken by Lim and Giles (1987) and Gordon et al (1993), and the microhabitat study Sharp's (1997) has been chosen here.

4.5 Methods

The primary aim of this study is to formulate a habitat model of *P. x. xanthopus.* This has been approached at two different scales. A secondary aim of study is to look at the decline of the species in the Flinders Ranges, S.A since the survey carried out by Copley in 1981. While a common method of determining species decline is to revisit sites previously surveyed and determine presence and absence (Strayer, 1999), visiting only past recorded sites would bias the habitat model. For this reason, other sites were also visited other than those surveyed by Copley in 1981 and aerial survey data was also included. In 2001 and 2002, under a Wildlife Conservation Fund grant and with the support of Bounceback 2000, a ground survey of 150 sites was conducted in the North Flinders Ranges. The primary objective of this survey was to measure any change of status of these *P. x. xanthopus* populations since 1981 as well as collect habitat information at the sites and relate this to presence and absence.

4.5.1 Ground Presence-absence survey

The presence of *P. x. xanthopus* was established from direct sightings or the detection of faecal pellets. The approach used here was to randomly visit a proportion of sites where there had been a recorded presence of *P. x. xanthopus* by Copley in 1981 from ground survey work or researched historical data. However, on many occasions wider searches around these sites were conducted to ensure animals sighted by Copley were not outliers of a nearby colony. On many occasions other gullies and hills were also searched on-route to these known sites and new sightings were made. For this reason great care needs to be exercised when comparing the data collected in 2001/2002 with the data collected in 1980/1981. As previously mentioned additional sites were also visited. These were randomly selected from topographic maps, but stratified such that they were confined to hills and mountain ranges. The extent of the areas surveyed also covered a wide geographical range and crossed several pastoral and private conservation properties. Alluvial plains or open rolling hills were not targetted.

Moro Gorge, Mt Chambers Creek and both the Flinders Ranges and Gammon Ranges National Parks were all known to have repeated regular sightings from aerial surveys, park staff and locals. Consequently these sites were not visited. An extensive amount of opportunistic data was also

provided by Lorraine Edmunds for the Arkaroola area. Most of this data was recalled from as early as 1995 and this did assist with the selection of survey sites in this area.

4.5.2 Study Area

The study area is approximately 130 x 80 kilometres. A total of 142 sites were visited between April 2000 and December 2002. Of the 142 sites visited in this study (marked as ticks in Figure 4.4), 27 were sites either surveyed between 1977 and 1981 or complied by Copley (1981) from historical sightings. A total of 125 points were survey and complied by Copley (1981) These are marked as dots in Figure 4.4).

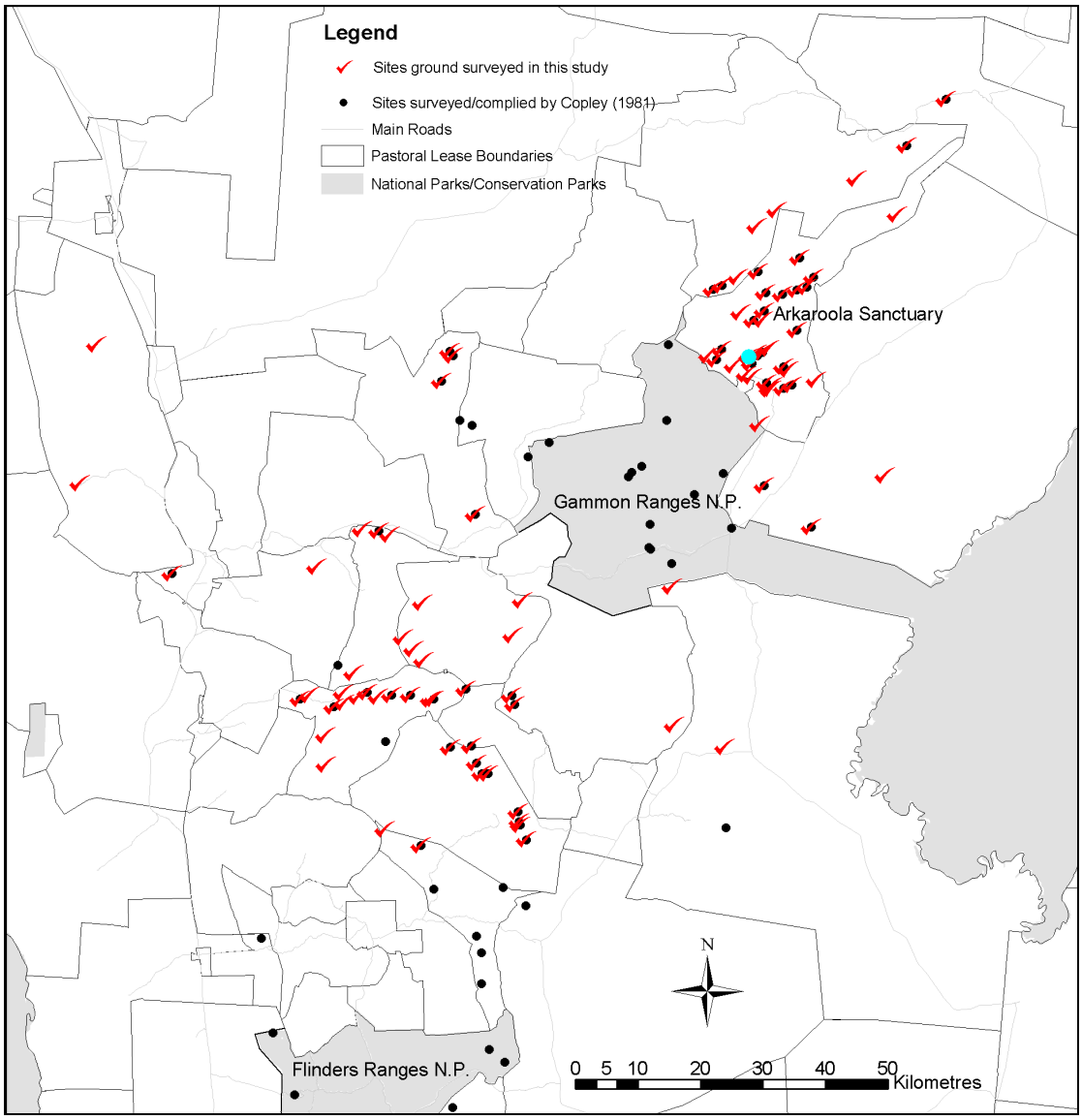


Figure 4.4 Study area and field survey points visited in this study with the points complied or surveyed by Copley (1981)

4.5.3 Aspatial Habitat Quality Scores

The following factors were recorded in relation to habitat quality:

- boulder fields,
- caves,
- water,
- resources.

A habitat scoring system was adapted from Lim and Giles (1987) and Gordon et al (1993) and Sharp (1997). Estimates were made about the availability of resources as well as the extent of boulder fields, presence of caves and water. It is difficult to ascertain the relative permanence of water, as such local property owners were consulted on this matter. The permanence of springs is also drought- and water table-dependent. For this reason, an assessment of water permanence is subjective. A scoring system of 0 (no water); 1 (water present) and 2 (permanent water) were devised. For caves, a score of 0 was assigned if they were absent, 1 if they were present but not suitable and a score of 2 where they were present and suitable for *P. x. xanthopus*. Despite previous researchers finding little correlation of wallaby abundance with caves, there was some evidence from the mark-recapture sites that caves found high in cliffs (usually limestone cliffs) and inaccessible to Euros and foxes did provide suitable refuge for *P. x. xanthopus*. Caves thought to be inaccessible to foxes and Euros were given a score of 2.

The absence of boulder fields was given a score of 0. If the boulder fields consisted of >0.5 metre rocks and provided some refuge but were over a limited area (< 10x10 metres), a score of 1 was used. A score of 2 was used if the extent of suitable boulder fields was much greater than 10 x 10 metres.

Key food resources include chenopods and succulent round or flat leafed plants with stellate trichomes: *Sida petrophila, Ptilotus obovatus, Solanum sturtianum, Abutilon leucopetalum, Ptilotus sessiliflorus, Solanum petrophilum* and *Solanum ellipticum*. To a lesser degree, forbs and grasses are also consumed. See Lapidge (1997) for a more complete review of diet. If an abundance of these plant species was evident a score of 2 was assigned otherwise a score of 1 was assigned. If no chenopods or plants with stellate trichomes were observed then a score of 0 was assigned. A score of 0 does not necessarily mean that the habitat has no available resources because *P. x. xanthopus* is

known to browse on a wide range of plants and eat forbs and grasses. Where there is permanent water, they may also persist in areas where there are few succulent plants.

4.5.4 Government Database

Data collected in this survey, the survey by Copley (1981) and other historical data have been integrated into a single government database held by DEH. This involved the assistance of DEH staff. This database has also been re-formatted to accommodate three modes of data collected about *P. x. xanthopus* including opportunistic data collected by park staff; and locals as well as personal knowledge imparted by locals; ground survey data collected by DEH staff and the DEH aerial data (discussed in chapter 2). A 'master' table including site coordinates and a site description was linked to three other tables, 'aerial survey', 'ground survey' and 'opportune data' using a unique site identifier. The intellectual property rights over this database are formally held by the DEH.

4.5.5 Habitat Modelling Strategies

The aspatial data is explored using a classification tree. This is thought to be more suitable because the ground survey data consist primarily of class variables. The spatial habitat modelling strategy is underpinned by three separate steps.

- Data Exploration.
- Model Comparison.
- Model Validation.

Three separate spatial modelling strategies are tested. A classification tree and a regression tree are first used to find significant contributing explanatory variables and interactions in the data. Following Hilborn and Mangel (1997), the performance of the GAM, MARS and PolyMARS approaches are then compared in terms of their fit of the data. Finally the model having the best fit of the data is extrinsically tested with a quarantined set of independent data and used to predict the species distribution over the entire landscape.

4.5.6 Interpolation of Rainfall data for the Spatial Model

Rainfall data has been used as one of the explanatory variables in the spatial habitat model. In this study the technique Co-kriging described by Burrough (1986) was used to derive a rainfall surface. This approach was chosen because unlike the thin-plate spline technique (Hutchinson, 1998b), Kriging is founded on a meaningful statistical framework that utilises an experimental variogram.

Rainfall data were supplied by the Australian Bureau of Meteorology on the 'Climate Data Australia' version 2.2 database (2002). In this database, all data for every rainfall gauge in Australia has been recorded as individual monthly precipitation records in a single table. This database is stored in a Microsoft Access database format. The rain gauge location, height and other details resides on a second table in this database.

The Flinders Ranges rainfall gauge data therefore had to be extracted from the Climate Data Australia database in Microsoft Access using a series of Structured Query Langauage (SQL) scripts. These scripts were developed to simultaneously cut out the Flinders Ranges data, join the monthly precipitation data with the gauge location data and aggregated this into quarterly and annual averages. The locations of rain gauges were then transformed from latitude and longitude in AGD84 to GDA94 and then projected into Map Grid of Australia (MGA) coordinates for Zone 54. The correlation of rainfall intensity at these locations was then compared with the associated Digital Terrain Model (DTM) (the elevation data) of the Flinders Ranges. Having established a correlation between elevation and the quarterly and annual rainfalls, Co-kriging was used to interpolate the rainfall data.

4.5.7 Spatial Habitat Model Variables

The choice of habitat variables at a landscape scale covering most of the Flinders Ranges has been driven partly by the findings of the aspatial model described later in Section 4.6.2. Another determining factor in the choice of habitat variables at a landscape scale has been the limited availability of spatially explicit data over a large area. The source data that was obtained and used to derive the explanatory variables in the model are listed in Table 4.4.

Table 4.4 Source datasets used to derive the explanatory variables in the Spatially Explicit Habitat Model

Dataset	Currency Year	Source	Format	Coordinate System
1:50,000 scale, 10 metre contours.	2002	DEH	ESRI Vector Polyline Shape File	GDA94, MGA Zone 54.
Vegetation Community Data (see 4.5.7)	1999	DEH	ESRI Vector Polygon Coverage	GDA94, MGA Zone 54.
1:50,000 scale, rocky outcrop delimitation.	2002	DEH	ESRI Vector Polygon Shape File	GDA94, MGA Zone 54.
1:50,000 scale, stream data.	2002	DEH	ESRI Vector Polyline Shape File	GDA94, MGA Zone 54.

Other explanatory variables that were considered included lithology, temperature and solar radiation data. However, these data were not available at the time. Obviously, spatial data related to the location of caves and boulder fields was not available over the entire Flinders Ranges. Otgoid (1999) attempted to derive a habitat model of *P. x. xanthopus* in South Australia using a range of BIOCLIM derived climate variables. However, for the purpose of testing a spatially explicit PVA over a smaller area of the Flinders Ranges, he used 1:50,000 topographic data indicating the location of rocky outcrops. The rocky outcrop polygons provided by DEH are derived from interpretation of aerial photography using photogrammetry. In densely vegetated areas these outcrops may be obscured, thereby biasing the data. Furthermore, the definition of a rocky outcrop is unclear and interpretation may be subjective. Despite these problems, it is obvious from the ground surveys that areas where rock outcrops are seen may be important for *P. x. xanthopus*.

Soil data was not available for the Flinders Ranges and soil moisture estimates derived from flow accumulation algorithms were not considered relevant in the rocky terrain as the rocks retain water.

Data pertaining to the permanence of water in the region was also not available. However, it was observed that on many occasions permanent springs were found along major creek-lines and gorges and it was also possible to separate major and minor creeks in the vector stream data supplied by DEH. Using the vector data pertaining to major creeks and gorges it was possible to derive a raster grid where each grid cell depicted the distance from a major creek or gorge.

The vegetation data was also converted to a raster grid for convenience (see Section 4.5.8 for a detailed description of this data). The 1:50,000 metre contour data was first converted to a Triangular Irregular Network (TIN) using the contour lines as break-lines. This ensured that the TIN triangles were constrained between the contour lines. The TIN was then converted to a raster Digital Elevation Model (DEM) with a 20 metre cell size. The selection of a small cell size was to ensure a high level of precision was maintained during format transformation. The DEM raster grid was also converted to a raster grid depicting percentage slope using the slope function in ArcGIS (ESRI, 2003).

The explanatory variables used to construct a spatial habitat models are:

- mean annual rainfall (Co-kriged with elevation),
- slope (the maximun in a 200 metre radius),
- elevation,
- distance from major creeks and gorges,
- distance from rocky outcrops and,
- dominant vegetation type in the community.

While elevation was clearly correlated with the Co-kriged rainfall, it was left in the model and significance tested for its separate contribution. The presence and absence input data were obtained from three sources. This included a total of 177 presence data and 97 absence data collected from ground surveys by Copley (1981) and from this study, as well as 712 presence data and 597 absence data recorded electronically with GPS during aerial surveys conducted between 1997 and 2002. Finally 50 opportunistic (historical) presence-only data points, compiled by Copley (1981) were included in the model. These 1633 points were then divided into two separate datasets. One dataset consisting of 1143 points (70%) was used for training the model and the other dataset consisting of 490 (30%) points was set aside to extrinsically validate the model.

As previously mentioned, the spatial accuracy of the aerial data is in the order of 100 to 300 metres. This is likely to depend on the direction of flight (see Section 4.2.2). Ground observations are also

likely to have up to 200 metres of error. *P. x. xanthopus* is also known to live on or near rocky cliffs but may forage away from these cliffs. However, accounting for all of these uncertainties was likely to be detrimental to the intended scale of the model so I decided to compromise and assume a conservative estimated uncertainty of +/- 200 circular error. The explanatory variable most sensitive to positional uncertainty in the presence and absence data was deemed to be slope. To accommodate this error, I made used of a Focal Maximum function in ArcGIS (ESRI, 2003) and applied this function to the slope raster grid. This function was applied over a 200 metre radius. The effect of this operation is that every 20 metre raster cell of slope subsequently depicted the maximum slope obtained in a 200 metre radius of the cell centre. The effect of this operation is that the presence or absence data is correlated with the maximum slope in a 200 metre radius from the recorded location.

4.5.8 Vegetation Data

Vegetation data was obtained from the DEH. This dataset is in the form of a vector polygon shape file and identifies the floristic and general structural classification of the native vegetation in these polygons. This data was collected in 1999 as part of the Biological Survey of S.A, Survey 104 (Brandle, 2001). Following the collection of survey site data, aerial photography and Landsat TM satellite imagery were used to interpret patterns in the landscape. These were used delineate vector polygons that defined each community. The primary vegetation mapping class, reflected the most dominant vegetation community for a given polygon (Brandle, 2001). These classes are shown in Table 4.5 with the community type and descriptions.

Table 4.5 Vegetation descriptions for each class number.

Class	Community Type	Description
2	Open tussock grassland	*Eragrostis australasica* (Swamp Canegrass) over +/- *Halosarcia* spp. or *Sclerostegia* spp. (Samphires).
3	Woodland	*Eucalyptus camaldulensis* (Redgum) over +/- *Meleuluca glomerata* (Paperbark) *Acacia victoriae* (Elegant Wattle) *Maireana pyramidata* (Blackbush) *Enchylaena tomentosa* (Ruby Saltbush) Herb spp. *Cymbopogon ambiguus* (Lemon Scented Grass).
4	Tall shrubland	*Acacia victoriae* (Elegant Wattle) over *Maireana pyramidata* (Blackbush) *Maireana aphylla* (Cottonbush).
5	Low shrubland	*Nitraria billardierei* (Nitrebush) *Rhagodia spinescens* (Spiny Saltbush) *Maireana pyramidata* (Blackbush) +/- *Atriplex nummularia* ssp. *nummularia* (Oldman Saltbush).
6	Tall open shrubland	*Acacia ligulata* (Umbrella Bush) *Dodonaea viscosa* ssp. *angustissima* (Sticky Hopbush) over +/- *Zygochloa paradoxa* (Sandhill Canegrass) +/- *Casuarina pauper* (Blackoak).
7	Low open woodland	*Acacia aneura* (Mulga) and/or *Acacia papyrocarpa* (Western Myall) over +/- *Senna* spp. *Chenopodiaceae* spp. or *Graminaea* spp.
8	Low shrubland	*Atriplex vesicaria* (Bladder Saltbush) *Maireana astrotricha* (Low Bluebush) *Maireana sedifolia* (Pearl Bluebush) *Maireana pyramidata* (Blackbush) +/- *Zygophyllum aurantiacum* (Shrubby Twinleaf).
9	Open tussock grassland	Enneapogon spp. (Bottle washers) Sporobolus actinocladus (Rat-tail Couch) +/- Astrebla pectinata (Mitchell-grass) +/- Sclerolaena spp.
10	Tall open shrubland	*Acacia victoriae* (Elegant Wattle) +/- *Eremophila duttonii* (Harlequin Emubush) *Alectryon oleifolius* (Bullock Bush) over *Chenopodiaceae* spp. or *Gramineae* spp.
11	Open tussock grassland	*Cymbopogon ambiguus* (Lemon Scented grass) *Stipa nitida* (Balcarra Spear Grass) *Enneapogon* spp. *Aristida* spp. +/- *Asphodelus fistulosus* (Onion weed).
12	Tall open shrubland	*Acacia victoriae* (Elegant Wattle) *Acacia tetragonophylla* (Dead Finish) *Acacia oswaldii* (Umbrella Wattle) and/or *Sida petrophila* (Rock Sida) over *Ptilotus obovatus* (Silver Mulla Mulla).
13	Shrubland	*Acacia anuera* (Mulga) and/or *Acacia* spp. *Eremophila* spp. *Senna* spp. *Dodonaea* spp. over *Ptilotus obovatus* (Silver Mulla Mulla) and *Chenopodiaceae* spp.
14	Open hummock grassland	*Callitris glaucophylla* (White Cypress-pine) or *Eucalyptus* spp. or *Acacia* spp. or *Meleuluca uncinata* (Mallee Broombush) or *Xanthorrhoea quadrangulata* (Rock Grass-tree) over *Triodia* spp. (Spinifex).
15	Mallee	*Eucalyptus socialis* (Red Mallee) *Eucalyptus dumosa* (White Mallee) +/- *Eucalyptus gracilis* (Yorrell) over *Eremophila* spp. or *Zygophyllum* spp.
16	Mallee	*Eucalyptus gillii* (Curly Mallee) +/- *Eucalyptus socialis* (Red Mallee) over +/- *Triodia* spp. (Spinifex).
17	Mallee	*Eucalyptus flindersii* (Flinders Mallee) over +/- *Meleuluca uncinata* (Mallee Broombush) +/- *Triodia* spp. (Spinifex).
18	Mallee	*Eucalyptus porosa* (Mallee Box) +/- *Eucalyptus odorata* (Peppermint Box).
19	Open woodland	*Eucalyptus intertexta* (Gum-barked Coolibah) over *Dodonaea* spp. *Cassinia laevis* (Curry Bush) or *Senna* spp.
20	Tall shrubland	*Allocasuarina verticillata* (Drooping Sheaoak) +/- *Allocasuarina muelleriana* (Slaty Sheaoak) over *Lepidosperma* spp.
21	Low open woodland	*Casuarina pauper* (Blackoak).
22	Woodland	*Callitris glaucophylla* (White Cypress-pine).
23	Hummock grassland	*Triodia* spp. (Spinifex).

(Source: Brandle, 2001).

4.6 Results

4.6.1 Population Trends

As previously mentioned, Copley (1981) suggests that the species had declined since early European records despite maintaining the extent of its former geographical range in South Australia. Eight local colony extinctions out of 190 known colonies in the Flinders and Willouran Ranges were known to have occurred since 1970. Three of these extinctions were known to have occurred since 1981 (Copley and Alexander, 1997).

As previously mentioned, of the 142 sites visited in this study, 27 were sites either surveyed between 1977 and 1981 or complied by Copley (1981) from historical sightings. A total of 22 of these 27 sites indicated a presence between 1977 and 1981. It is difficult to ascertain whether old pellets simply represent infrequent visits (i.e. outliers) or a recent extinction (in the absence of fresh pellets), consequently these results have been presented under both assumptions.

Since 1981, five of the 22 sites above no longer indicated signs of persistence and an additional six had old pellets (see Table 4.6). However, six of these 11 sites (five with no signs and six with old pellets) are within 1.5 km of extant colonies. Interestingly, of the five sites where Copley (1981) had recorded an absence of *P. x. xanthopus*, fresh faecal pellets were found in 2000 to 2002.

An additional 15 sites were also investigated that were not surveyed in the period between 1977 and 1981. Fifteen of these were either historical sightings or Copley (1981) had commented on their potential. Of these 15 sites, four no longer indicated any signs of persistence although one of these sites was within 1.5 km of an extant colony (see Table 4.7).

Table 4.6 Of the 22 positive sightings (inc pellets) recorded between 1977 and 1981, 11 are now absent or have old faecal pellets.

Site Number	Description	N - No Signs O - Old Pellets	Distance to nearest 2000/2001 presence
148	Henry's Range View	N	400
147	Henry's Range View	N	1200
143	Camel Gap	N	2300
375	Mt. Painter	N	1400
371	Yudnamutana Gorge	N	600
34	Patawarta Hill	O	1600
144	Mt. Brooke	O	800
159	Ann Hill	O	4900
149	SW Mt Andre	O	600
374	Mt. Gee	O	>8000
377	Split Rock	O	4600

Table 4.7 Of the 22 positive sightings pre-1977, four are now absent or have old faecal pellets.

Site Number	Description	N - No Signs O - Old Pellets	Distance to nearest 2000/2001 presence
4	Barbararana Creek	N	2300
9	Moocatoona Hill	N	>8000
171	E of Stirrup Iron Rng.	N	1400
162	SW Mt. Hack	N	3200

4.6.2 Aspatial Habitat Model Exploration

Of the 142 sites surveyed in this study, 138 sites have a complete set of scores for boulders, caves, water and food resources. These scores have been modelled with the presence-absence data in an attempt to find correlations between the habitat and persistence of *P. x. xanthopus*. Two scenarios were explored using the Classification Tree software Quest (Shih, 2003). In scenario one, a presence-absence score of one was assigned to sites that had either fresh faecal pellets or where *P. x. xanthopus* was sighted. In scenario two, a presence-absence score of one was assigned to sites that had any sign

of faecal pellets (old pellets or fresh pellets) or where *P. x. xanthopus* was sighted. In scenario one there are 53 presences and 85 absences (see Figure 4.5). In scenario two there are 76 presences and 62 absences (see Figure 4.6).

A classification tree was constructed for each scenario using the unbiased discriminate splitting approach (Loh and Shih, 1997). The minimum node size of the pre-pruned trees was set at five. Each tree was pruned such that the cross-validation estimate of misclassification cost was given by a SE = 1.0. A ten-fold cross-validation pruning test was selected. Equal prior probabilities were assigned to presences and absences. In Figures 4.5 and 4.6, the terminal nodes at the base of the tree indicate the model's classification of presence and absence. All of the rules along each branch further up from each terminal need to be satisfied for that classification.

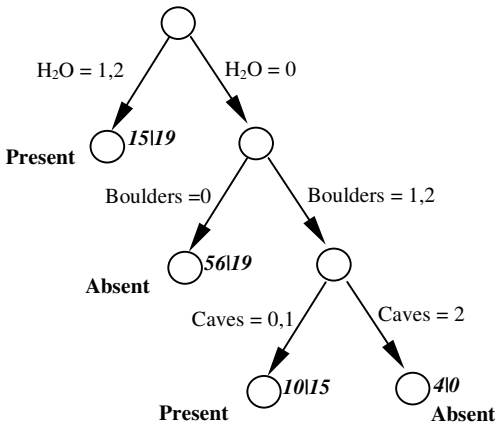


Figure 4.5 Scenario One

Sites that had either fresh faecal pellets or where *P. x. xanthopus* was sighted; a\p denote the absence\presence counts indicating misclassifications at each terminal node. See Section 4.5.3 for scoring descriptions.

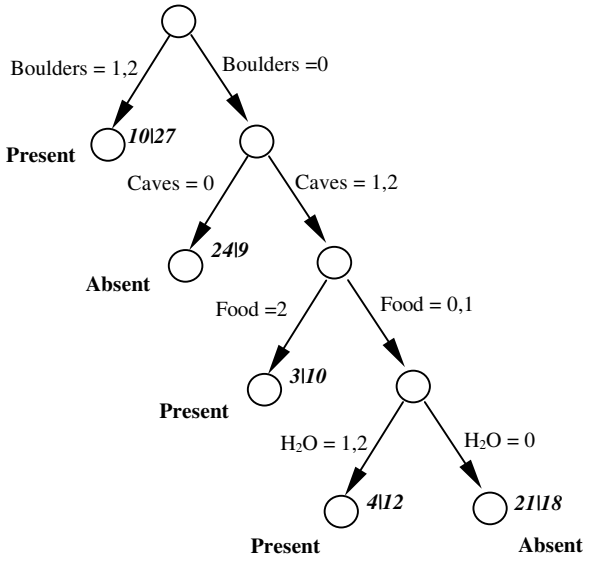


Figure 4.6 Scenario Two

A presence-absence score of 1 was assigned to sites that had any sign of faecal pellets (old pellets or fresh pellets) or where *P. x. xanthopus* was sighted; a|p denotes the absence|presence counts indicating misclassifications at each terminal node. See Section 4.5.3 for scoring descriptions.

The ratio depicted at the each terminal node (a|p) denotes the absence|presence counts. This indicates the purity of the classification at each terminal node. These misclassifications present at the terminal nodes suggests there is still much unexplained variation in the data. However, some trends are evident. For example, in scenario 1, the absence of boulders, is nearly three times more likely to indicate an absence of *P. x. xanthopus* and in scenario 2, a lack of boulders and caves is three times more likely to indicate an absence. It is also interesting that the presence of water overarches all other classifications in scenario 1 when only fresh faecal pellets and animal sightings indicate a presence.

4.6.3 Spatial Habitat Model Exploration

Table 4.14 depicts the hyper-envelope of explanatory variables in which the presence-only data resides.

Table 4.14 Explanatory Variable Ranges for Presence Data

% Slope	Elevation	Distance from Major Creeks	Annual Average Rainfall	Distance from Rocky Outcrops
232.5365	1025.717	20134.52	337.8973	39789.95
7.51	123.4575	0	0	0

The only categorical variable used in this model is vegetation. Figure 4.7, is a bi-directional histogram of the presences (shown as positive) and absences (shown as negative) for each vegetation class. In Figure 4.7, there is a considerably higher presence of *P. x. xanthopus* in the dominant vegetation class 13, shrublands of *Acacia anuera* and/or other *Acacia* spp, *Eremophila* spp, *Senna* spp, *Dodonaea* spp over *Ptilotus obovatus* and *Chenopodiaceae* spp.

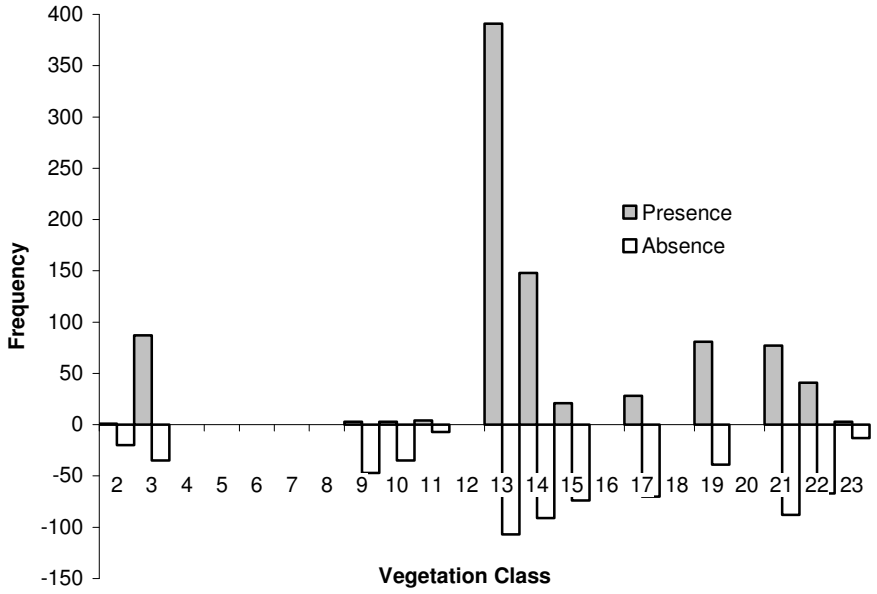


Figure 4.7 Frequency of presences and absences for each vegetation class.

Figure 4.8 also shows the presence and absence data in relation to each vegetation class. The magnitudes of the bars here represent the median slopes on which the presences and absences fall. *P. x. xanthopus* is overall found in higher median slopes. A major peak in presences at a high median slope occurs when the species falls in vegetation class 15, a Mallee community of *Eucalyptus socialis* and *Eucalyptus dumosa* with *Eucalyptus gracilis* over *Eremophila* spp or *Zygophyllum* spp. The class 2 vegetation community is dominated by *Eragrostis australasica* or swamp canegrass. This plant species clearly does not occur on steep slopes. The slope may be an artifact of the 200 metre radius in which the highest slope is derived and/or the level of aggregation in the vegetation polygons. This may also indicate relatively permanent water located near cliffs or rocky outcrops.

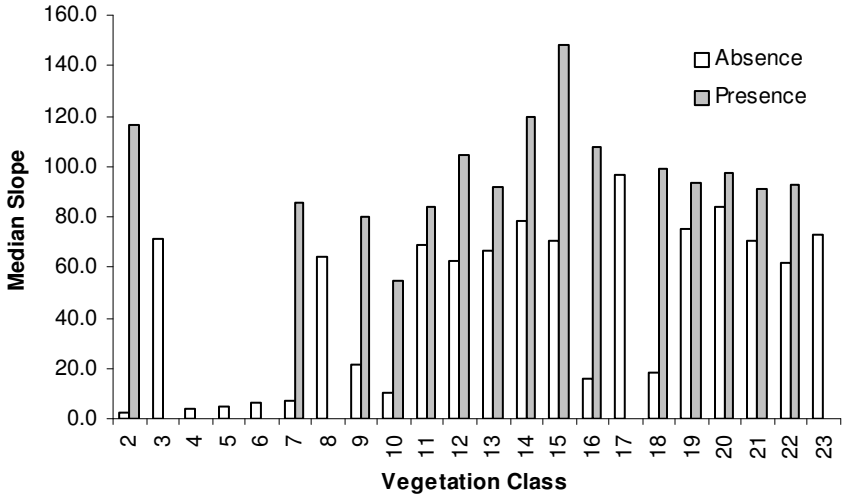


Figure 4.8 The median slopes for each vegetation class.

Using the ArcGIS Geostatistical Analyst (ESRI, 2003), a correlogram was derived (Figure 4.9). This correlogram (Figure 4.9) reveals a spatial dependency of up 0.26 at distance lags of under 150 metres with little or no spatial dependency at approximately 1000 metres. This level of autocorrelation may be sufficiently high enough to violate the assumption in most Modelling approaches of data independence.

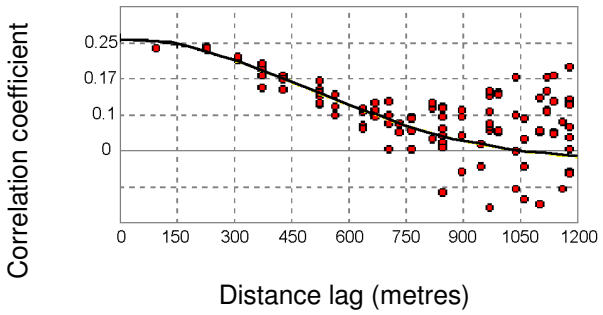


Figure 4.9 Correlogram of presence and absence data.

A classification tree (Figure 4.10) was used to explore possible interactive effects in the data using QUEST (Shih, 2003). The explanatory variables used were: vegetation, distance from water, elevation, slope and average annual rainfall. An unbiased discriminate splitting approach was used (Loh and Shih, 1997) where the minimum node size of the pre-pruned trees was set at five. A ten-fold cross-validation pruning test was selected and equal prior probabilities were assigned to presences and absences. A SE of 0.75 was found to be the best compromise between over-fitting the data with a precise model and sufficient generalisation in the model to be able to interpret the results. Interestingly, the presence of the species appears to be further away from rocky outcrops, which is counter-intuitive since Rock-wallabies live in rocks. Table 4.15 is confusion matrix showing the percentage correctness of the model.

Table 4.15 Confusion matrix of the percentage correctness of the fit for the tree in Figure 4.10.

Actual	Predicted Absent	Predicted Present	Total	% Correct
Absent	361	6	367	98.4
Present	102	565	667	84.7

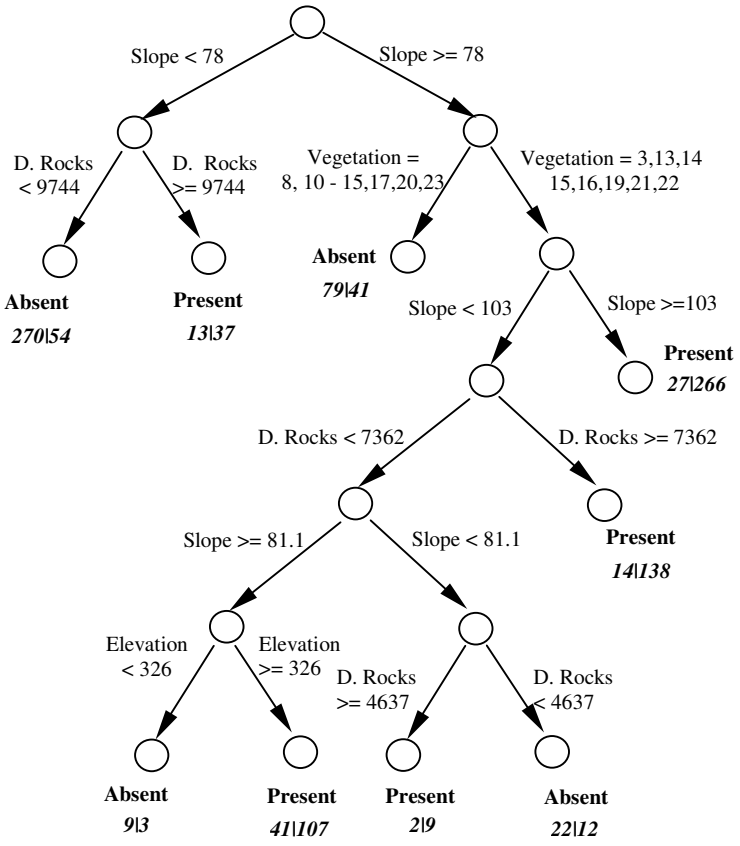


Figure 4.10 Classification Tree showing presence and absence in relation to significant environmental variables.

a|p denotes the absence|presence counts indicating the correctly and incorrectly classified data at each terminal node. D. Rocks is an abbreviation of the variable 'Distance to Rocky Outcrops'. Distance and elevation units are in metres, slope units are shown as a percentage.

A regression tree was also used to explore the vegetation classes and their interactive effects with other variables. The regression tree was modelled using the application GUIDE (Loh, 2002). A constant regression tree was used where the values were split from sample quantiles. The minimum node size of the pre-pruned tree was set at 15. A search was conducted over 38% of sample data. This search was conducted over a systematic sample of the ordered data values. Each tree was pruned with a mean and SE estimation. The best SE threshold was found to be 1.0. A five-fold cross-validation pruning test was selected. The explanatory variables used were: vegetation, distance from water, elevation, slope and average annual rainfall.

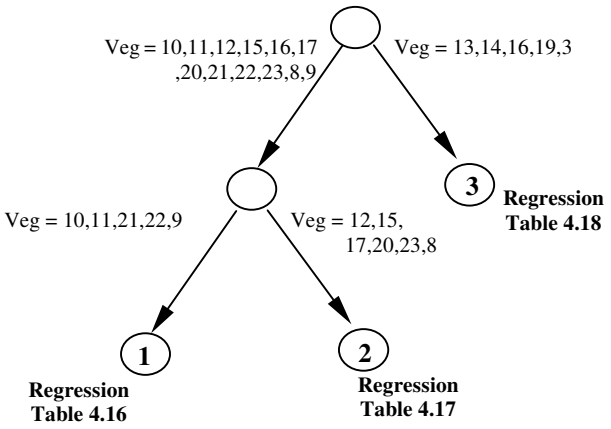


Figure 4.11 A Regression Tree using linear regression equations in Tables 4.16, 4.17 and 4.18

Tables 4.16, 4.17 and 4.18 show the parameter estimates β_i and the Student's 't' tests from the Ordinary Least Squares (OLS) of the data, which has already been partitioned according to the rules higher in the tree in Figure 4.11.

Table 4.16 Linear Regression coefficients at terminal node 1 in Figure 4.10.

Term	β_i	t-stat
Constant	6.445045E-03	7.951
Slope	2.985707E-04	1.450
Elevation	1.782438E-04	-2.092
Dist. to Major Creeks	-1.746409E-05	1.139
Annual Rainfall	6.919663E-04	8.433
Dist. to Rocky Outcrops	1.555968E-05	2.559

Table 4.17 Linear Regression coefficients at terminal node 2 in Figure 4.10.

Term	β_i	t-stat
Constant	2.113672E-01	0.940
Slope	6.777541E-03	6.673
Elevation	-2.717026E-04	-1.358
Dist. to Major Creeks	-1.900491E-05	-1.469
Annual Rainfall	-1.170016E-03	-1.150
Dist. to Rocky Outcrops	-6.944394E-07	-0.085

Table 4.18 Linear Regression coefficients at terminal node 3 in Figure 4.10.

Term	β_i	t-stat
Constant	6.139078E-01	4.845
Slope	5.423934E-03	12.869
Elevation	1.103515E-04	0.962
Dist. to Major Creeks	-1.681214E-06	-0.384
Annual Rainfall	-1.959293E-03	-4.784
Dist. to Rocky Outcrops	7.308581E-06	4.856

Unfortunately, as GUIDE does not facilitate logistic regression equations and only uses OLS regression at each of the terminal nodes. This assumes the response is linear and normally distributed. GAMs provide a solution to this problem.

4.6.4 Generalised Additive Model

As previously mentioned, GAMs are able to model non-linear responses using splines. However, the vegetation variable is categorical and is not able to be fitted with a continuous spline function. To avoid this problem, a hybrid model was constructed that uses the regression tree in Figure 4.11, replacing the linear functions at the three terminal nodes with three GAM models.

The software extension to the R statistical package called GraspeR was used. This is adapted by Fivaz (2003) from the S-Plus extension GRASP by Lehmann et al (2003a) and described by Lehmann et al (2003b). This software uses penalized regression splines to fit the species response to each explanatory variable. The data partitioned in terminal node was explored for the responses to each predictor and the correlation between predictors. Following this, a separate GAM model was constructed at each terminal node.

The histogram distributions at each node are shown in Figures 4.13, 4.14 and 4.15 for each variable response. The darker (lower) component of the bars represents absences and the lighter component represents presences. The histogram counts are measured on the *y* axis. The skeletal bars represent the ratio of presences to absences. These are shown for each histogram bin in relation to a dashed line representing the overall proportion of presences. Any trends apparent in the skeletal bars across each explanatory variable's range (along the x-axis) indicates a likely trend in the response of the presence and absence of species.

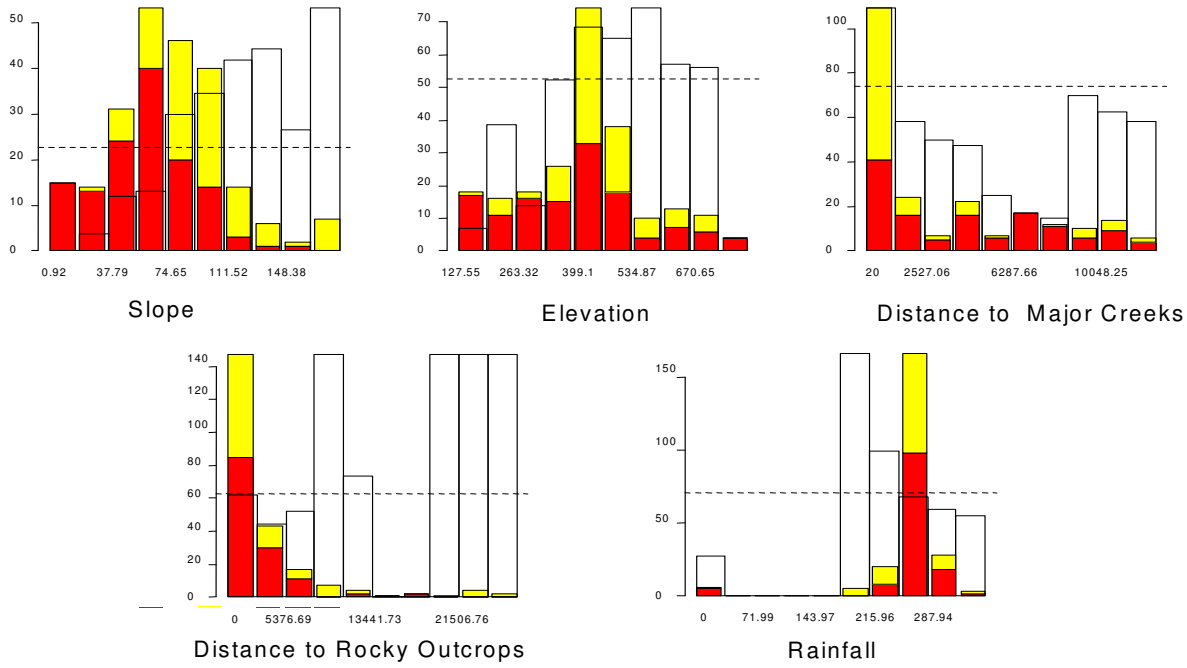


Figure 4.13 The histogram distributions of node 1 in Figure 4.11 for each explanatory variable.

Lower component of bars - absences. Upper component of bars - presences. Skeletal bars - ratio of presences to absences. Dashed line – overall proportion of presences. Distance and elevation units – metres. Slope units - percentage.

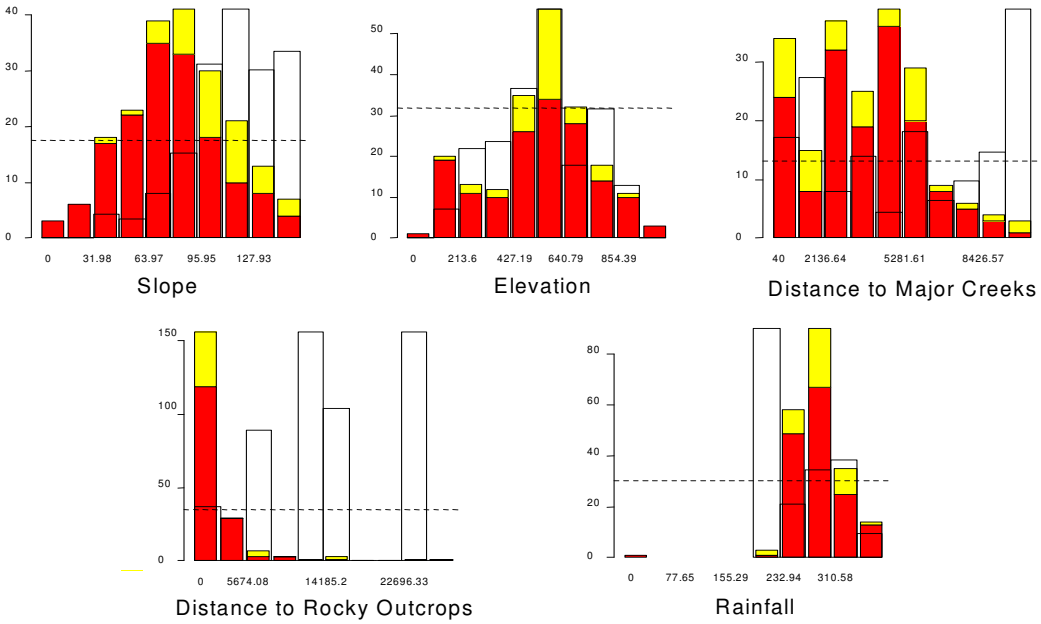


Figure 4.14 The histogram distributions of node 2 in Figure 4.11 for each explanatory variable.

Lower component of bars - absences. Upper component of bars - presences. Skeletal bars - ratio of presences to absences. Dashed line – overall proportion of presences. Distance and elevation units – metres. Slope units - percentage.

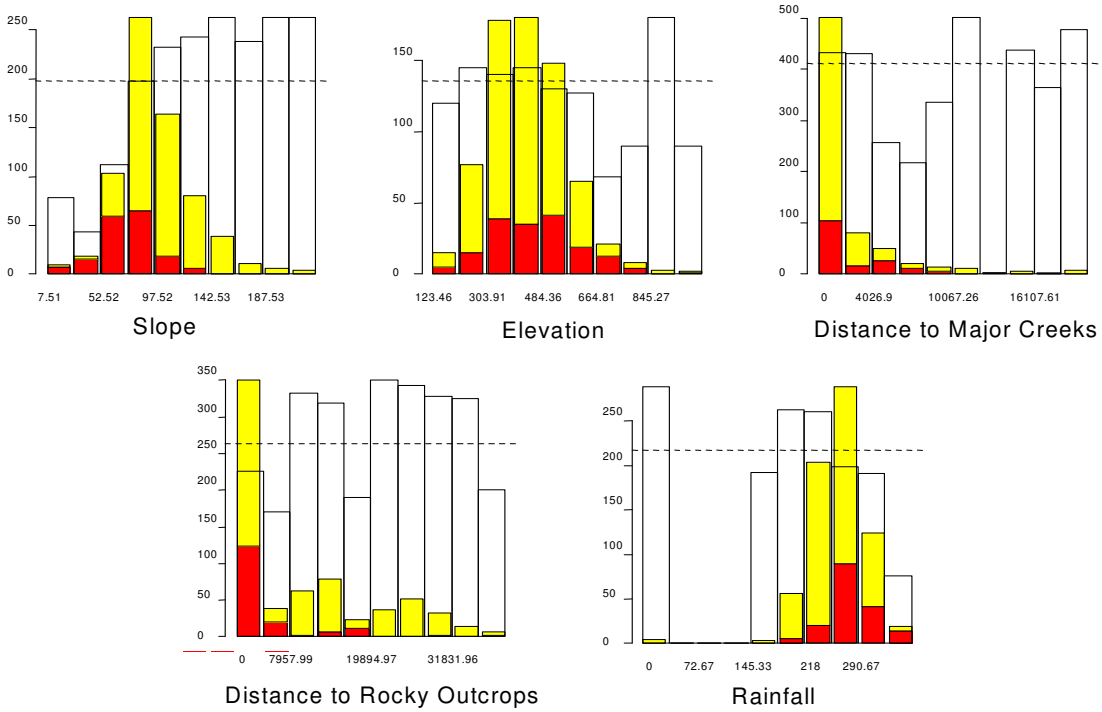


Figure 4.15 The histogram distributions of node 3 in Figure 4.11 for each explanatory variable.

Lower component of bars - absences. Upper component of bars - presences. Skeletal bars - ratio of presences to absences. Dashed line – overall proportion of presences. Distance and elevation units – metres. Slope units - percentage..

The correlation matrices in Tables 4.19 to 4.21, show the correlations between each explanatory variable. All of these correlations were relatively low.

Table 4.19 Correlation Matrix of node 1 in Figure 4.11.

Variable	Slope	Elevation	Dist.Maj.Crks	Rainfall	Dist.Rky.Outc.
Slope	1.00	0.209	-0.234	-0.174	-0.054
Elevation		1.00	-0.208	0.118	-0.164
Dist. to Major Creeks			1.00	-0.190	-0.255
Rainfall				1.00	-0.075
Dist. to Rocky Outcrops					1.00

Table 4.20 Correlation Matrix of node 2 in Figure 4.11

Variable	Slope	Elevation	Dist.Maj.Crks	Rainfall	Dist.Rky.Outc.
Slope	1.00	0.509	0.164	0.453	0.026
Elevation		1.00	0.039	0.676	-0.235
Dist. to Major Creeks			1.00	0.268	-0.222
Rainfall				1.00	-0.116
Dist. to Rocky Outcrops					1.00

Table 4.21 Correlation Matrix of node 3 in Figure 4.11

Variable	Slope	Elevation	Dist.Maj.Crks	Rainfall	Dist. Rky.Outc.
Slope	1.00	-0.083	-0.192	-0.077	0.055
Elevation		1.00	0.256	0.295	-0.267
Dist. to Major Creeks			1.00	0.054	-0.247
Rainfall				1.00	-0.389
Dist. to Rocky Outcrops					1.00

Equation 4.6 was the final model derived in the forward stepwise model selection process at node 1. All of the explanatory variables were retained. The simple validation ROC area under the curve was 0.910 and the cross validation ROC area under the curve was 0.847. Lehmann et al (2003b) suggest that the close agreement between the simple validation ROC area and cross validation ROC areas indicate model stability. These values are also high indicting a good model fit. The null hypothesis area = 0.5.

$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \text{s(Slope)} + \text{s(Elevation)} + \text{s(Dist. to Major Creeks)} + \text{s(Rainfall)} + \text{s(Dist. to Rocky Outcrops)}$$

Equation 4.6

Figure 4.16 shows the partial response curves and 95% CIs for each of the terms in the final GAM model at node 1 (Equation 4.6). This is called a partial response curve because it represents the response distributions before the logit transfomation.

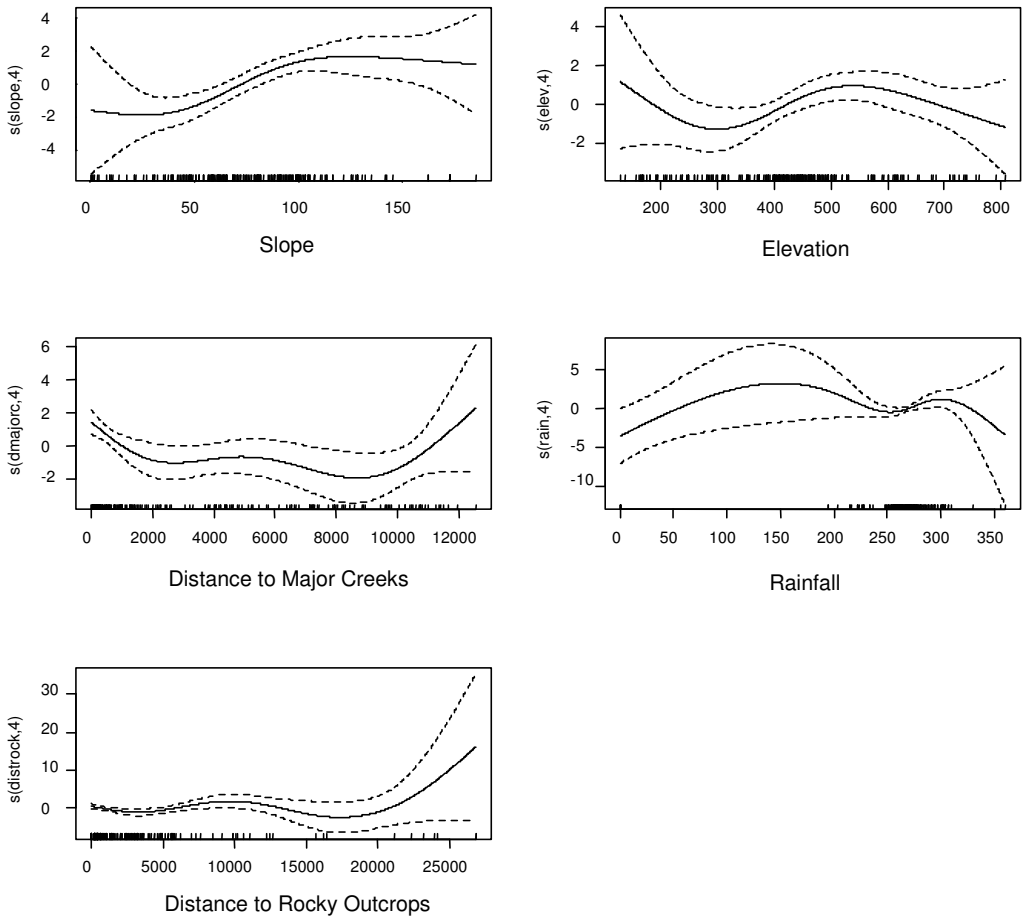


Figure 4.16 Node 1 partial response curves and 95% CIs for each of the terms in the final GAM model.

Distance and elevation units are in metres, slope units are shown as a percentage.

Equation 4.7 was the final model derived in the forward stepwise model selection process at node 2. The distance from major creeks explanatory variable was again removed. The simple validation ROC area under the curve was 0.890 and the cross validation ROC area under the curve was 0.809. Again, there is good model stability. These values are also high indicting a good model fit.

$$\ln(\frac{p}{1-p}) = \beta_0 + \text{ s(Slope)} + \text{s(Elevation)} + \text{s(Dist. to Rocky Outcrops)} \qquad \textbf{Equation 4.7}$$

Figure 4.17 shows the partial response curves and 95% CIs for each of the terms in the final GAM model at node 2 (Equation 4.7).

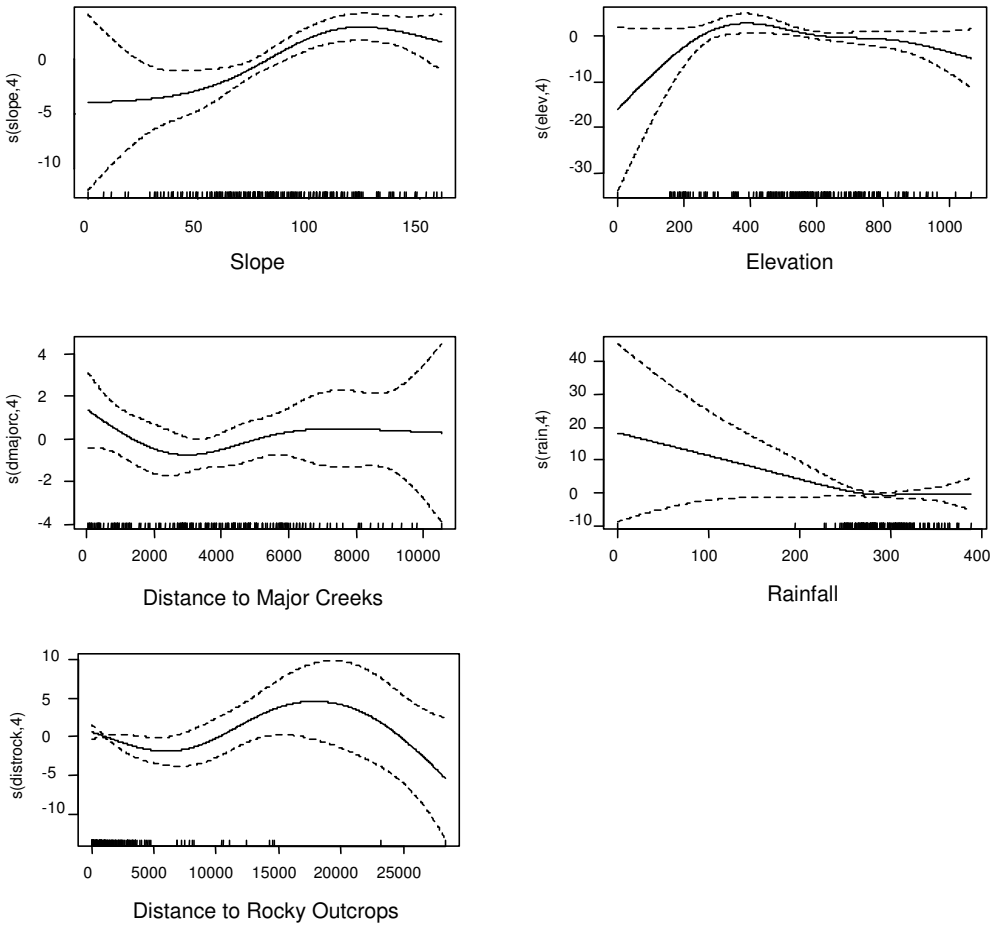


Figure 4.17 The node 2 partial response curves and 95% CIs for each of the terms in the GAM model.

Distance and elevation units are in metres, slope units are shown as a percentage.

Equation 4.8 was the final model derived in the forward stepwise model selection process at node 3. The distance from major creeks explanatory variable was again removed

$$\ln(\frac{p}{1-p}) = \beta_0 + \text{ s(Slope) + s(Dist. to Major Creeks) + s(Rainfall) + s(Dist. to Rocky Outcrops.)}$$

Equation 4.8

The simple validation ROC area under the curve was 0.862 and the cross validation ROC area under the curve was 0.841. Again there is good model stability. These values are also high indicting a good model fit.

Figure 4.18 shows the partial response curves and 95% CIs for each of the terms in the final GAM model at node 3 (Equation 4.8).

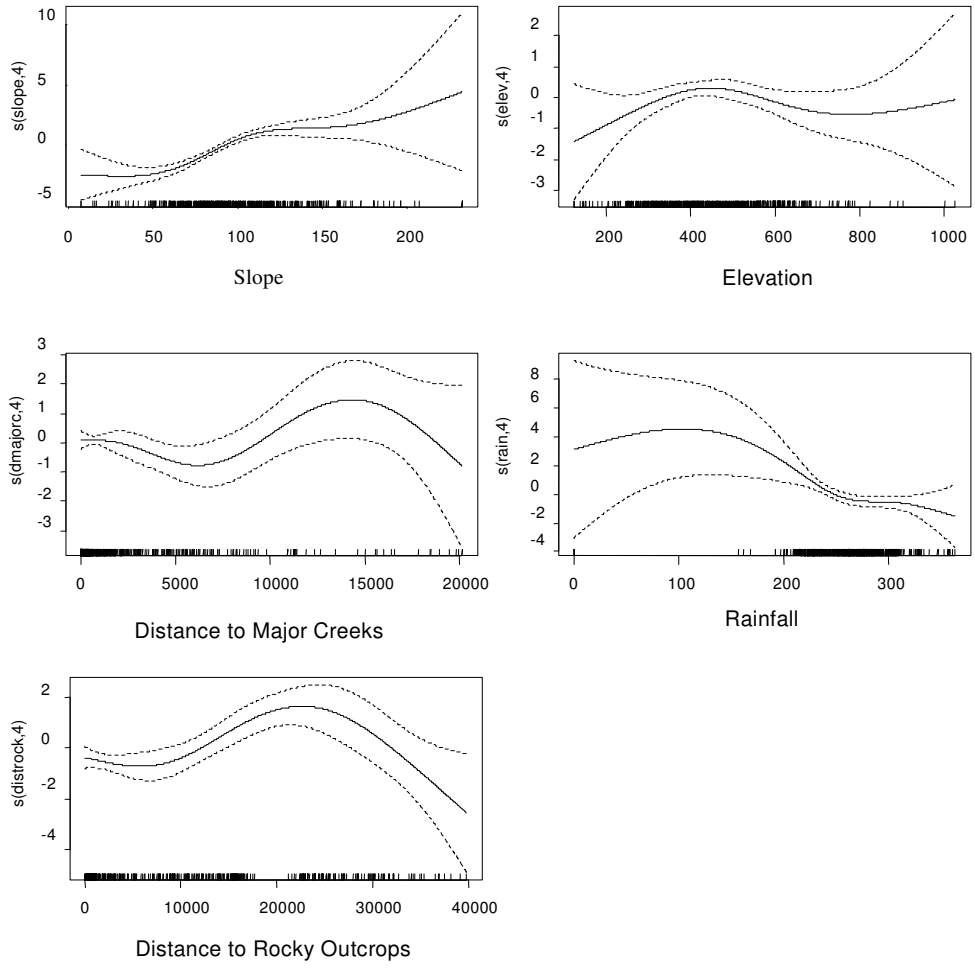


Figure 4.18 Node 3 partial response curves and 95% CIs for each of the terms in the GAM model.

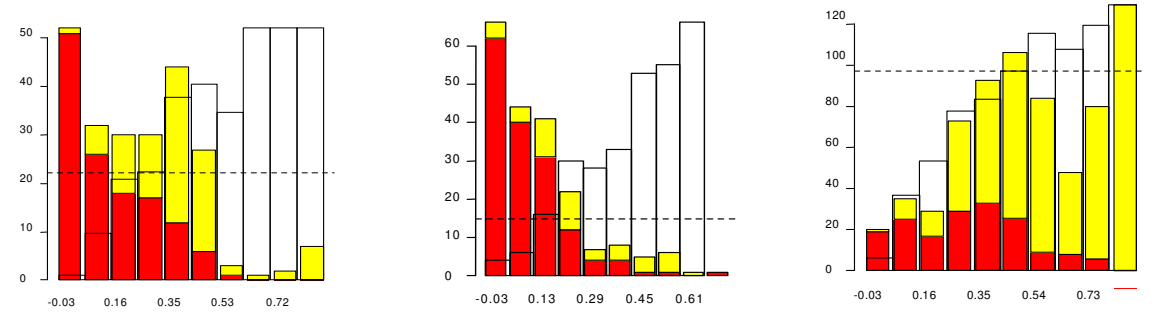
Distance and elevation units are in metres, slope units are shown as a percentage.

4.6.5 GAM incorporating autocorrelation

Three new GAM models at each terminal node were tested with each now including the autocorrelation term suggested by Augustin et al (1996). Equation 4.5 described a GLM with an autocorrelation term. This has been adapted to incorporate a GAM (Equation 4.9).

$$g(y) = \beta_0 + s_1(x_1) + s_2(x_2) + ..s_i(x_i)..+ s_n(x_n) + s_{n+1}\left(\frac{\sum_{k=1}^{m_j} w_{jk}\, y_k}{\sum_{k=1}^{m_j} w_{jk}}\right) + \varepsilon \quad \textbf{Equation 4.9}$$

Each $s_i(x_i)$ is again a non-parametric spline fit of the response to explanatory variable x_i. However, the final term is a spline fit of the inverse distance weight function estimating how much of the value y_j is contributed by the values from surrounding cells as distinct from causal effects within cell *j*. In other words, the predicted presence or actual presence at the j^{th} cell is ignored and its value is re-sampled by distance weighting the surrounding cells. As previously mentioned, the prevalence of 'no data' in the surrounding grid cells confounds the use of this weight function. Using the Gibbs sampler methodology (Augustin et al, 1996) the predicted presences and absences at un-sampled grid squares were derived from the GAM model predictions in Section 4.5.4. A Visual BASIC Application (VBA) script was written for ArcGIS to carry out the distance weighted re-sampling. The $s_{n+1}(.)$ term in Equation 4.9 here on is be labeled *s*(Autocorrelation).



Autocorrelation Term – Node 1 Autocorrelation Term – Node 2 Autocorrelation Term – Node 3

Figure 4.19 Histograms of the autocorrelation responses at each node in Figure 4.11.

The contribution of each explanatory variable to the node 1 model is shown in Figure 4.20. On the left-hand-side of Figure 4.20, the bars indicate the effect of dropping each explanatory variable. For any given variable, a lower contribution on the left-hand-side when compared with the right-hand-side indicates the other variables have adequately compensated for the removal of this variable. At node 1 the contribution of slope and autocorrelation are least compensated by other variables when dropped.

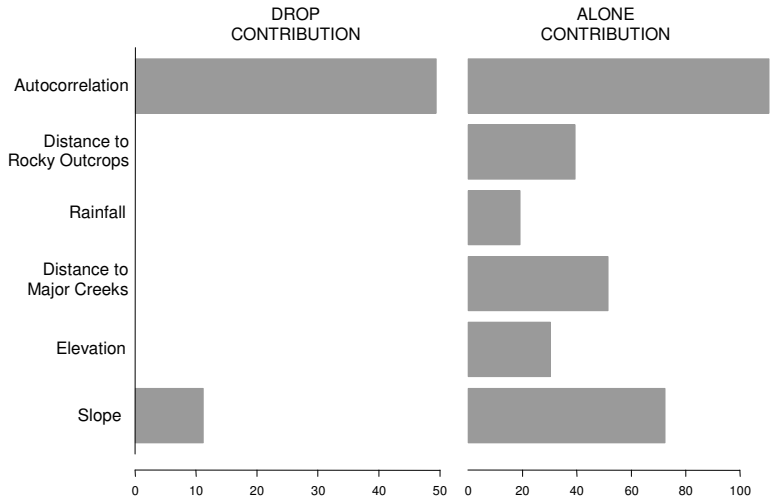


Figure 4.20 The contribution of each explanatory variable to the model at node 1.

The contribution of slope and autocorrelation are least compensated by other variables when dropped.

$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \text{ s(Slope) + s(autocorrelation)} \qquad \textbf{Equation 4.10}$$

Equation 4.10 was the final model derived in the forward stepwise model selection process at node 1. All of the explanatory variables are retained. Model fit and model stability are reasonable good, with a ROC area under the curve of 0.885 and cross validation ROC area of 0.861. At node 2 in Figure 4.21, the contribution of slope, distance to rocky outcrops and autocorrelation are least compensated by other variables when dropped.

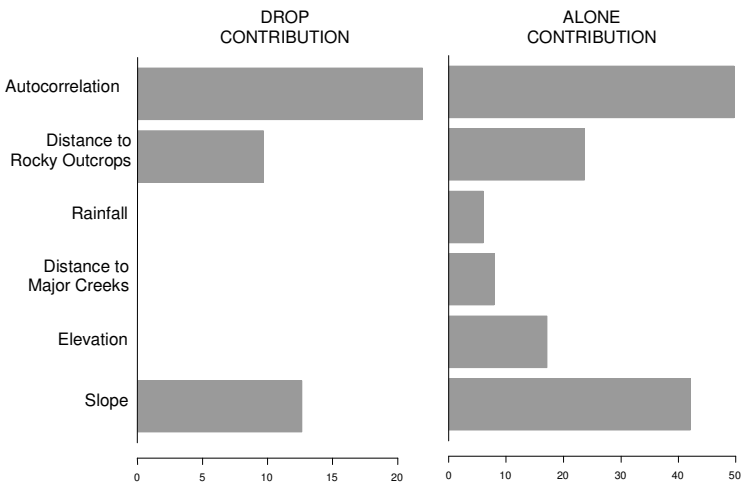


Figure 4.21 The contribution of each explanatory variable to the model at node 2.

The contribution of slope, distance to rocky outcrops and autocorrelation are least compensated by other variables when dropped.

$$\ln(\frac{p}{1-p}) = \beta_0 + \text{ s(Slope) + s(Dist. to Rocky Outcrops) + s(Autocorrelation)} \qquad \textbf{Equation 4.11}$$

Equation 4.11 was the final model derived in the forward stepwise model selection process at node 2. The 'distance from major creeks' explanatory variable was again removed. Model fit and model stability are again reasonable good, with a ROC area under the curve of 0.825 and cross validation ROC area of 0.885. At node 3 in Figure 4.24, the contribution of slope, rainfall, distance to rocky outcrops and autocorrelation are least compensated by other variables when dropped.

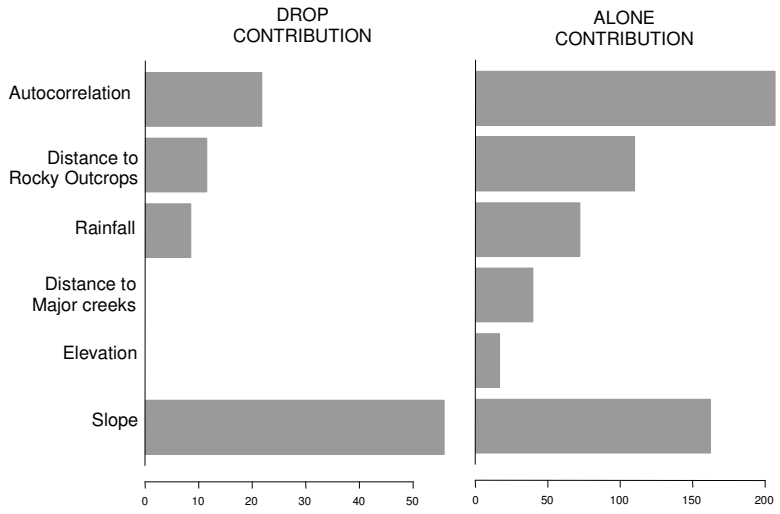


Figure 4.22 The contribution of each explanatory variable to the model at node 2.

The contribution of slope, rainfall, distance to rocky outcrops and autocorrelation are least compensated by other variables when dropped.

$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \text{ s(Slope) + s(Rainfall) + s(Dist. to Rocky Outcrops) + s(Autocorrelation)}$$

Equation 4.12

Equation 4.12 was the final model derived in the forward stepwise model selection process at node 3. The 'distance from major creeks' explanatory variable was again removed. The ROC area was 0.867 and the cross validation ROC area was 0.845.

The intrinsic validation of the combined GAM/regression tree models have been presented in Tables 4.22 and 4.23 in the form of confusion matrices. These confusion matrices measure the percentage correctness of each model using a 0.5 threshold. This threshold determines which probability predictions are rounded up to a presence classification and which are rounded down to an absence classification. The first model in Table 4.22 ignored the autocorrelation term. The second model in Table 4.23 uses the first model to calculate an autocorrelation term. This term is subsequently added as a new explanatory variable.

Table 4.22 Confusion matrix of the percentage correctness of the fit of the GAM/regression tree model *without* the autocorrelation term.

Actual	Predicted Absent	Predicted Present	Total	% Correct
Absent	364	113	477	76.3
Present	81	586	667	87.9

Table 4.23 Confusion matrix of the percentage correctness of the fit of the GAM/regression tree model *with* the autocorrelation term.

Actual	Predicted Absent	Predicted Present	Total	% Correct
Absent	375	102	477	78.6
Present	77	590	667	88.5

4.6.6 PolyMARS Comparison

The data used in the GAMs in Sections 4.5.4 and 5.5.5 were regressed using PolyMARS (Stone et al, 1997). As previously mentioned, PolyMARS uses a maximum likelihood approach, which is a more robust framework for presence-absence responses (Hastie et al, 2001). PolyMARS allows up to two-way interactions between the explanatory variables.

Equations 4.13 and 4.14 show the final models that were obtained for the model excluding autocorrelation and the model including autocorrelation respectively. There were no significant interaction terms.

$$\ln(\frac{p}{1-p}) = \beta_0 + \text{ s(Slope) + s(Dist. to MajorCreeks) + s(Dist. to Rocky Outcrops) + s(Elevation)}$$

Equation 4.13

$$\ln(\frac{p}{1-p}) = \beta_0 + \text{ s(Slope) + s(Autocorrelation)}$$

Equation 4.14

Table 4.24 shows the ANOVA derived contributions of each term's in the final models as percentages for the two models. Tables 4.25 and 4.26 are confusion matrices showing the percentage correctness of each model using a 0.5 threshold. MARS found no significant interaction terms.

Table 4.24 ANOVA derived Percentage Parameter Contributions: PolyMARS

Excluding the Autocorrelation Term		**Including the Autocorrelation Term**	
Parameter	% Contribution	Parameter	% Contribution
Slope	51.7	Autocorrelation	78.98
Distance to Rocky Outcrops	26.8	Slope	15.78
Distance to Major Creek lines	12.6		
Elevation	2.3		

Table 4.25 Confusion matrix of the percentage correctness of the fit of the PolyMARS model without the autocorrelation term.

Actual	**Predicted Absent**	**Predicted Present**	**Total**	**% Correct**
Absent	387	90	477	81.1
Present	77	590	667	88.5

Table 4.26 Confusion matrix of the percentage correctness of the fit of the PolyMARS model *with* the autocorrelation term.

Actual	**Predicted Absent**	**Predicted Present**	**Total**	**% Correct**
Absent	363	114	477	76.1
Present	75	592	667	88.8

4.6.7 MARS Comparison

The data used in the GAMs in Sections 4.5.4 and 5.5.5 were also regressed using MARS (Friedman, 1991). As previously mentioned, MARS uses piecewise linear functions, called basis functions to fit the data. These basis functions can also be multidimensional. The MARS package (Salford Systems, 2001) can potentially allow up to an infinite number of interactions or multivariate splines.

Unfortunately, unlike PolyMARS, MARS outputs the relative parameter contributions making it difficult to directly compare with PolyMARS. The relative importance of the parameters is determined by comparing the estimated cost of omitting each parameter from the model. As this is a relative cost, the percentages will not sum to 100%. Table 4.27 shows the relative contributions of each term's parameter as percentages for the two models while Tables 4.28 and 4.29 are confusion matrices showing the percentage correctness of each model using a 0.5 threshold.

Table 4.27 Relative Parameter Contributions: MARS

Excluding the Autocorrelation Term		**Including the Autocorrelation Term**	
Parameter	% Relative Contribution	Parameter	% Relative Contribution
Slope	100.0	Autocorrelation	100.0
Vegetation	61.4	Slope	31.6

Table 4.28 Confusion matrix of the percentage correctness of the fit of the MARS model *without* the autocorrelation term.

Actual	Predicted Absent	Predicted Present	Total	% Correct
Absent	119	358	477	24.95
Present	5	662	667	99.25

Table 4.29 Confusion matrix of the percentage correctness of the fit of the MARS model *with* the autocorrelation term.

Actual	Predicted Absent	Predicted Present	Total	% Correct
Absent	379	98	477	79.5
Present	109	558	667	83.7

4.6.8 Summary of Intrinsic Tests

Tables 4.30 and 4.31 summarise the intrinsic tests using confusion matrices for both models, with and without the autocorrelation term. While intrinsic tests using confusion matrices do not provide a comprehensive test of each model's performance, they do provide some insights about the likely biases of each approach. For example, the MARS model fails to adequately describe absences when the autocorrelation term is left out. Instead the MARS model predicts presences very well. This anomaly is likely to be caused by the lack of a logistic link function in MARS, which constrains the output range on a zero to one scale. Overall the predictability of each approach appears to improve slightly overall when the autocorrelation term is included.

Table 4.30 Summary of confusion matrix intrinsic tests for each approach *without* the autocorrelation term.

	GAM/Regression tree	PolyMARS	MARS
Actual	% Correct	% Correct	% Correct
Absent	76.3	81.1	24.95
Present	87.9	88.5	99.25

Table 4.31 Summary of confusion matrix intrinsic tests for each approach *with* the autocorrelation term.

	GAM/Regression tree	PolyMARS	MARS
Actual	% Correct	% Correct	% Correct
Absent	78.6	76.1	79.5
Present	88.5	88.8	83.7

The final model chosen was the GAM/regression tree model. The reason for this is two-fold. Firstly, neither MARS nor PolyMARS found any significant interactive effects in the data. This suggests that the univariate splines produced by the GAMs adequately fit of the data. Secondly, the simplicity in the hierarchical structure of the GAM/regression tree model allows one to more easily understand which vegetation classifications are more likely to explain the variation in the data. The vegetation data are the only categorical data in the suite of explanatory variables.

4.6.9 Extrinsic Tests

As previously mentioned, intrinsic tests using confusion matrices do not provide a comprehensive assessment of a model's performance. Intrinsic validation involves either cross validation or an analysis of the residuals between the training data and the predictions. Extrinsic validation on the other hand involves using a separate sub-set of recorded presence and absence data to test the model. In this study, 1143 points (70%) were used as training data and 490 (30%) points were used in the extrinsic validation.

ROC areas have been used to validate the accuracy of the two GAM/regression tree models in Table 4.32. ROC areas provide a relative assessment of the performance of each model but unlike confusion matrices, the assessment is made across the whole range of probabilities in the predicted distribution between zero and one. The residual ROC areas have already been described for each GAM at each terminal node. However, Table 4.32 reveals the combined model residual ROC areas. A ROC area of 1.0 is a perfect fit of the model to the data.

Table 4.32 ROC areas

		ROC Area	Standard Error	Asymptotic Significance	Asymptotic 95% Confidence Interval	
					Lower Bound	Upper Bound
Model 1: Excluding the Autocorrelation Term	Intrinsic validation	**.896**	.010	.000	.878	.915
	Extrinsic validation	**.885**	.016	.000	.853	.916
Model 2: Including the Autocorrelation Term	Intrinsic validation	**.908**	.009	.000	.892	.925
	Extrinsic validation	**.897**	.014	.000	.869	.926

In Table 4.32, although not significant, there has been some gain in model accuracy by adding the autocorrelation term. Unfortunately, ROC areas are a non-parametric summary statistic and do not provide any indication of how the residuals are spread. To reveal the spread of the residuals, box plots have been used to describe the presence and absence residuals. Figure 4.23 and Table 4.33 describe the extrinsic residuals of the two GAM/regression models, separately for the presence and absence data. The error bars in these figures show 95% CIs, while the boxes show the first quartile of spread in the data around the median centers of the box.

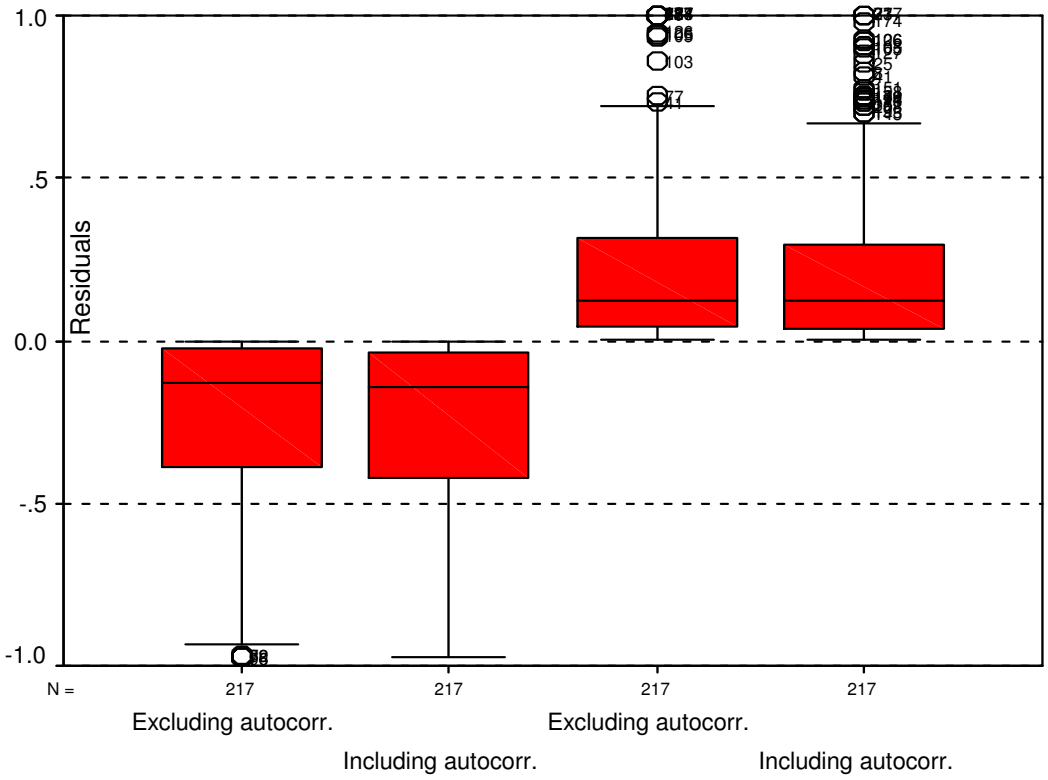


Figure 4.23 Summary bi-directional box plots of the *extrinsic* validations of both GAM/regression tree models (with and without autocorrelation).

Error bars are 95% CIs. The absence residuals are depicted as negative residuals and presence residuals are depicted as positive residuals.

The box plots show a greater range of residual error in the absence data however, the net gain of adding the autocorrelation term appears to be minor. Table 4.34 shows the actual median error values of the centres of the boxes in Figures 4.23 and 4.24. This test shows that there are very minor gains in the predictability of presences when adding the autocorrelation term while some loss in predictability is evident with the absences using extrinsic validation.

Table 4.33 Summary of the extrinsic residuals of the autocorrelation and non-autocorrelation models.

Absence residuals are depicted as negative residuals and presence residuals are depicted as positive residuals.

	Absence		Presence	
	Excluding Autocorrelation	Including Autocorrelation	Excluding Autocorrelation	Including Autocorrelation
Median Error	-0.130	-0.142	0.124	0.120
Mean Error	-0.249	-0.262	0.232	0.213

Finally, confusion matrices related to the extrinsic data for each model, with and without the autocorrelation term, are shown in Tables 4.35 and 4.36.

Table 4.35 Confusion matrix of the percentage correctness using extrinsic data for the fit of the GAM/regression tree model *without* the autocorrelation term.

Actual	Predicted Absent	Predicted Present	Total	% Correct
Absent	175	42	217	80.6
Present	42	232	274	84.7

Table 4.36 Confusion matrix of the percentage correctness using extrinsic data for the fit of the GAM/regression tree model *with* the autocorrelation term.

Actual	Predicted Absent	Predicted Present	Total	% Correct
Absent	169	48	217	77.8
Present	37	237	274	86.5

These tables again indicate a lowering of the percentage correctness of absence data when including the autocorrelation term but a raising of the percentage correctness of presence data.

4.6.10 Model Prediction Surfaces

Prediction surfaces for the combined GAM/regression tree models were constructed in ArcGIS (ESRI, 2003). Appendix A shows the final prediction surface for the GAM/regression tree model that ignores autocorrelation. Appendix B shows the final prediction surface for the GAM/regression tree model where an autocorrelation term has been included.

The net effect of including the autocorrelation term is minor. In areas where there were few or no recorded presences, the inclusion of the autocorrelation term has marginally lowered the prediction probability. Conversely, in areas where there is a concentration of recorded presences, the inclusion of the autocorrelation term has marginally lifted the prediction probability. The GraspeR (Fivaz, 2003) software also provides Standard Error (SE) estimates of the prediction surfaces. The SE estimates for the surface for the GAM/regression tree model that ignores autocorrelation is shown in Appendix C. As there was little difference between this model's SE and the SE for the model with the autocorrelation term, the latter has not been attached as an Appendix.

4.7 Discussion and Summary

4.7.1 Aspatial Habitat Model

Figures 4.5 and 4.6 show classification trees of the presence of *P. x. xanthopus* using two different scenarios. The first scenario is where presence represents an animal being sighted or fresh faecal pellets found. The second scenario is where presence represents an animal sighted, fresh faecal pellets or old faecal pellets found. The classification tree was pruned using a SE = 1.0. This determined the level of homogeneity acceptable after partitioning the data. A total of 138 sites were used in this model. Twenty-three absences in scenario one shifted to presences in scenario two. Classification trees are adversely affected by outliers (Miller and Franklin, 2002) so the shift of these 23 data had a large effect on the structure of the tree.

In addition, the partitioning of the data between presences and absences at the terminal nodes in many cases was weak. For example in scenario one the number of presences verses absences when water is present (H_2O =1,2) is a|p =15|19. In scenario two when water is absent (H_2O =0), a|p =21|18. These ratios indicate the partitioning of the status of water lacks the power to draw any definitive conclusions.

In scenario one, there was a strong partitioning between absence and presence related to boulder fields (a|p =56|19, Figure 4.5). Conversely, there was a slightly weaker partitioning of presences and absences in relation to caves (presence: a|p =10|15; absence a|p =4|0, Figure 4.5). While the shift of 23 records to presences in scenario two alters the interaction of caves and boulders, the partitioning of the absence and presence remains relatively strong with boulder fields (a|p =10|27, Figure 4.6) and a lack of caves (a|p = 24|9, Figure 4.6). However, boulder fields alone did not contribute to presence. Only 20 out of the 138 sites indicated presence when boulders =1 or 2 in scenario one and 27 indicated presence in scenario two. There are three possible explanations for this.

In Queensland, Sharp (1997) found that the use of caves and boulder fields varied between season. He also proposed that the primary importance of these sites was linked to a need for nursery sites and providing there is sufficient protection in the narrow confines of the cave and rockpile system, juveniles may be able to escape larger predators, whereas adults may not (Sharp, 2002). While Lim (1987) suggests that boulder fields and deep narrow caves provide refuge from the heat, dense vegetation is also likely to provide a suitable microclimate (Sharp, 2002). In these areas, the strength

of the relationship of presence-absence data to boulder fields may also be weaker. Unfortunately the density of vegetation was not recorded in this field study.

Lehmann et al (2002) pointed out the importance of understanding the effects of the field sampling strategy on the habitat model. In this study a stratified random approach was attempted, due to the configuration of the landscape and its abrupt changes in land system. The average nearest neighbor distance between sites was 1258 metres extending over a 115km by 55km area. However, the closest distance between sites was approximately 100 metres. This may have introduced autocorrelation biases into the results, particularly if transient animals move between the sites. For example, 19 of the 34 sites having water were within 1500 metres of sites with boulder fields.

The correlation between *P. x. xanthopus* presence and the availability of key resources (plants with stellate tricomes) only enters the scenario two model. Here the 'food =2' terminal node in Figure 4.6 appears under the rules 'boulders=0' and 'caves =1, 2'. Since mainly old faecal pellets were found here, sites that are rich with food resources and absent of sufficient refuge may still be infrequently used. Alternatively, the old faecal pellets found at these sites may indicate recent extinctions, particularly if little protection is afforded by the caves.

4.7.2 Population Trends

A very real danger when comparing presence and absence surveys is the problem of making Type II errors and concluding there is a decline when in fact the population is stable. Here observation biases may invalidate the statistical tests of the power in the differences (Strayer, 1999). Strayer (1999) used Monte Carlo simulation to assess the power of presence-absence surveys to detect decline. He concluded that unless the declines were severe, presence-absence surveys had only a low to moderate power in detecting these changes. However, despite the cryptic behavior of *P. x. xanthopus*, the detectability was increased markedly by using faecal pellets as an indication of presence, as these were easy to identify.

As previously mentioned, of the 22 sites indicating a presence between 1977 and 1981, five of these sites no longer show signs of persistence and 6 had old pellets. However, approximately half of these 11 sites are close to other extant colonies (< 1500 metres). Of the 15 sites where animals have been sighted before 1977, four showed no signs of persistence although one is close to an extant colony (< 1500 metres). Using < 1500 metres as a crude measure of site independence, it would appear that there has only been one extinction out of 22 sites since 1981, and four extinctions out of a total of 37 sites overall. It is obvious that these figures do not sufficiently indicate any decline.

4.7.3 Spatial Habitat Model

A key objective of this study was to derive a spatial habitat model for *P. x. xanthopus*. Determining the 'fundamental niche' requires species distribution data in the absence of disturbance (Peters, 1991). In an attempt to overcome some of the effects of disturbance, present and historical data were pooled. Seventy percent of the pooled data was randomly selected for model training with the remaining 30% of the data quarantined for extrinsic model validation.

The explanatory variables used to construct a spatial habitat models were: mean annual rainfall (co-Kriged with elevation), slope (the maximum in a 200 metre radius), elevation, distance from major creeks and gorges, distance from rocky outcrops and dominant vegetation type in the community. The vegetation variable was categorical. A preliminary exploration of the data was conducted using a classification tree and following this, three modelling approaches were intrinsically tested for their best fit of the data.

The first model involved hybridising a regression tree with a GAM. Intrinsic tests were also carried out on the MARS and PolyMARS approaches by way of comparison. MARS uses multidimensional piecewise basis functions to fit the data whereas PolyMARS uses a logistical framework to work with categorical variables and presence-absence responses (Hastie et al, 2001). Neither the MARS nor PolyMARS techniques had any significant interactive effects in the explanatory variables. Interactions between explanatory variables occur in classification trees when the same variable appears on separate branches. This occurred in Figure 4.10 for the variable 'distance to rocky outcrops'. Interestingly, this variable does appear in the final GAM model but was dropped by MARS and PolyMARS when the autocorrelation term was added. Interestingly, the species tended to be absent near rocky outcrops. This may be due to the fact that rocky outcrops identified on maps at a 1:50,000 scale are larger exposed rock faces rather than smaller boulder fields, and afford little protection.

Confusion matrices were used to compare the intrinsic fit of the GAM/regression tree, PolyMARS and MARS models. These matrices indicated only marginal differences between the three approaches. Given there are not likely to be substantial interactions in the data, the simpler GAM/regression tree model was chosen as final model.

4.7.4 Spatial Autocorrelation

Most spatially explicit predictive models assume observation data to be independent and rarely investigate neighborhood relationships in the observation data (Guisan and Zimmermann, 2000). If the observation data are spatially dependant, part of the variation in the model may be explained by neighborhood values (Overmars et al, 2003). Figure 4.9 revealed a spatial dependency of up 0.26 at distance lags of under 150 metres. The autocorrelation in the data indicates that the presence of the species at some locations may in part be due to the geographical proximity of other presences and not independent responses to the explanatory variables.

A spatial autocorrelation term was derived using the Gibbs sampling approach suggested by Augustin et al (1996). Interestingly, the inclusion of the autocorrelation term did not have a significant impact on the predictability of the model although it did have the effect of making the explanatory variable "elevation" insignificant at nodes 1 and 2 and "distance from major creeks" insignificant at node 3. These variables were subsequently removed from the model. This effect of altering the significance of explanatory has also been observed by Overmars et al (2003). The autocorrelation term was least compensated by all other terms.

There are three important issues concerning this technique. Firstly, sample bias could potentially the influence the final model, particularly since the autocorrelation term is heavily dependent on the values in surrounding cells. The second issue concerns the robustness of the autocorrelation error term approach. The inverse distance weighting function, suggested by Augustin et al (1996), is deterministic and is not derived from the distributional properties of the spatial dependence in the data. Its application to derive the autocorrelation error surface is therefore dubious. A better approach may have been to use a semi-variogram to derive a stochastic spatial proximity weight function. Kriging interpolation for example, uses an autocorrelation weight function based upon the statistical shape of the data dependence (Burrough, 1986).

The use of Kriging to derive an autocorrelation error surface has been attempted by Miller and Franklin (2002). However, the approach taken by these authors was seriously flawed because the calculation of the autocorrelation error at each observation point must be based only on the data surrounding the cell. In their study, Miller and Franklin (2002) did not precluded the data in the prediction cell when they applied a weight function. This may account for the unusually high and unrealistic smoothing Miller and Franklin (2002) encountered.

Finally, Augustin et al (1996) suggest that the autocorrelation error term should be included in spatial models, when the main objective of the study is to map the probably spatial distribution of a species. However, when the objective is to understand the average response of the species to environmental variables, Augustin et al (1996) suggest excluding the autocorrelation error term. In this study, in areas where there were few or no presences, the autocorrelation model lowered the prediction probability. Whereas in areas where there is a concentration of presences or a high distribution probability, the autocorrelation model lifted the prediction probability. If the aim of the study were to predict the distribution of *P. x. xanthopus* for the purpose of targeting management strategies or designing more rigorous sampling strategies, a distributional model including an autocorrelation term would be more appropriate. However, if the aim of the study is to locate areas in the landscape favorable to this species, a model precluding the autocorrelation term may be more appropriate.

4.7.5 Interpretation of data distributions

It is important that predictive models are able to provide the researcher with a better understanding of the biologically meaningful causal relationships in the model (Guisan and Zimmermann, 2000). This is what distinguishes the CART, GLM, GAM, MARS and PolyMARS approaches from 'black box' models like ANNs.

Using the dominant descriptions provided in Table 4.5, the regression tree in Figure 4.11 distinguishes three separate groups of vegetation communities. The first group defining terminal node 1 includes communities of tall open shrublands dominated by of *Acacia victoriae,* open tussock grasslands of *Cymbopogon ambiguous* and *Enneapogon* spp.*,* and low open woodlands dominated by *Casuarina pauper* or *Callitris glaucophylla* (classes 10, 11, 21, 22, 9 in Figure 4.11). The histograms in Figure 4.13 show the response of the species to the continuous explanatory variables at terminal node 1 in these vegetation communities. The highest proportion of presences occurs in high slopes and elevations from 400 – 700 metres. Both presences and absences decline with distance to rocky outcrops although close to rock outcrops there are more absences.

The second group defining terminal node 2 includes communities of tall open shrublands dominated by *Acacia victoriae,* Mallee*,* tall woodlands dominated by *Allocasuarina verticillata,* hummock grasslands of *Triodia* spp. or low shrublands dominated by *Atriplex vesicaria, Maireana astrotricha, Maireana sedifolia, Maireana pyramidata* (classes 12, 15, 17, 20, 23, 8 in Figure 4.11). The histograms in Figure 4.14 show the response of the species to the continuous explanatory variables at terminal node 2 in these vegetation communities. In these communities there are fewer presences and

more absences overall. Again the highest proportion of presences occurs in high slopes with a sharp peak of presences between 450 – 650 metres elevation.

The third group defining terminal node 3 includes communities of shrubland dominated by *Acacia anuera* and/or *Acacia* spp., open hummock grasslands with *Callitris glaucophylla* or *Eucalyptus* spp., Mallee, open woodlands of *Eucalyptus intertexta* or woodlands of *Eucalyptus camaldulensis* (classes 13, 14, 16, 19, 3 in Figure 4.11). The histograms in Figure 4.15 show the response of the species to the continuous explanatory variables at terminal node 3 in these vegetation communities. In these communities there is a three to four-fold number of presences compared with the other two terminal nodes and a greater proportion of presences overall. The peak number of presences occur at slopes of around 80% and between 300 to 500 metres elevation. Clear trends are also apparent in relation to other explanatory variables. Many more presences are found in close proximity to rocky outcrops and major creeks. The presences also peak around 250mm rainfall.

Dependencies are more evident in the classification tree in Figure 4.10 because of its simpler rule-based structure. For example, in Figure 4.10 absences are shown to be primarily found in communities of low shrublands dominated by *Atriplex vesicaria, Maireana astrotricha, Maireana sedifolia* and *Maireana pyramidata*, tall open shrublands dominated by of *Acacia victoriae* and *Acacia tetragonophylla,* open tussock grasslands of *Cymbopogon ambiguous, Stipa nitida* and *Enneapogon* spp., Mallee, tall woodlands dominated by *Allocasuarina verticillata,* hummock grasslands of *Triodia* spp. or low shrublands dominated by *Atriplex vesicaria*, shrublands dominated by *Acacia anuera,* open hummock grasslands with *Callitris glaucophylla* or *Eucalyptus* spp.

Apart from Mallee, most of these communities are not associated with the microclimate afforded by rocky outcrops and deep gorges. In these rocky microclimates, not surprisingly there is a distinct absence of chenopod shrubs like *Atriplex vesicaria, Maireana astrotricha, Maireana sedifolia* and *Maireana pyramidata*. Instead there is usually a rich mix of rock plants including herb, *Eremophila* spp, *Senna* spp., *Dononaea* spp., *Sida* spp., *Ptiolotus obovatus, Xanthorrhoea quadrangulata* but also *Triodia* spp., *Cymbopogon ambiguous, Acacia victoriae, Acacia anuera.* Many of these species are known to be in the diet range of this species (Lapidge, 1997). This is also confirmed in Figure 4.7, where there was a considerably higher presence of *P. x. xanthopus* in the dominant vegetation class 13, shrublands of *Acacia anuera* and/or other *Acacia* spp, *Eremophila* spp., *Senna* spp, *Dodonaea* spp. over *Ptilotus obovatus* and *Chenopodiaceae* spp. Dense Mallee found on higher slopes is also known to provide a microclimate suitable for this species. This was evident in Figure 4.8, where the presences occurred in Mallee at higher median slopes. Areas where this has been observed in the field include the Warraweena and Narrina leasehold properties in the north Flinders

Ranges, as well as Scrubby Peak and Yandinga Gorge in Gawler Ranges on the Eyre Peninsula in South Australia.

There is general agreement between the final GAM/regression tree and the classification tree. In the classification tree, a higher number of presences were found in vegetation classes 3, 13, 14, 15, 16, 19, 21 and 22. This is similar to the results at terminal node 3 in the regression tree in Figure 4.11, where a higher number of presences overall were found in Figure 4.15 in vegetation classes 3, 13, 14, 16 and 19.

4.7.6 Data Limitations

Habitat models, particularly those over small geographical areas, often do not take into consideration the importance of dispersal and its associated barriers as well as other species interactions (Pearson et al, 2002). Goats and foxes are known to be present over the greater extent of the spatial model with net reductions in the Flinders Ranges National Park, the Gammon Ranges National Park, Arkaroola and, most likely, the properties immediately surrounding these land parcels. Hence the data is likely to be negatively biased due to the effects of disturbance and the final habitat model is more likely to lie somewhere between a 'fundamental niche' prediction and a 'realised niche' prediction.

As previously mentioned, spatially explicit habitat models are scale-dependant. This dependency is has two aspects. The first aspect relates to the ability of the model to adequately predict the geographic distribution or habitat properties of the species at the intended scale. For example, stochastic environmental and demographic processes may deem the model invalid at a microhabitat scale. The second aspect relates to the spatial precision and level of spatial aggregation in the variables that underpin the model. While this will determine the optimal scale domain of the predictions, stochastic processes may still swamp these predictions even if the prediction scale matches the scale of the underpinning variables. Unfortunately, many government-supplied spatial data are often expensive to capture and restricted to broad scale mapping and modelling. For example, the vegetation data in this study was highly aggregated and is likely to have missed much of the heterogeneity in the vegetation.

Another problem is the inadequate model specification. This is when other causal variables are missed. If available at the time of this study, additional data might have improved the model. For example, data including lithology, temperature and solar radiation were not available for this study and in light of the field observations, particularly pertaining to lithology, it is likely that these additional variables might have improved the habitat model for this species.

CHAPTER 5

A new Population Viability Model (PVA)

5.0 Introduction

Population modelling for conservation management is generally applied in three areas: the protection of endangered species; the control of pests; and the sustainable harvest of a species (Caswell, 2001). Population Viability Modelling (PVA) more particularly, focuses on estimating the probability of extinction with the aim of reducing the risk of extinction (Lindenmayer and Possingham, 1994; Possingham et al, 1993; Possingham and Davies, 1995).

PVAs incorporate Monte Carlo simulation to assess how stochastic processes affect the probability of extinction of a population sometime into the future (Lindenmayer et al, 1993a; Lindenmayer and Possingham, 1994; Possingham et al, 1993; Beissinger, 2002; Caswell, 2001; Marmontel et al, 1996; Morris and Doak, 2002; Reed et al, 2002). These stochastic processes include chance birth and death processes (demographic stochasticity); short term climate fluctuations (which also affect resource availability - environmental stochasticity); catastrophes and chance movement events (Burgman et al, 1993; Possingham and Davies, 1995; Possingham et al, 2001; Berec, 2002; Turchin, 1998). Stochastic population models are thought to be more appropriate than their deterministic counterparts because they acknowledge natural variation in the environmental and demographic processes that drive a population (Beissinger and Westphal, 1998; Possingham and Davies, 1995; White, 2000). This is important for small populations, which are particularly susceptible to chance events (Boyce, 1992; Lacy, 1993; Shaffer, 1981).

PVAs are used to assess the relative risks to extinction and thereby provide a framework for affecting positive management actions and identifying important ecological processes. PVAs are also useful inputs into a more formal risk assessment process (Maguire, 1986; Shea and Management, 1998), where risks are weighed up against other considerations such as economic factors (Possingham et al, 1993). In this context, PVA has a formal role as a decision support tool in Active Adaptive Management frameworks (Possingham, 2001).

PVA begin by randomly simulating demographic and environmental processes from defined probabilities and then modelling their cumulative effects over time (Lacy, 1993). The population's viability is assessed after repeated simulations by measuring either the median time to extinction (usually in years) or the probability of extinction within a specified time interval (Lindenmayer and Possingham, 1994; White, 2000).

Spatially explicit PVAs combine population models with representations of the landscape (Wiegand et al, 1998). These have the distinct advantage of being able to model metapopulations where the landscape structure and patch dynamics (movement) between local populations can affect population viability (Keymer et al, 2000). Given that species interact with their environment in space and time, PVA models that are explicitly spatial can assist with answering questions about where management actions should be prioritised (Akçakaya, 1994; Burgman and Possingham, 2000) or how fragmentation and patch geometry affect a population (Kindvall and Petersson, 2000; Lindenmayer et al, 1993b).

Many spatially explicit PVA computer programmes including ALEX, (Possingham and Davies, 1995) RAMAS/GIS (Akçakaya, 1994), and Vortex (Lacy, 1993) have been used to assess the threat of species extinction in a range of applications. They have been used to assist with habitat or reserve design (Lindenmayer and Possingham, 1994; Shaffer, 1983), forest resource management (Lindenmayer, 1996; Lindenmayer and Possingham, 1994) and reintroduction/translocation strategies (Southgate and Possingham, 1995 - see Table 5.1).

Table 5.1 PVA Computer Software

Software	**Spatially Explicit**?	**Individual-based**?	**Single Sex or Both Sexes**	Includes Genetic Modelling
Vortex (Lacy and Kreeger, 1992)	No	Yes	Both	Yes
Alex (Possingham et al, 1991)	Yes	No	Single	No
@Risk (Palisade Corp)	No	No	Single	No
RAMAS (Akçakaya, 1994)	Yes	No	Single	No

The aim of this Chapter is to describe a new PVA model that has been built, not only to be able to answer key questions related to *P. x. xanthopus,* but also to be applied to a wider range of mammals in semi-arid environments in future studies. The model has been written in the C++ programmeming language and Avenue®, an extension to the Environmental Systems Research Institute (ESRI) ArcView® 3.2 Geographical Information System (GIS).

There are several reasons for producing an alternative model to the spatially explicit PVA models listed in Table 5.1. Firstly, there is a requirement for a seamless and robust interface between the GIS and the PVA simulation engine. This enables one to more easily alter landscapes rather than importing new landscapes. Secondly, this model is individual-based and models both sexes. This is better suited for simulating small populations where the distance between potential breeding partners may be large (Allee et al, 1949). Thirdly, the model simulates some of the unique environmental characteristics of semi-arid environments including highly skewed rainfall distributions. Most of the approaches listed in Table 5.1 characterise the landscape as discrete and shapeless patches. However, this is not considered to adequately represent the continuously varying and richly textured heterogeneous landscape (Wiegand et al, 1999; Weins, 2001). For this reason a GIS raster grid has been chosen to represent landscape habitat quality, where the landscape is divided into a regular grid of cells, each holding a habitat quality index. Finally, this model includes an optional genetic sub-model. This enables the researcher to explore different dispersal strategies and their likely relative effects on inbreeding.

5.1 Applications of PVA

The most appropriate PVA model depends on the ecology of the species, availability of data on population parameters and questions to be answered (Burgman and Lindenmayer, 1998). While PVAs are more commonly used to guide the management of threatened species, there are many other applications of PVA in conservation biology (Morris and Doak, 2002). While not an extensive list, a sample of the many PVA applications is summarised in Table 5.2.

Table 5.2 Applications of PVA

Adapted from Morris and Doak (2002).

Application	Examples
1. Assessing the extinction risk of a single population	(Wiegand et al, 1998), (Foley, 1994), (McCarthy et al, 1994), (Wang et al, 2001), (Crone and Gehring, 1997), (Cross and Beissinger, 2001), (Akçakaya et al, 1995), (Morita and Yorkota, 2002)
2. Comparing relative risks of two or more populations.	(McCarthy et al, 2000)
3. Identifying life stages of demographic process as management targets.	(Vucetich and Creel, 1999)
4. Determining the effects of patch size or geometry on extinction risk.	(Lindenmayer et al, 1993b), (Kindvall and Petersson, 2000), (Goldingay and Possingham, 1995)
5. Captive release or translocation strategies for threatened species.	(McCallum, 1994), (McCarthy, 1994), (McCallum et al, 1995), (Akçakaya et al, 1995)
6. Managing sustainable harvesting.	(Chaloupka, 2002)
7. Assessing the impacts of population sub-division.	(Lacy and Lindenmayer, 1995)
8. Balancing resource management with threatened species management.	(Possingham et al, 2002), (Possingham, 1995)
9. Testing PVA Accuracy	(Lindenmayer et al, 2000), (McCarthy and Broome, 2000), (McCarthy et al, 2001), (Lindenmayer et al, 2001)

5.2 Criticisms of PVA

Conservation biology is a crisis discipline (Soulé, 1985) and decisions must be made quickly, in the face of financial constraints, scant and incomplete data (Burgman et al, 1993; Crone and Gehring, 1997; Brook et al, 2002). Brook et al (2002) contend that given that there are no alternative tools currently available in conservation decision making, PVAs are still better than subjective decision making. Unfortunately, the critics of PVAs argue that model predictions are unreliable because of the scarcity of data. Moreover, models that estimate the risk of extinction over a given time period are difficult to test because empirical data cannot be replicated (Burgman et al, 1993). Consequently, few researchers have tested the accuracy of these predictions (Lindenmayer et al, 2001).

PVA tends to focus on the more immediate causes of small population extinctions rather than exploring the historical causes of population decline and Caughley and Gunn (1996) contest that this is a narrow view and too focused on the more immediate stochastic events that cause small populations to go extinct. They argue that in many instances the population may have declined from historical events that have been succeeded by new threats and decline cannot be completely mitigated by removing the new threats alone. For example, isolation and possibly inbreeding depression are not solved necessarily by simply removing more recent threats. However, finding the historical causes of decline is more problematic because very little is known about the historical species' interactions and dynamics.

5.3 PVA Model Description

This model a variation of the PVA model described by Lethbridge et al (2001) with a few important differences highlighted throughout this chapter. After selecting a GIS habitat quality layer and the input parameters, the model begins a simulation loop (see Figure 5.1). Inside the simulation loop, the initial population is input from a GIS layer and the period loop begins. The demographic response of the species to changing environmental conditions is simulated by using an environmental variable drawn from a statistical distribution. This variable relates resource availability at time *t*, to survival and fecundity. Inside the period loop, four sub-models are run in the following order: dispersal events, fecundity events, survival events and, should the option be selected, breeding events.

Dispersal is allowed to occur first so that sub-adults are given the opportunity to disperse before the probability of survival determines their fate and before sub-adult females breed. At the end of each period, the model records information about the final population. The period loop is repeated *t* times before repeating a simulation loop. The number of simulations is then repeated *s* times.

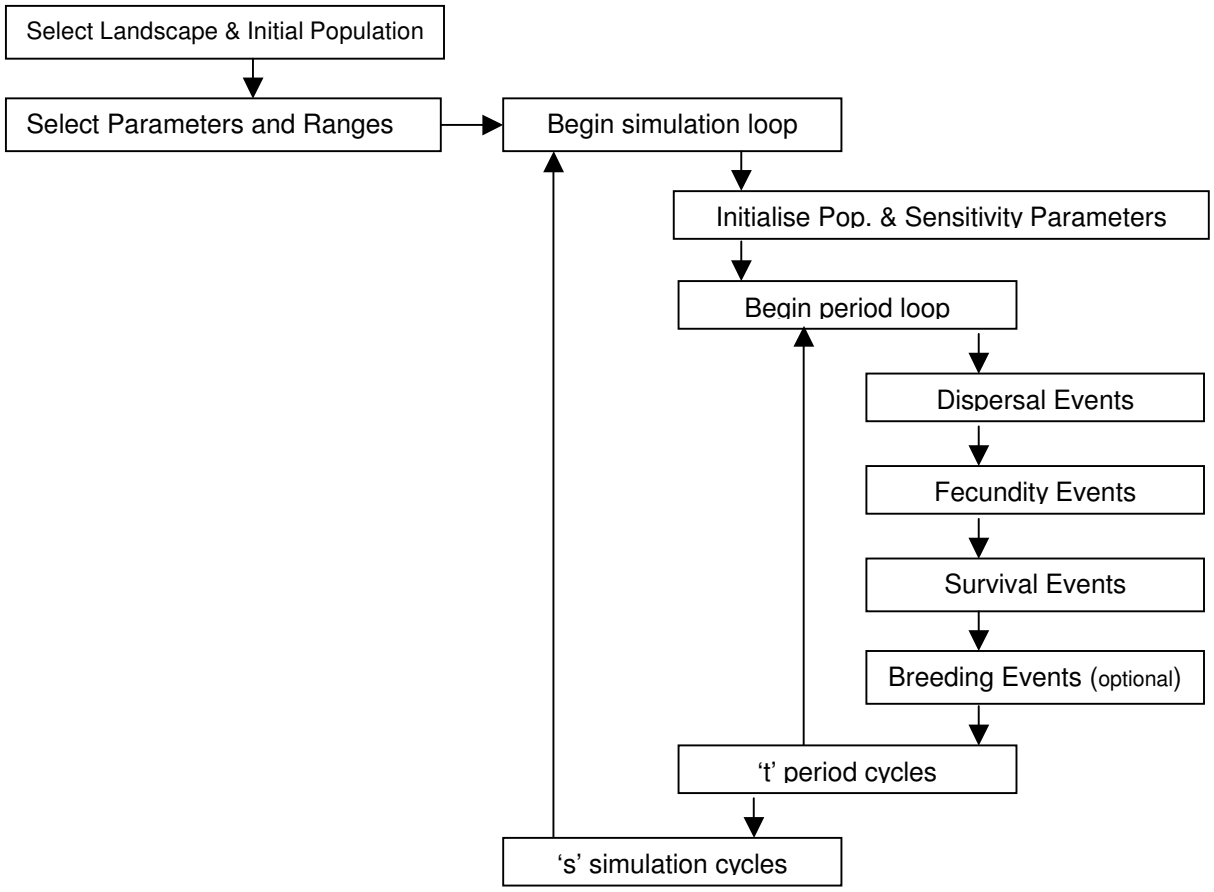


Figure 5.1 Model structure.

Extinction by definition means that the population in question has no animals left. An alternative coined by Ginzburg et al (1982) is quasiextinction. This is when the population falls below a minimum number of animals, adults, or females (in the case of single sex models). At the beginning, this minimum is set by the user. After the model has completed cycling through 't' periods and 's' simulations, the number of simulations having a total population less than the quasiextinction minimum is recorded. Other information including occupancy data are also recorded.

5.3.1 Survival and Fecundity

Demographic stochasticity in this model includes chance fluctuations in survival, fecundity and sex determination. Chance birth and death events are simulated using a binomial pseudo-random variate generator (Equations 5.1 and 5.2). The model can support up to three age classes (e.g. juveniles, sub-adults and adults), although only two age classes were used in this study (see Chapter 6).

Individual-based PVAs allow one to model the fate of each individual throughout its lifetime. Modelling both sexes also allows one to specify a maximum distance between potential mates because as the distance between potential mates increases, it becomes increasingly unlikely they will breed. This may adversely affect a small population (Allee et al, 1949; Boyce, 1992).

Moreover, the maximum distance between breeding partners is defined as the number of cell rows or columns in the habitat grid around a female's location, that she is able to find a male, in order to breed. For example, if this parameter was set to three cells, a 3 x 3 block of cells is searched for a male (including the cell in which the female resides). The minimum distance between breeding partners therefore depends upon the cell size nominated by the user in the underlying habitat grid. If no male is found, the female cannot breed. The mating system is polygamous.

Each age-class is assigned a survival probability. Males and females in a particular age class have the same survival probability. The number of animals in an age class that survive from time *t* to *t*+1 for grid cell *i*, is a binomially distributed random variable:

$$n_{i,t+1} =\sim Binomial\left(n_{i,t}, s_{i,t}\right) \qquad \textbf{Equation 5.1}$$

where, $n_{i,t}$ is the number of animals (the number of Bernoulli trials) in a particular age class for grid cell *i* at time *t* and $s_{i,t}$ is the survival probability in cell *i* at time *t* (see Equation 5.3).

The number of offspring $b_{i,t}$ born in a particular time step is also a binomially distributed random variable:

$$b_{i,t} =\sim Binomial\left(l * f_{i,t}, m_{i,t}\right) \qquad \textbf{Equation 5.2}$$

where, $f_{i,t}$ is the number of potential breeding females (the number of Bernoulli trials) in cell *i* at time *t*; $m_{i,t}$ is probability of birth success in cell *i* at time *t* (see Equation 5.4) and *l* is the maximum number of offspring per female in each time step. The binomial generator in all cases uses the 'n' Bernoulli trial algorithm described by Kachitvichyanukul and Schmeiser (1988). This algorithm is also used to draw the sex of each offspring for a given sex ratio.

5.3.2 Environmental Stochasticity

The fecundity and survival probabilities, $m_{i,t}$ and $s_{i,t}$ in Equations 5.1 and 5.2 vary annually with available resources. This is called environmental stochasticity. Rainfall is a useful surrogate of resource availability and its temporal distribution in semi-arid environments tends to be highly skewed (McCallum, 1994). Here environmental stochasticity has been simulated by sampling an "environmental variable" from a log-normal rainfall distribution at each time step. The mean environmental variable and variance are entered as two global parameters. Possingham and Davies (1995) used simple linear functions to relate survival and fecundity to an environmental variable. However, the model in this study allows survival and fecundity to have a logistic relationship with the environmental variable following McCallum (1994).

$$s_{i,t} = S(x)\left(\frac{\exp(a_s + b_s u_{i,t})}{1+\exp(a_s + b_s u_{i,t})}\right) \qquad \textbf{Equation 5.3}$$

$$m_{i,t} = M(x)\left(\frac{\exp(a_f + b_f u_{i,t})}{1+\exp(a_f + b_f u_{i,t})}\right) \qquad \textbf{Equation 5.4}$$

Here $u_{i,t}$ is the environmental variable generated for cell *i* (see Equation 5.5) at time step *t*; $S(x)$ and $M(x)$ are multipliers representing the maximum attainable survival and fecundity probabilities for each age class *x*; $s_{i,t}$ and $m_{i,t}$ are the derived survival and fecundity probabilities in cell *i* and time step *t*. The parameters a_s, b_s, a_f and b_f are held fixed however, $S(x)$ and $M(x)$ are varied in the sensitivity analysis.

Under extreme conditions, a perfect correlation between patches could mean that all populations become extinct at the same time. Using the global environmental variable, drawn from a distribution defined by a global mean and variance, a correlation coefficient '*c*' is used to alter the inter-cell environmental correlation using Equation 5 (Burgman and Possingham, 1993).

$$u_{i,t} = cx_{g,t} + x_{i,t}(1 - c^2)) \qquad \textbf{Equation 5.5}$$

Here $u_{i,t}$ is the environmental variable for a given cell *i*; $x_{g,t}$ is a global environmental variable generated for all cells in one time step and $x_{i,t}$ is an environmental variable independently generated for an individual cell using the same distribution as $x_{g,t}$. When c =1, $u_{i,t}$ is the same for all patches. Conversely, when c = 0, each patch is given independent environmental variables, $u_{i,t}$. Equation 5.5 does not allow for spatial correlation between cells.

5.3.3 Density Dependence

Invoking density dependence follows approaches taken by Possingham and Davies (1995), South (1998) and Morita and Yorkota (2002), where the population is capped to the maximum carrying capacity for that cell. Here, individuals are removed randomly across all ages at the end of each time step down to the maximum carrying capacity. This is distinct from the model described by Lethbridge et al (2001), which starts by removing animals from the earlier stages. In the absence of any data to the contrary, the approach taken here is thought to have less assumptions. The carrying capacity for each cell is static. It is calculated by multiplying the GIS habitat quality grid cell value (on a 0 to 1 scale) with a parameter *K,* where *K* is the maximum number of animals if the habitat was ideal. The habitat quality does not vary with $u_{i,t}$ but is affected by catastrophes (see Section 5.3.4).

The multiplication of *K* with the habitat score in the PVA model is an attempt to reflect the maximum attainable capacity that the habitat resources and refuge can support. The environmental variable $u_{i,t}$ (described in Section 5.3.2) conversely controls the fluctuations in resources that directly affect survival and fecundity. Capping the population is not true density dependence because the population density does not effect survival until the population reaches carrying capacity.

5.3.4 Catastrophes

Here catastrophes can be extreme environmental events such as fire or prolonged drought, which affect the habitat and lower survival and fecundity (Possingham and Davies, 1995). In this model, following ALEX (Possingham and Davies, 1995), catastrophes can affect either a proportion of the population (local catastrophes) or the entire population (global catastrophes). The advantage of separating catastrophes from unusual environmental events is the ability to stipulate the probability (or frequency) of a global catastrophe, its maximum duration and net effect on carrying capacity,

survival and fecundity. The frequency of catastrophes is drawn from a binomial variate generator using a specified probability. The duration of the catastrophe (in years) is drawn from a uniform random number generator up to a specified maximum duration. The severity of catastrophes is specified using an environmental modifier. This is multiplied by the environmental variable $u_{i,t}$ in Equation 5.5 before it is used in Equations 5.3 and 5.4. The environmental modifier is also multiplied by the carrying capacity.

Another catastrophe that can affect a population is disease. Disease can also spread through a local population. Individuals moving between two connected local populations may also transport the disease (Burgman et al, 1993). This has not been considered in this study but will be included in a future version of the model.

5.3.5 Dispersal

The role of dispersal is an important question in population studies (Burgman et al, 1993; Grant, 1978; Lidicker, 1975; Sharp, 1997a; Turchin, 1998) and spatially explicit PVA need to incorporate dispersal behavior. Movement affects a local population through the processes of emigration and immigration (Lidicker, 1975). Movement is also interrelated with environmental and demographic stochasticity (Burgman et al, 1993).

Dispersal behavior has a complex interrelationship with demographic processes and landscape composition (South, 1998). Unfortunately, dispersal is also one of the least understood areas of ecology (Weins, 2001). However, this does not prevent attempts to model dispersal. Indeed, South (1998) argues in favour of models incorporating dispersal to test whether our lack of knowledge is likely to cause unacceptable uncertainty in our predictions. For example, spatially explicit PVAs that incorporate landscape structure and dispersal, allow the researcher to test the influence of the landscape on dispersal probabilities (Forney and Gilpin, 1989; Weins, 2001), examine the factors influencing departure from a patch and examine the process of selecting a new patch (Bennettes et al, 2001), and explore the effects of landscape structure on gene flow**.** These questions can be tested under different assumptions depending upon the number options available in a model. Models of dispersal are generally underpinned by three fundamental hypotheses (Johnson and Gains, 1990). These include density dependence models, models that consider competition for mates and social hierarchy, and models that consider inbreeding avoidance (Dobson, 1982; Peacock and Ray, 2001; Ronce et al, 2001).

The simplest dispersal model assumes the disperser is moving in a constant direction, and providing there is a constant probability that the disperser stops per unit of time, the probability distribution of one or more dispersers follows a negative exponential function (Turchin, 1998). This also assumes the disperser is travelling through a spatially homogeneous landscape in a random direction. This a well known limitation and in heterogeneous landscapes dispersal dynamics are likely to be more complicated (Burgman et al, 1993; Franklin, 1993; Gustafson and Gardner, 1996).

To model non-random movement, Turchin (1998) suggests the use of dynamic models such as Individual-Based Movement Models (IBMM). IBMMs, like individual-based PVA, fall under a more general approach called Agent-Based Modelling. Spatially explicit IBMMs adopt a Lagrangian philosophy, where a set of rules govern how an individual moves or disperses through the landscape (Turchin, 1998). This flexibility allows a range of movement rules to be tested (Gustafson and Gardner, 1996). IBMMs that incorporate landscape characteristics also allow one to explore dispersal processes in heterogeneous landscapes (Pulliam et al, 1992; South, 1998).

Ims and Hjermann (2001) and Ronce et al (2001) stress the importance of condition-dependent dispersal. They argue that in spatio-temporally varying environments, animals maximise their fitness prospects by matching their phenotypical condition with the prevailing environmental conditions and may choose to do this through dispersal. Thus environmental conditions trigger dispersal directly by affecting behavior or indirectly by affecting body condition (Ims and Hjermann, 2001). South (1998) modelled a spatially explicit population with two different dispersal initiation mechanisms. The first of these, coined "saturation dispersal", involves individuals dispersing only when the carrying capacity is reached (Lidicker, 1975). The second mechanism, coined "presaturation dispersal" (Lidicker, 1975), involves applying a percentage dispersal probability for the potential dispersers in the population before the carrying capacity is reached. In both scenarios South (1998) allowed for only random dispersal and capped the carrying capacity after all dispersal events. Saturation dispersal occurs when resources are fully exploited (Grant, 1978), and although the causes of presaturation dispersal behavior in mammals is still being debated, this model aligns more closely to an inbreeding avoidance hypothesis.

Only natal dispersal is considered in this model. This is where a subadult permanently disperses from its natal patch to another patch. There are three components to the dispersal sub-model. The first involves the factors that influence an individual's decision to stay or leave its natal patch. The second component involves the way in which an individual selects a new patch. The third component is concerned with the cost associated with finding a new patch. These three components are defined

probabilistically and are interrelated with other demographic processes in the population, as well as environmental conditions and landscape composition.

The PVA model offers two options in relation to an individual's decision to stay or leave its natal patch. The first is a saturation dispersal approach similar to South's (1998) resource competitive model. However, unlike South's (1998) saturation approach, the model allows animals to begin to disperse when the population in one cell reaches a percentage of the carrying capacity rather than after the population has reached carrying capacity. This also prevents the model deterministically oscillating in and out of dispersal events in artificial cycles. This oscillation consistently destabilises the population's age distribution. Alternatively, the second assumption allows all subadults to disperse from their natal patch regardless of the density of the population.

The second part of the dispersal algorithm relates to the way in which an individual selects a new patch. Here the model accommodates both active and passive dispersal strategies. An active dispersal strategy is when an individual seeks suitable habitat for survival and reproductive success (Pulliam, 1996), whereas a passive disperser moves randomly.

Active dispersers move through the landscape by stopping at each raster cell and choosing a new raster cell before moving on. This algorithm has been adapted from Wiegand et al (1999). At each step, the individual chooses from the surrounding cells before making the next move. Wiegand et al (1999) define this as local dispersal. Global dispersal on the other hand involves the individual searching a large proportion of the whole landscape for a suitable destination and moving directly to that location. For example, larger bird species are more likely to be global dispersers. An active disperser would usually choose to move to a surrounding cell with the highest habitat score whereas a passive disperser would move randomly. Many species are likely to fall somewhere between these two extremes.

However, in contrast to Wiegand et al (1999), this model incorporates stochasticity in the individual's cell selection using a search parameter n. This number is set by the user and represents an individual's search effort of the cells immediately surrounding the individual's current cell. This is thought to simulate an individual checking the surrounding cells for the best habitat, n times before making a decision. A high n therefore indicates a greater search effort. Parameter n represents the number of Bernoulli trials from which a binomially distributed random variable:

$$h_j = \sim Binomial\ (n, p_j) \qquad \textbf{Equation 5.6}$$

is drawn for each surrounding cell. The cell habitat scores are used as the probability p_j of success.

After generating a value h_j for each surrounding cell, the individual is moved into the cell with the highest value of h_j. The task of selecting a new cell for the next move is then repeated. If n is zero, a surrounding cell is chosen randomly. The individual cannot move back into the cell from where it last moved.

Wiegand et al (1999) distinguish between an "all" disperser and a "minimum" disperser. They define an "all" disperser as an individual that samples all sites in its path and selects the best habitat as the final destination. Conversely a "minimum" disperser selects the first suitable habitat in its path as the final destination. Here, the "minimum" disperser approach has been adopted where the individual will cease to move once it has reached a cell that has sufficient resources. This is where the carrying capacity minus any existing occupants will support one or more individuals. Territorial behavior is not considered.

All moves by the individual to the final destination occur within one time step. The 'minimum' disperser approach used here, forces the individual to make at least three moves. However, in three moves it is possible for the individual to return to its natal cell. This is not regarded as a deficiency in the model. Under conditions of extreme isolation, having returning individuals that don't permanently disperse allows the natal patch to continue to recruit sub-adults. Inevitably, if the population has reached carrying capacity some of these individuals may be randomly selected to die.

The third part of the dispersal algorithm relates to dispersal mortality. This is defined as a probability of survival decaying exponentially with distance (Equation 5.7).

$$f(x) = e^{-ax} \qquad \textbf{Equation 5.7}$$

Here $f(x)$ is a negative exponential probability density function of survival for a given distance x. Parameter 'a' is the inverse of the average dispersal distance specific to each sex (Burgman et al, 1993). Equation 5.7 is calculated after the individual has moved through the landscape and landed in its destination cell. The probability of survival $f(x)$ is calculated using the Euclidian distance between the natal cell and destination cell. This is thought to better relate to empirical studies as the exact distance an individual travels to search for a patch can never be determined. In the model described by Lethbridge et al (2001), this function was used to determine the distance an individual traveled rather than penalise its survival. This was thought to be a distinct limitation of this model (Lethbridge et al, 2001).

5.3.6 Inbreeding Simulation

The idea of linking demographic and genetic attributes in models is relatively new (Richards, 2000). Gene flow between subpopulations also reduces the loss of genetic diversity through genetic drift and inbreeding (Dudash and Fenser, 2000; Thrall et al, 2000). These effects may reduce mean population fitness and the viability of small populations, particularly in the presence of environmental and demographic stochasticity (Dudash and Fenser, 2000; Daniels et al, 2000). The risk may also increase as a result of a small population becoming isolated (Dudash and Fenser, 2000; Thrall et al, 2000).

Dominance may either have a positive or negative effect on inbreeding depression depending upon the level of fitness of the dominant gene and how dominant individuals are selected (Dudash and Fenser, 2000). For example, does a female prefer to breed with the largest and presumably genetically fitter male in favor of other males, and will she select an immigrant male on the basis of these attributes in favor of a resident dominant male (Ball, 2000)? Moreover, to what extent can a resident male defend his territory against immigrant males? Are immigrant males that have dispersed from other patches likely to have higher levels of genetic fitness?

In this study a genetic sub-model was developed to explore the effects of a range of dispersal strategies and landscapes on inbreeding depression.

5.3.7 Pedigree Simulation

Individual-based simulation models allow pedigrees to be simulated (Falconer and Mackay, 1996). The idea of an individual-based simulation model that tracks individual mating pairs follows work carried out by Daniels et al (2000).

The pedigree sub-model tracks mating pairs in a nominated area within the PVA landscape. Choosing a local population in a smaller area of the landscape reduces the computer processing time, and enables one to focus on isolated populations, where gene flow through dispersal is likely to increase the effective population size and reduce the effects of inbreeding depression (Richards 2000). The sub-population is geographically selected by a coordinate and radius.

The pedigree sub-model makes the following assumptions about the breeding patterns:

1. Mating is non-random.
2. A female will not mate with a father or son.
3. A dominant female is selected randomly from the older age class for each cell. This female will always be allocated the first successful offspring in the population.
4. A dominant male is selected randomly from the older age class for each cell. The dominant male will always be chosen first to breed with females in his vicinity unless the female is his daughter or mother, in which case another male is selected to breed.
5. Siblings are only able to breed when the population is low and all other options are exhausted.
6. Founders are not related.
7. Immigrants to the sub-population are not related.

At the end of the PVA simulation, a pedigree file is generated for each year and each simulation. Table 5.3 is an example of a typical pedigree file for a given year and simulation. This contains not only the breeding individuals for that year, but also the family tree back to the founding population.

Table 5.3 Example of a pedigree file for a sub-population.

The first column contains information about the year and simulation number. Entries marked 'x' infer the mother or father is unknown due to the individual being an immigrant or a founder.

Sim/Year	ID	Father	Mother	Sex
16015	43	x	x	f
16015	14	x	x	f
16015	3	x	x	m
16015	33	3	14	m
16015	54	33	43	m
16015	39	3	14	m
16015	64	39	43	m
16015	55	33	43	f
16015	16	x	x	f
16015	32	3	16	f
16015	5	x	x	m
16015	46	5	32	f
16015	59	33	46	m
16015	41	3	16	f
16015	57	33	41	m
16015	61	33	46	f
16015	31	3	14	f
16015	50	33	31	f
16015	65	39	50	f
16015	38	3	14	f
16015	48	33	38	f
16015	66	39	48	f
16015	67	39	41	f
16015	62	x	x	m
16015	63	x	x	f
16015	51	x	x	f
16015	44	5	14	m
16015	68	44	51	f
16015	26	x	x	m

Following the work carried out by Daniels et al (2000), the mean kinship coefficient of all successful breeding pairs is calculated for each year and each simulation for the sub-population using the pedigree generated files. The coefficient of kinship is the probability that two alleles, one from each of the parents are identical by descent (Falconer and Mackay, 1996; Gillespie, 1998). The kinship coefficient of a breeding pair is equal to the inbreeding coefficient of the offspring (Daniels et al, 2000; Falconer and Mackay, 1996; Gillespie, 1998).

The kinship coefficient calculation requires the full pedigree history back to the founding population. As previously mentioned, in this study all founders and immigrants are assumed to be unrelated and hence not inbred. The programme 'Sib-pair' by Duffy (2002) was used to calculate the kinship coefficients from the simulation pedigree files. This programme was selected because of its ability to batch process large numbers of pedigree files from multiple simulation replicates.

5.3.8 **Random Mating**

As an alternative to the pedigree approach, a simpler and less computer-intensive breeding sub-model is also offered in the PVA model. This uses Wright's (1931; 1951) random mating equation. This links migration and population size with inbreeding. He defined an inbreeding coefficient F as the correlation between presence or absence of an allele in uniting gametes compared with an expected correlation if these pairs were randomly drawn from the population (Raybould et al, 2001). The term 'uniting gametes' infers self-breeding can take place. However, in the context of mammal populations, this correlation can be thought of as the probability of alleles that are identical-by-descent being combined in zygotes (Neigel, 2002) or the correlation between a randomly selected allele from one individual and a randomly selected allele from another individual (Raybould et al, 2001). The effective number of breeding individuals N_e is related to the average rate of inbreeding ΔF according to Equation 5.8 (Falconer and Mackay, 1996).

$$\Delta F = \frac{1}{2N_e} \qquad \textbf{Equation 5.8}$$

This equation assumes that mating is random, there is no immigration and there is a neutrality of alleles. Wright (1931; 1951) also provides a useful equation that enables an average inbreeding coefficient F_t at time *t* to be calculated from the average inbreeding coefficient F_{t-1} at time *t-1*. This equation (Equation 5.9) also allows for immigration. Here *m* is the fraction of immigrants in relation to N_e.

$$F_t = \left\{ \frac{1}{2N_e} + (1 - \frac{1}{2N_e}) F_{t-1}) \right\} (1-m)^2 \qquad \textbf{Equation 5.9}$$

The effective number of breeding individuals N_e can be estimated from *N,* the total number of individuals using a range of formulae discussed by Wright (1969) and later Falconer and Mackay (1996). Falconer and Mackay (1996) also discuss formulae that adjust N_e to exclude sibling and self breeding and allow for unequal representation of the sexes in the breeding pool, non-random distributions of family size, unequal numbers in successive generations, overlapping generations, migration, mutation and selection.

5.3.9 Sensitivity Analysis

Sensitivity analysis can indicate the relative contribution of a suite of demographic and environmental parameters to the population's persistence. In PVAs, this involves determining their relative impact on the probability of extinction. This may be used in a retrospective context or a prospective context (Caswell, 2001; Cross and Beissinger, 2001). For example, predicting the effects of changes in future demographic parameters may be use to assess management strategies and guide management effort (Caswell, 2001; McCarthy et al, 1995; Possingham et al, 1993). Conversely, using empirical data from several field studies might also provide a retrospective and quantitative assessment of the effects of past changes (Caswell, 2001).

The demographic parameters for which the model is most sensitive will also be responsible for the most error propagation. These parameters are also likely to require more sampling and monitoring effort (Caswell, 2001). This is particularly useful when the parameters are derived from limited data (Goldingay and Possingham, 1995) as sensitivity analysis can direct the researcher to the parameters that with more precise measurement will improve the model's precision. Sensitivity analysis also draws our attention to the important system dynamics that lead to extinction, shifting the emphasis away from predicting absolute extinction times (Cross and Beissinger, 2001).

In Monte Carlo simulation models, sensitivity analysis involves explicitly varying model input parameters in order to ascertain their relative influence on the results (Jørgensen, 2001; McCarthy et al, 1995; Turchin, 1998; Cross, 2001). This is distinct from analytical models or matrix models where differential calculus and Eigen analysis are used to derive parameter elasticities or sensitivities (Caswell, 2001).

Conventional sensitivity analysis is exhaustive and usually involves running a number of simulations for a given parameter set and then varying only one parameter at a time by a set percentage and re-running the simulations (Cross and Beissinger, 2001). Varying the parameter by a percentage of its range is considered to be a relative approach. However, exhaustive sensitivity analysis necessitates a very large number of fixed parameter combinations to assess each parameter independently and an unwieldy number of combinations to assess possible interactive effects between fixed levels of each parameter (McCarthy et al, 1995).

Alternatively, McCarthy et al (1995) recommend a more expedient approach that summarises the parameter contributions using logistic regression. This approach involves varying each input parameter randomly within a stipulated range for each simulation and regressing these parameter variates with the results. Sample-based methods of sensitivity analysis where the simulation results for a given range of input parameters are regressed is also known as meta-modelling (van Groenendaal and Kleijnen, 2001). This is discussed in detail by Frey (2002), Helton and Davis (2002), and Frey and Patil (2002). If a binary output is used (for example quasiextinction in 100 years), the input parameter variates can be regressed against the results using logistic regression (McCarthy et al, 1995) as shown in Equation 5.10.

$$\ln\left(\frac{y}{1-y}\right) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots \qquad \textbf{Equation 5.10}$$

Here *y* is the probability of extinction (or quasiextinction) for a nominated period. The explanatory variables $x_1, x_2 \ldots$ etc are the parameter variates and $\beta_0, \beta_1, \beta_2 \ldots$ etc are the estimated coefficients. The coefficients $\beta_0, \beta_1, \beta_2 \ldots$ reflect the contribution of each variable and their units of measure. Accordingly, the coefficient estimates require standardising to remove their scale differences (McCarthy et al, 1995).

How one standardises $\beta_0, \beta_1, \beta_2 \ldots$ largely depends on the question being asked. For example, McCarthy et al (1995) suggest scaling the coefficients using their parameter uncertainties. This provides a unitless comparison of the relative contribution of $x_1, x_2 \ldots$ (McCarthy et al, 1995; Selvin, 1995). However, this might only be appropriate when the problem is retrospective and involves determining the parameters that most affect the population from given a set of empirical estimates. Here the scaling can be achieved by dividing $\beta_0, \beta_1, \beta_2 \ldots$ by $SE_{x_1}, SE_{x_2} \ldots$ derived from empirical replicates (Cross and Beissinger, 2001). According to Cross and Beissinger (2001), there are two problems with this approach. Firstly, standard error estimates from empirical studies often reflect the combined effects of process and observation error (Hilborn and Mangel, 1997; White, 2000) and standard error estimates for the purpose of parameter scaling $\beta_0, \beta_1, \beta_2 \ldots$ should only reflect process error. Secondly, empirically derived estimates of the standard errors may not be comparable between studies. Varying parameters by a fixed percentage of their range may be more comparative between studies and have both retrospective and prospective elements because future changes can be explored based upon known past variations (Cross and Beissinger, 2001).

Alternatively, Helton and Davis (2002) suggest standardising the coefficients by correcting them using the standard deviation estimates from the regression equation. The standardised coefficients therefore provide a measure of the importance of the parameter based on the effect of moving it a fixed fraction of its standard deviation from its central value (Helton and Davis, 2002). As the standard deviations are proportional to the uniform ranges of the input parameters, this is analogous to varying parameters by a fixed percentage of their range. The relative influence of each parameter depends on the derived range of values for each parameter.

The relative influence of each parameter will also depend on the central value about which each parameter is being varied. For example, varying a survival parameter +/- 0.2 around a central value of 0.7 may alter the importance of survival compared with varying survival the same amount around a central value of 0.5. Similarly, the effect of a survival parameter's range of +/-0.2 as compared with +/-0.4 will alter the relative influence of parameter. It is critical that these ranges and central values are selected carefully. Their selection will largely depend upon the questions being asked of the model. Moreover, the regression model may not be useful when extrapolating beyond these ranges (Devore and Peck, 1996).

McCarthy et al (1995) and Frey (2002) suggest testing for non-linear relationships between the independent variables and the response variable *y* and recommend testing for parameter interactive effects. Non-linearities are often removed using a simple transformation (Hosmer and Lemeshow, 1989; Rice, 1995; Zar, 1996). In this study the non-parametric Multivariate Adaptive Regression Spline (MARS) data mining software by Friedman (1991) has been used to regress the parameter variates with the probability of extinction following McCarthy et al (1995). A more detailed description of this methodology was provided in Section 4.2.7.

MARS has three distinct advantages. Firstly, being a non-parametric approach, it makes no assumptions about linearity in the contribution of each parameter to the dependent variable. Secondly, MARS explores the likely significance of potential interactive effects between all parameters. In the MARS software (Salford Systems, 2001), the relative importance of the parameters is determined by comparing the estimated cost of omission of each variable with the highest cost of omission of all variables. The cost of omission is derived by calculating the goodness of fit of the model after the variable in question has been dropped. This is better than standardising coefficients because it combines the direct contribution of a parameter and its indirect contribution from an interactive relationship with another parameter.

Latin Hypercube Sampling (LHS) has also been employed in the PVA software in this study. LHS is a sampling refinement of sensitivity analysis that efficiently stratifies the parameter ranges that are being varied. Consider *i* parameters where each parameter range is divided into *n* bins and each bin has an equal number of samples drawn. Samples are drawn such that every bin in each parameter is paired with every bin of all other parameters (Helton, 2004; Helton and Davis, 2002; van Groenendaal and Kleijnen, 2001). This ensures that samples are drawn across the entire range of likely parameter combinations (i.e. *n* x *i* tuples - Helton and Davis, 2002). Hence the term hypercube refers to the full multidimensional set of all tuple combinations of bins for all variables. The model uses up to ten bins for each parameter. There is also and option to impose correlations between the parameter samples.

5.4 Summary of Model Inputs

Table 5.4 is a summary of the input parameters required to execute the model. The pedigree parameters are optional. These inputs are entered by the user in a Windows® Graphical User Interface (GUI) with a series of dialog boxes.

Table 5.4 Summary of PVA model input parameters

Module	Input Parameters
Start	Output file(s).
	Number of Simulations.
	Number of time steps (years).
	Minimum population for quasi-extinction calculation.
	Map option. An animated view of population changes over the landscape for visualisation and qualification of model behavior.
	Random number seed.
	Latin Hyper cube sampling option.
Demographic	Age of sexual maturity (time steps).
	Litters per time step.
	Litter size.
	Allee search area (in cells). The Allee search parameter is the number of cell rows or columns (including the target cell) that a female can find a mate in order to breed.
	Survival logistic parameters a_s, b_s in Equation 5.3.
	+/- a_s range for sensitivity analysis.
	Fecundity logistic parameters a_f, b_f in Equation 5.4.
	+/- a_f range for sensitivity analysis.
	S(j), juvenile survival multiplier. Multiplied by Equation 5.3.
	+/- *S(j)* range for sensitivity analysis.
	S(sa), sub-adult survival multiplier. Multiplied by Equation 5.3.
	+/- *S(sa)* range for sensitivity analysis.
	S(a), adult survival multiplier. Multiplied by Equation 5.4.
	+/- *S(a)* range for sensitivity analysis.
	M(x), female fecundity multiplier. This is the probability that a female successfully gives birth to a male or female.
	+/- *M(x)* range for sensitivity analysis.
	Maximum juvenile age.
	Maximum sub-adult age.

	Maximum adult age.
	The percentage of sub-adults in the initial population.
	The percentage of juveniles in the initial population. The percentage of Adults is deduced.
Pedigree simulations or Wrights equation (optional)	Pedigree analysis position. The centre of the statistically quarantined area for tracking pedigrees and immigrants.
	Pedigree analysis radius. The radius of the statistically quarantined area.
Environmental Stochasticity	Mean rainfall (or some other environmental variable defining available resources). Used in Equation 5.5.
	Rainfall variance.
	Choice of normal rainfall distribution or log-normal rainfall distribution.
	Minimum rainfall. This prevents zero rainfall events.
	Carrying capacity, K. The habitat quality of each cell in the landscape is on a 0 to 1 scale. Multiplied by the habitat cell values.
	Catastrophe modifier. If a catastrophe occurs that year this value is multiplied $u_{i,t}$ and the carrying capacity (should this option be selected).
	Maximum catastrophe duration. A random number is drawn from this range for each catastrophe.
	Probability of a catastrophe, P_c.
	+/- P_c, range for sensitivity analysis
	Fraction of cells effected, F_c
	+/- F_c, range for sensitivity analysis
Dispersal	Dispersal can be turned off for single population studies without movement.
	Dispersal trigger. All sub-adults disperse despite density or, sub-adults begin to disperse as population exceeds X% of the carrying capacity.
	Average female dispersal distance to a 50% survival probability.
	+/- range of average female dispersal distance to a 50% survival probability for sensitivity.
	Maximum female dispersal.
	Average male dispersal distance to a 50% survival probability.
	+/- range of average male dispersal distance to a 50% survival probability for sensitivity.
	Maximum male dispersal.
	Dispersal queue order. Males or females first.
	Dispersal search mode. 0 to ∞ scale where 0 is a passive (random disperser). Dispersers with high dispersal mode values (>=10.0) actively search for higher habitat quality cells as they step through the landscape.

CHAPTER 6

A Population Viability Analysis of the Yellow-footed Rock-wallaby (*Petrogale xanthopus xanthopus*) in South Australia.

6.0 Introduction

This chapter presents an application of the PVA model described in Chapter 5 to assess the effect of several ecological and environmental parameters on the probability of extinction and inbreeding depression of *P. x. xanthopus*. This has been used to answer three key questions.

The first question, raised in Chapter 3, relates to the closeness of the constant survival estimates obtained in this study and from Sharp (2002) using the Jolly-Seber-Cormack mark recapture methodology. These estimates assume there is no emigration. Moreover, the constant survival estimates described in Chapter 2 from Eregunda Creek and Wilkawillina Gorge were not significantly different despite each site having different pest management strategies. This either indicates that these populations are not sensitive to these survival fluctuations and naturally vary, they do not respond to different pest strategies or the observation errors are inflated. The danger is that these apparently insignificant differences could be the difference between a population being viable or not.

One way to reduce observation uncertainty is to undertake repeated long-term sampling (Hilborn and Mangel, 1997; White, 2000). However, the investment in long-term studies is expensive and conservation mangers need to know how useful additional sampling will be before committing to this level of effort. Hence the first aim of this Chapter is to determine how small changes in survival might affect the population's long-term viability. This is an important step before continuing sampling to reduce the observation errors.

The second question raised is: what are the factors that most affect the viability of *P. x. xanthopus*? Here the aim is to use sensitivity analysis and a spatially explicit PVA to rank the importance of a wide range of ecological and environmental parameters (including dispersal parameters) by assessing how they affect the probability of extinction of a metapopulation of *P. x. xanthopus* in the Flinders Ranges, South Australia. This will help prioritise further monitoring and management in this area.

As this PVA requires a GIS raster grid to describe habitat quality, to test that the predictions are not merely artifacts of cell size, a sensitivity analysis was first conducted for three separate cell sizes, 500 x 500 metres, 1000 x 1000 metres and 1500 x 1500 metres.

Little is known about the movement of *P. x. xanthopus* (Sharp, 2002). In Chapter 3, a genetic assignment test carried out by Eldridge (unpublished) revealed that little recent movement was evident over four kilometres between Wilkawillina North and Wilkawillina South and that no movement was evident between these sites and Eregunda Creek (>20 kilometres). However, the few samples collected (n = 43) and limited geographical area from which these were collected, limits the utility of this information. No published studies about *P. x. xanthopus* have revealed how individuals move and what triggers them to disperse. Hence the third question is: how do different dispersal strategies affect the inbreeding? This question will be answered by using the genetic sub-model described in Chapter 5, to explore a range of dispersal strategies in two different landscapes and the effect these have on inbreeding depression. Here the aim is to better understand the implications of different dispersal processes and set an agenda for more focused questions that are able to test specific hypotheses related to dispersal.

6.1 Methods

6.1.1 Study Area

The geographical area chosen for this study is north of the Flinders Ranges National Park and south of the Gammon Ranges National Park in the Flinders Ranges, South Australia. The target area in Figure 6.1 was selected because the area has been chosen by the Natural Heritage Trust (NHT) appointed rangelands Natural Resource Management committee as a regional priority project area. The proposed threat abatement area in Figure 6.1 is shaded. Threat abatement in this area is hoped to consist of fox and goat control. The point symbols in Figure 6.1 indicate positive sightings of *P. x. xanthopus* from ground and aerial surveys (see Chapter 4). Figure 6.2 shows the actual area chosen for PVA modelling.

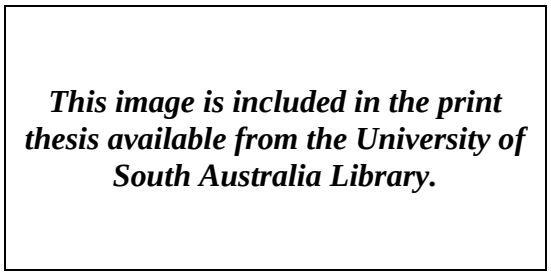


Figure 6.1 Proposed priority project area.

6.1.2 Habitat Model

The PVA described requires a spatial representation of the habitat quality of *P. x. xanthopus*. It is thought that the disturbance of *P. x. xanthopus* is not associated with the more common problems of vegetation clearing, excavation and urban growth but is more likely due to the gradual loss of resources through competition from introduced herbivores and predation from foxes (Copley, 1981). Figure 6.2 is an enlargement of Figure 6.1 showing the probability distribution model derived in Chapter 4 and the extent of the PVA simulation area in red.

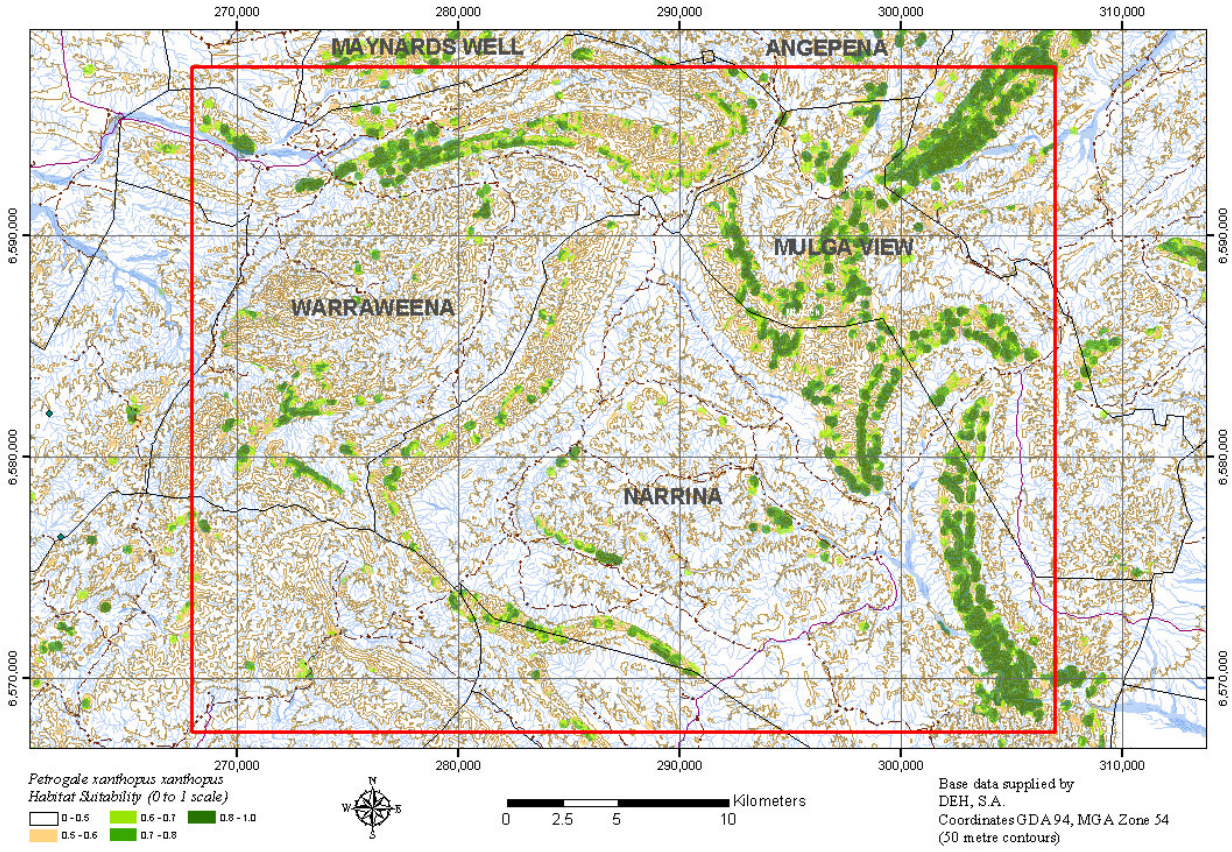


Figure 6.2 Enlargement of Figure 6.1 with the PVA simulation area marked in red.

As discussed in Chapter 4, presence-absence models that ignore spatial autocorrelation, focus only on the habitat characteristics that determine presence and absence. The predicted presence-absence probabilities in these models are independently derived for each cell and are not influenced by the proximity of that location to nearby presence data. This is thought to be more suitable for depicting the landscape in a spatially explicit PVA because these PVAs effectively incorporate autocorrelation by simulating movement.

Presence-absence models often fail to indicate the quality of biotic and abiotic components of the landscape that support a viable population (van Horne, 1983). Hence the utility of presence-absence models as habitat quality models depends upon the explanatory variables used to derive them. In this study more abiotic variables were used to explain presence and absence. However, many of these abiotic variables are thought to indirectly explain the capacity of the habitat to hold food resources. For example, rock plants are more likely found in steeper slopes and in rocky outcrops. It is therefore reasonable to suggest that the habitat model from Chapter 4 loosely reflects the capacity of the abiota and biota to support this species. Figure 6.2 is an enlargement of Figure 6.1 showing the habitat scored derived from Chapter 4, ignoring autocorrelation.

6.1.3 Rainfall

While the rainfall patterns will vary across the study area, the distributional properties of the rainfall used to generate an environmental variable in the PVA model (described in Section 5.3) was taken from the Narrina Station rainfall gauge located nearest to the centre of the study area. This has a mean rainfall of 245 mm and variance of 9000. This rainfall data exhibited a log-normal distribution. The data was obtained from the Australian Bureau of Meteorology on the 'Climate Data Australia' database, version 2.2, 2002.

6.1.4 Age Classes

It is generally agreed that the survival of juvenile macropods is usually lower than sub-adults and adults. However, few juveniles were trapped in this study and it was not possible to separate juvenile survival from sub-adult survival. Juveniles and sub-adults were consequently grouped into one age class. Despite this, the mark recapture estimate of survival for this age class was not found to be significantly different from the adult age class. The ability to adequately separate age classes is a limitation of the Jolly-Seber-Cormack method more than a lack of data. For the purpose of PVA modelling it was desirable to have at least two age classes to test the age-specific effects of survival on extinction. However, there was little justification for having three age classes. Consequently, two age classes were used in the PVA modelling. The survival multiplier $S(x)$ was separated into juvenile survival $S(j)$ and adult survival $S(a)$. All individuals under two years of age are called juveniles. Based upon data about the longevity of captive animals, the maximum age of an adult was set to 12 years of age (Royal Adelaide Zoological Society, 1999).

6.1.5 Local Population Survival

Closed populations have no emigration and immigration, so modelling a closed population allows one to focus on the demographic parameters that drive a population. Moreover, sensitivity analysis was used to rank the importance of a range of demographic parameters on the probability of extinction of a closed population. As the fluctuation in available resources in semi-arid environments is usually dependent upon rainfall, the dependency of survival on rainfall is also tested in relation to the probability of extinction.

The mark recapture data collected in this study was used to calculate six-monthly survival. While there is some evidence to suggest that six-monthly survival is related to rainfall, the rainfall coefficient was not significantly different from zero (see Figure 3.13). This is either an artifact of observation error or the relationship of survival with rainfall is weak. Interestingly, Sharp's (2002) study in NSW also indicated little evidence to support a relationship between survival and rainfall. However, the influence of rainfall on survival may also depend upon the microclimate afforded by the habitat. Assuming six-monthly survival is constant throughout the year, the square of this is a twelve-monthly estimate of survival (i.e. the joint probability of surviving two successive six-monthly intervals).

However, in Chapter 3, the six-monthly survival probability was related to a thirteen-monthly interval of rainfall, lagged by eleven months. This makes it difficult to derive an equivalent annual survival relationship with rainfall without either cycling the PVA model over six-monthly periods using thirteen-month rainfall distributions or changing the mark recapture intervals. Alternatively, a crude estimate of the twelve-monthly rainfall relationship (the line with squares in Figure 6.3) can be obtained by squaring the discrete estimates of six-monthly survival (the line with diamonds in Figure 6.3). This is a crude estimate because the six-monthly rainfall relationship is temporally correlated with a rainfall interval that overlaps with the following six-monthly survival's rainfall interval. Hence the joint probability of these two estimates is not based on independent probabilities. Nevertheless, the order of magnitude of this error is not thought to be great enough to confound modelling the effect of different strengths of the twelve-monthly survival/rainfall relationship.

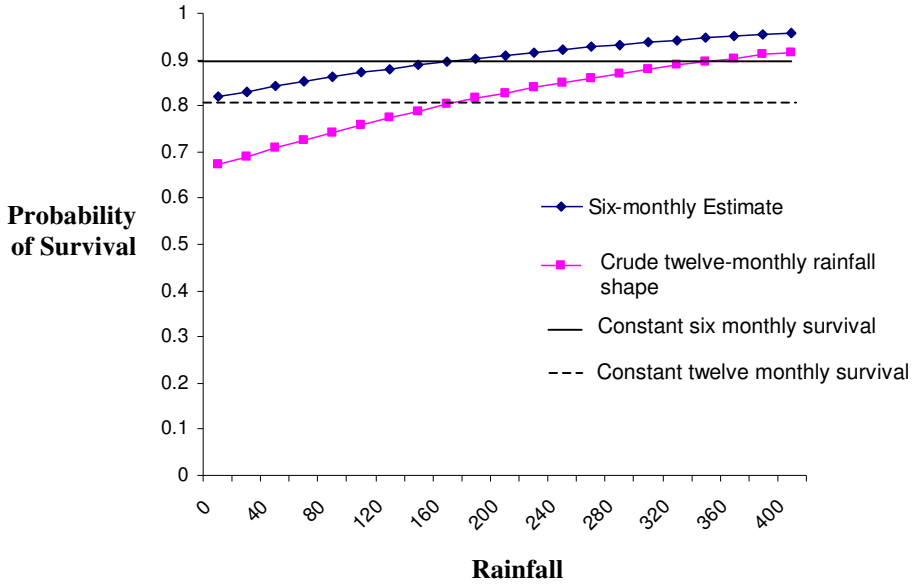


Figure 6.3 Comparison of different rainfall dependencies.

This shows the six-monthly survival curve, a crude twelve-monthly survival estimate and the equivalent mean (constant) six and twelve month survival lines.

In Equation 5.3, two parameters define the shape of the rainfall/survival curve. These are a_s and b_s. To be able to vary the strength of the relationship between rainfall and survival probability, the shape of the curve can be varied by holding parameter b_s fixed and varying parameter a_s (see Figure 6.4). This is better than varying both parameters, which can give spurious-shaped curves. The amplitude of these probability curves (the *y* intercept) is varied using the survival multiplier *S(x)* (from Equation 5.3).

In Chapter 3, twelve-monthly fecundity was related to a twelve-monthly interval of rainfall. From Equation 5.3, the parameters a_f and b_f are used to describe the relationship of fecundity probability in relation to rainfall for adult females. The fecundity multiplier *M(x)* defines the amplitude of fecundity probability an adult age class only. These parameters were also altered for the purpose of sensitivity analysis in the same way as survival (see Figure 6.4).

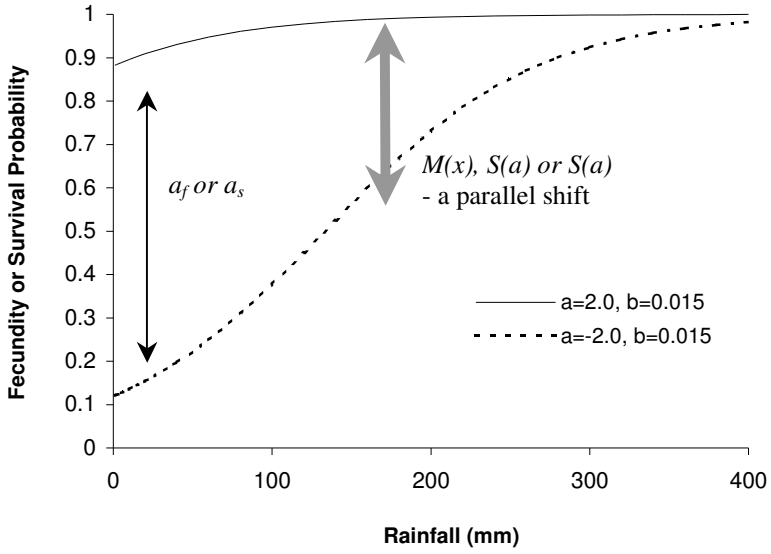


Figure 6.4 The effect of varying a_m or a_f and, *M(x)*, *S(j)* or *S(a)*

6.1.6 Spatially Explicit PVA Simulations

Current distribution data for *P. x. xanthopus* in the study area (Figure 6.2) was obtained from aerial surveys and used as the starting population in the simulations. However, only a fraction of the true population is ever seen in aerial surveys. To estimate true abundance, Lim (1987) suggested an aerial sightability multiplication factor of *P. x. xanthopus* in the range of 4.61 and 6.85. He derived this at Middle Gorge in South Australia (see Section 2.2.4). However, this range is thought to be conservative and based upon a limited field validation (Kinnear, 1994) and a wider sightability range of 3.85 to 7.85 is thought to be more appropriate. While the distribution data cannot be varied in the model, the sightability factor was varied according to this range for the purpose of sensitivity analysis.

The Allee parameter indicates the distance (in cell units) that is allowed between a female and the nearest male before breeding can occur. No information is known about the maximum distance required between *P. x. xanthopus* breeding partners in order for females to be able breed, so some assumptions had to be made about this distance. A 1000 metre cell size occupies an area of 100 hectares. Sharp (2002) calculated an average home range for this species of under 20 hectares but

found a significant overlap in the home ranges of 18 individuals living in 117 hectares. The physical layout of the landscape and distribution of resources will usually determine the shape of a home range. However, if it is assumed that the home ranges are regularly shaped with minimal perimeters, it is unlikely that a female will encounter a male more than 1500 metres away. For both 1500 and 1000 metre cell sizes, the Allee parameter was rounded off to three cells and for 500 metre cells it was set to seven cells.

Asb the habitat distribution model in Chapter 4, predicts the probability of occurrence on a continuous scale, habitat quality scores of under 0.2 required truncating to zero to prevent individuals from moving into unsuitable terrain (e.g. open plains).

As previously mentioned, a sensitivity analysis was first conducted for three separate cell sizes, 500 x 500 metres, 1000 x 1000 metres and 1500 x 1500 metres to test that the spatially explicit predictions are not merely artifacts of cell size. The carrying capacities were adjusted according to the area of each cell.

Following this, three other scenarios were explored, each having a different set of biological and environmental assumptions. In the first scenario (Model 1), all sub-adults were able to disperse regardless of population density. In Model 2, the severity and frequency of catastrophes is increased however unlike Model 1, in Model 2, dispersal is density dependent. In Model 3, all sub-adults are able to disperse regardless of population density but catastrophes and their effects are maintained at the higher levels set in Model 2. Spatially explicit PVA simulations can be computer intensive. Hence in order to reduce processing time only 60 years were projected for 10,000 simulations.

6.1.7 Dispersal and Inbreeding Potential

The simulations introduced in Section 6.1.5, focus on the importance of the model parameters in an ecological context. Here sensitivity analysis was used to test the effect of key parameters on inbreeding depression.

Initially two different approaches were compared. The pedigree approach tracked individual mating pairs. The rules governing the mating pairs were outlined in Section 5.3.6 in Chapter 5. After running the PVA simulations, the programme 'Sib-pair' by Duffy (2002) was used to calculate the kinship coefficients from the simulation pedigree files. The second approach assumed mating was random and used Wright's (1931; 1951) equation (Equation 5.8) to calculate an average inbreeding coefficient F_t at time *t* from the average inbreeding coefficient F_{t-1} at time *t-1*.

Only a small area within the entire study area was used to process the pedigree information o reduce processing time. This area is around Mt Stuart on the Warraweena property. This is thought to be a relatively isolated colony and therefore a useful area for testing the effects of different dispersal strategies on inbreeding (see Figure 6.6). The site has also attracted attention from DEH and the Warraweena management, who are interested in the genetic viability of the population. As such, genetic data are currently being sampled at this site in a separate study.

Tracking pedigree information significantly increased the computer processing time. Conversely, calculating the cumulative effects on F using Wright's random mating model (Equation 5.9) incurs no notable delays in computer processing time. In order to reduce the significant processing delays incurred using the pedigree model, subsequent simulations only used Wright's random mating model (Equation 5.8).

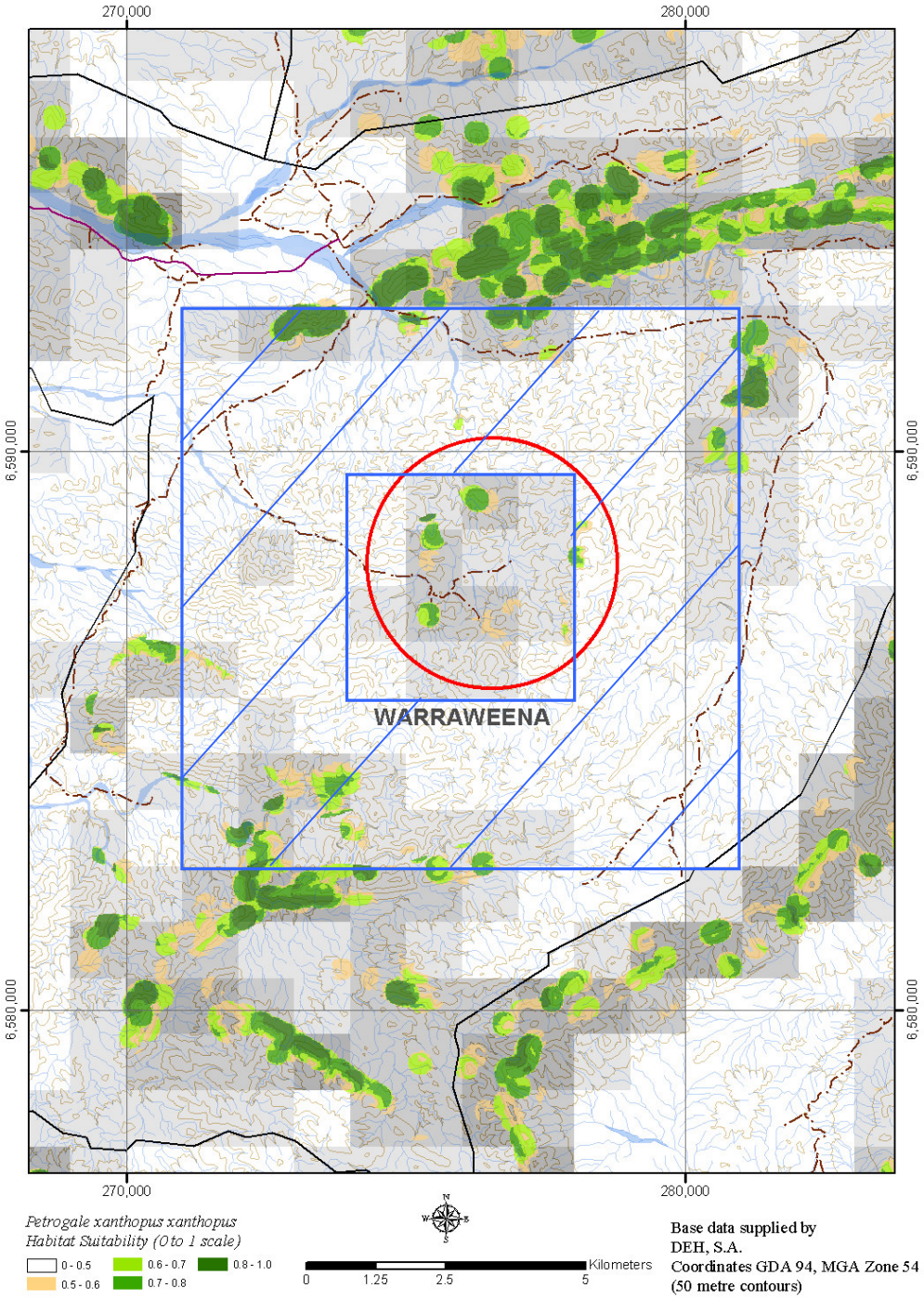


Figure 6.5 An enlargement of Figure 6.2.

The area in which inbreeding was simulated is circled in red. Tracks are depicted as brown dashed lines and the boundaries are black. Orange to Green colour represents habitat quality scores from Chapter 4 and grey shades represent the equivalent habitat scores aggregated to 10000 x 1000 metre cells. The lightly hatched blue area around the quarantine area indicates where the habitat is later removed in the PVA for fragmentation comparisons.

6.2 Results

6.2.1 Local Population Survival

A PVA was carried out using a hypothetical local population, which was assumed to be closed (i.e. not subject emigration or immigration). A sensitivity analysis of selected demographic parameters was conducted. This involved varying these parameters according to the ranges specified in Table 6.1 using a Latin Hypercube algorithm for each PVA simulation. After 10,000 simulations, the binary results (i.e. 0 - extinction or 1 - otherwise) over 100 years were regressed with the parameter variates using the non-parametric regression package MARS (Salford Systems, 2001). Up to five-way interactive effects were allowed in the penalized spline fitting.

The parameters *S(j), S(a)* and *M(x)* in Table 6.1 are the multipliers representing the maximum attainable survival and fecundity probabilities described in Equations 5.3 and 5.4 respectively. The fecundity parameter b_f was fixed at 0.015 while a_f was varied according to Table 6.1. The survival parameters a_s and b_s from Equation 5.3 were also set to 0.015 and varied from –2.0 to +2.0 respectively for both age classes. Carrying capacity 25 to 75 animals. This is thought to typify the range of carrying capacities in a landscape supporting local populations that are likely to remain viable. The population was given an initial abundance of 75 adults. This was set to the upper limit of the carrying capacity range. This allows the carrying capacity in the first year to define the initial population because the carrying capacity will cap the population in the first year. In the absence of any information to the contrary, a sex ratio of 1:1 was used.

Table 6.1 Aspatial Input Parameters for Sensitivity Analysis.

a_s and a_f are survival and fecundity parameters that define the shape of the logistic curves at lower rainfalls in equations 5.3 and 5.4.

Parameter	Value	Random Variation
Juvenile Survival *S(j)*	0.85	+/- 0.15
Adult Survival *S(a)*	0.85	+/- 0.15
Fecundity *M(x)*	0.85	+/- 0.15
Carrying Capacity	50	+/- 25
a_f	0.0	+/-2.0
a_s	0.0	+/-2.0

The Generalised Cross Validation GCV-R^2 measure of fit is described in Chapter 4. A GCV-R^2 of 0.79 was obtained here. Table 6.2 describes the cost of omission of and relative importance of each

variable. The relative importance of the parameters is determined by comparing the estimated cost of omitting each parameter from the model. As this is a relative cost, the percentages will not sum to 100%.

Table 6.2 Meta-model results from the MARS regression.
This shows the cost of omission of each parameters and the relative percentage importance of each parameter.

Parameter	Cost of Omission	% Relative Importance
a_s	0.080	100.0
Carrying Capacity	0.077	96.3
Juvenile Survival *S(j)*	0.066	73.1
Adult Survival *S(a)*	0.060	57.3
Fecundity *M(x)*	0.050	0.00
a_f	0.050	0.00

In Table 6.2, it can be seen that the parameter a_s, representing the dependency of survival on rainfall, is the most important parameter followed by carrying capacity, juvenile and adult survival. Figure 6.6 shows the MARS meta-model prediction of the probability of extinction for two carrying capacities $K = 40$ and $K = 60$, under an assumption that both fecundity and survival are constant and not affected by rainfall. This enables these simulations to be directly compared with the constant survival estimates (assuming no movement) in this study and the study by Sharp (2002). The fecundity parameter *M(x)* is held constant at 1.0.

The survival estimate by Sharp (2002) and the survival estimate from Chapter 3 are marked as vertical lines in Figure 6.6. Sharp (2002) calculated a quarterly constant survival probability of 0.93 (95% CI = 0.91 to 0.95). This equates to a 12-monthly survival of 0.75, the joint probability of his quarterly estimates. From Chapter 3, the constant six-monthly survivals at Eregunda Creek and Wilkawillina Gorge are estimated to be 0.91 (95% CI = 0.83 to 0.96) and 0.82 (95% CI = 0.74 to 0.87) respectively using the *p(site), χ(site)* model. This equates to 12-monthly estimates of 0.83 and 0.67 respectively. The Wilkawillina Gorge survival estimate is much lower (0.67). Interestingly, the Wilkawillina Gorge site has an integrated pest control programme in place and yet Sharp's (2002) site and the Eregunda Creek site do not.

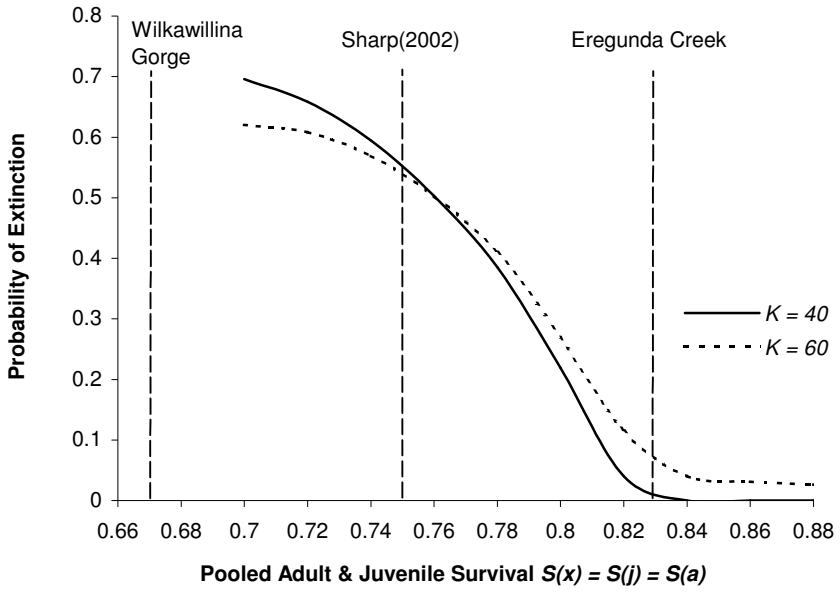


Figure 6.6 Probability of extinction in relation to the pooled adult and juvenile survival modifiers.

Figure 6.7 shows the probability of extinction in relation to parameter a_s for two carrying capacities K = 40 and K = 60, with the juvenile survival multiplier $S(j)$ = 0.85, the adult survival multiplier $S(a)$ = 0.85 and the fecundity parameter $M(x)$ = 0.85. Parameter a_f was held fixed at 0.0, although its contribution to the model was minimal. Similarly, the shape of the curves change little when $S(j)$, $S(a)$ and $M(x)$ are increased from 0.85. It can be seen that the influence of parameter a_s begins to diminish as K is increased.

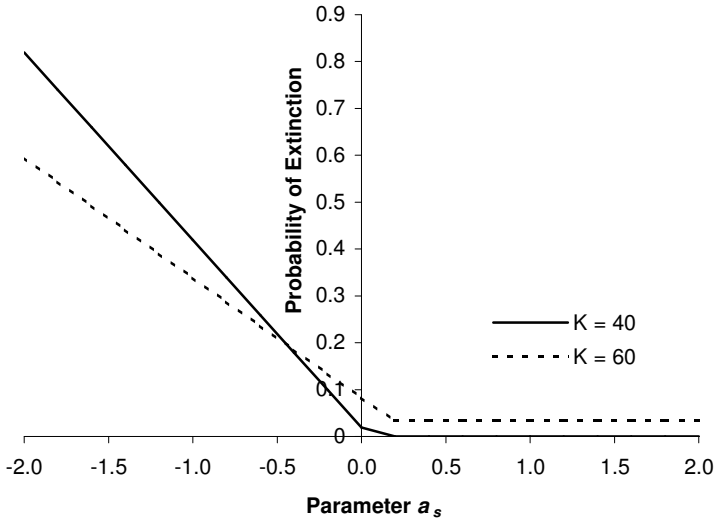


Figure 6.7 Probability of extinction in relation to parameter a_s

6.2.2 Spatial Scale Tests

Three different cell sizes of the same landscape were separately tested in the PVA model. These were 500 metres, 1000 metres and 1500 metres cells. The parameters in Table 6.4 were varied and a sensitivity analysis was conducted for each PVA model. For all of these tests, sub-adults disperse when the population exceeds 90% of carrying capacity. This avoided the imposition of artificial oscillations if they only dispersed at carrying capacity.

The simulation results were regressed using MARS with interactive effects allowed. The GCV- R^2 scores of the 500, 1000 and 1500 metre cell meta-models were 0.61, 0.66 and 0.68 respectively. These relatively low scores are a reflection of the very high percentage of extinctions predicted from the parameter ranges in Table 6.3. The relative importance and cost of omission of the parameters for each model are shown in Tables 6.4, 6.5 and 6.6 respectively.

Table 6.3 Parameters Varied in Scale Tests

Parameter	Value	Random Variation
Juvenile Survival *S(j)*	0.85	+/- 0.15
Adult Survival *S(a)*	0.85	+/- 0.15
Fecundity *M(x)*	0.85	+/- 0.15
Male Dispersal to chance survival (50%)	3000	3000
Female Dispersal to chance survival (50%)	3000	3000
Carrying Capacity	500m cells: 10	+/- 6
	1000m cells: 40	+/- 25
	1500m cells: 90	+/-56
Initial Population sightability factor	5.85	+/- 2.0

Table 6.4 Relative importance of parameters in the 500 m cell model.

Variable	Cost of Omission	% Relative Importance
Carrying Capacity	0.083	100
Juvenile Survival *S(j)*	0.057	69.0
Adult Survival *S(a)*	0.056	68.2
Fecundity *M(x)*	0.034	18.4
Initial Population I	0.033	9.5
Male Dispersal to 50% chance survival	0.033	0
Female Dispersal to 50% chance survival	0.033	0

Table 6.5 Relative Importance of parameters in the 1000 m cell model.

Variable	Cost of Omission	% Relative Importance
Juvenile Survival *S(j)*	0.179	100
Adult Survival *S(a)*	0.156	86.9
Carrying Capacity	0.096	34.6
Fecundity *M(x)*	0.092	26.8
Male Dispersal to 50% chance survival	0.085	0
Female Dispersal to 50% chance survival	0.085	0
Initial Population I	0.085	0

Table 6.6 Relative Importance of parameters in the 1500 m cell model.

Variable	Cost of Omission	% Relative Importance
Juvenile Survival *S(j)*	0.174	100
Adult Survival *S(a)*	0.16	92.6
Fecundity *M(x)*	0.086	27.1
Male Dispersal to 50% chance survival	0.079	0
Female Dispersal to 50% chance survival	0.079	0
Carrying Capacity	0.079	0
Initial Population I	0.079	0

Clearly as the cell size increases, the importance of carrying capacity diminishes from 100% for 500m cell sizes to 0% for 1500m cell sizes. To understand the reason for the diminishing importance of carrying capacity, an investigation of dispersal events, abundance and extinction of each of these models was conducted. Table 6.7 is a summary of the results of each model.

Table 6.7 Summary of the results of 500m, 1000m and 1500m models

Model	% Extinctions	Number of Dispersal Events	Average Realised Dispersal Distances (metres)	Average N after 60 years (if extant)
500 x 500m	91	2651	1621	60
1000 x 1000m	51	96,754	1213	271
1500 x 1500m	42	248,990	1848	521

Notable differences were found between the results of these three models, despite each having identical initial populations and average habitat quality indicies for the entire landscape. Clearly cell size has had a large effect on the number of dispersal events, the final population abundance (for populations extant after 60 years) and the probability of extinction.

The original habitat grid cell size in Chapter 4 was 30 metres. This has been progressively aggregated to three levels (500 metres, 1000 metres and 1500 metres). This effectively smoothes the habitat. Figure 6.8 is an arbitrary profile taken across the artificial landscape through the 1500m habitat grids and equivalent 500m habitat grids. The artificially smoothing the landscape changes the way in which and individual will select habitat during dispersal. This is discussed in detail in Section 6.3.2.

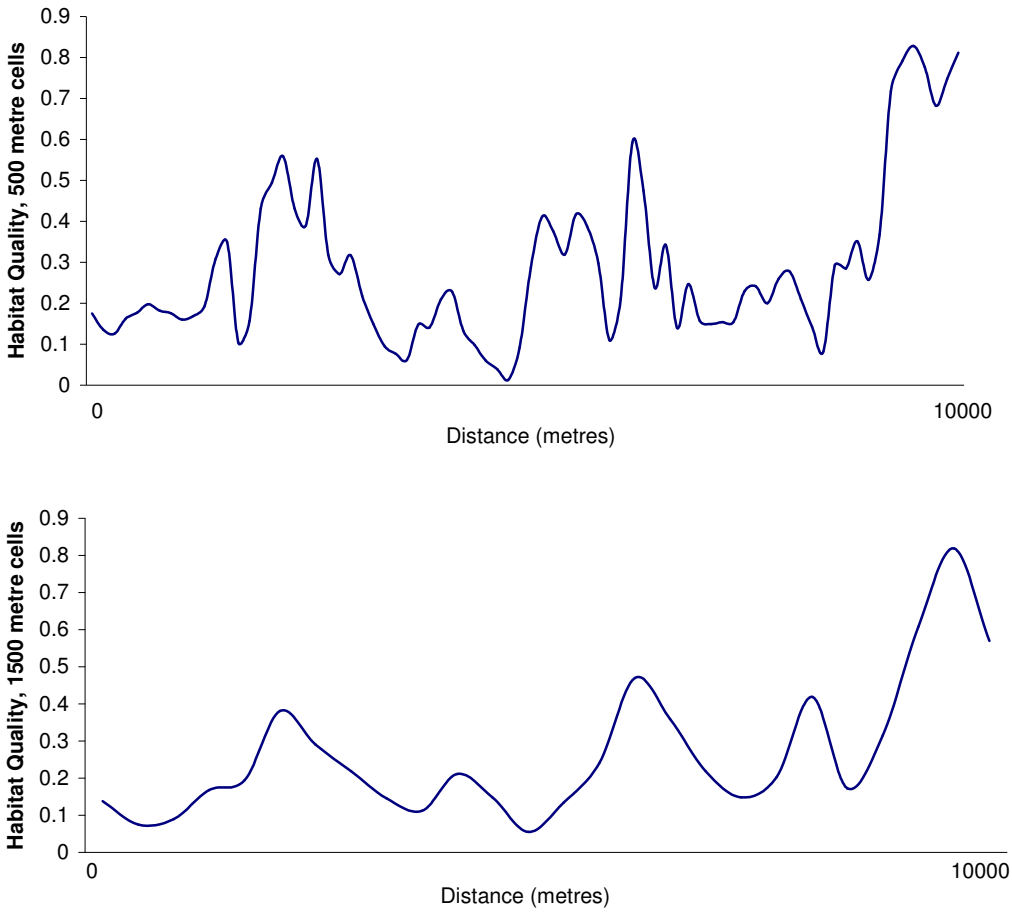


Figure 6.8 Arbitrary habitat quality profile through the landscape for 500m & 1500m cells

A 1000m cell size was finally selected for all of the PVA simulations that follow. The reasons for this decision are discussed in Section 6.5.2.

6.2.3 Model 1

In Section 6.2.2, dispersal events were triggered when the population exceeded 90% of the carrying capacity. In contrast to this assumption, the following model allows all sub-adults to disperse independent of the population density. The Allee parameter remained set to three cells. The cell correlation was held at 1.0. This means that the environmental variable has a global influence on all of the cells in the landscape. The carrying capacity was capped. Habitat quality scores of under 0.2 were again truncated. All other parameters were varied according to Table 6.3 for the purpose of sensitivity analysis. The GCV-R^2 of the MARS regression was 0.61.

Table 6.8, shows a lift in the importance of female dispersal compared with Table 6.5. Under the assumption that dispersal is not density dependent and all sub-adults attempt to disperse, female dispersal now appears to play a more important role in affecting the viability of the population.

Table 6.8 Relative Importance of the parameters in Model 1

Variable	Cost of Omission	% Relative Importance
Juvenile Survival *S(j)*	0.165	100
Adult Survival *S(a)*	0.137	80.9
Female Dispersal to 50% chance survival	0.104	47.4
Fecundity *M(x)*	0.093	29.2
Carrying Capacity	0.089	19.0
Initial Population	0.086	0
Male Dispersal to 50% chance survival	0.086	0

6.2.4 Model 2

Here the influence of catastrophes is tested. The cell correlation was also set to 0.8. The probability of a catastrophe was varied between 0% and 20%. This range of values is thought to reflect the extreme range of fire and drought events likely to occur in the region. In the advent of a catastrophe a variation of between 0% and 100% of patches could be affected. The reduction in carrying capacity due to any catastrophes was a decrease of 40%. Catastrophes could continue for up to two years. The carrying capacity was capped. Habitat quality scores of under 0.2 were truncated. Individuals disperse when the population exceeds 90% of the carrying capacity. The parameters variations are summarised in Table 6.9. The MARS regression GCV- R^2 was again 0.61.

Table 6.9 Summary of the parameters varied in Model 2

Parameter	Value	Random Variation
Juvenile Survival *S(j)*	0.85	+/- 0.15
Adult Survival *S(a)*	0.85	+/- 0.15
Fecundity *M(x)*	0.85	+/- 0.15
Male Dispersal to chance survival (50%)	3000	3000
Female Dispersal to chance survival (50%)	3000	3000
Carrying Capacity	40	+/- 25
Initial Population sightability factor	5.85	+/- 2.0
Probability of Catastrophe	0.1	+/- 0.1
Percentage of Cells affected by a Catastrophe	0.5	+/- 0.5

Table 6.10 Relative importance of the parameters in Model 2

Variable	Cost of Omission	% Relative Importance
Juvenile Survival *S(j)*	0.172	100
Adult Survival *S(a)*	0.145	81.1
Carrying Capacity	0.103	36.4
Probability of a catastrophe	0.111	47.6
Percentage of cells effected	0.111	47.6
Fecundity *M(x)*	0.099	27.6
Initial Population	0.093	0
Male Dispersal to 50% chance survival	0.093	0
Female Dispersal to 50% chance survival	0.093	0

Not surprisingly, increasing the effect of catastrophes raises the level of importance of catastrophes and carrying capacity (Table 6.10) when compared with Table 6.8 from Model 1.

6.2.5 Model 3

Model 3 has the cell correlation and catastrophes at the same settings as Model 2. However, dispersal is now no longer density-dependent and all sub-adults will attempt to disperse. All other parameters remain the same as Model 2 (see Table 6.11). The meta-model had a GCV- $R^2 = 0.57$. Table 6.12 shows the relative importance of each of the parameters.

Table 6.11 Summary of the parameters varied in Model 3

Parameter	Value	Random Variation
Juvenile Survival *S(j)*	0.85	+/- 0.15
Adult Survival *S(a)*	0.85	+/- 0.15
Fecundity *M(x)*	0.85	+/- 0.15
Male Dispersal to chance survival (50%)	3000	3000
Female Dispersal to chance survival (50%)	3000	3000
Carrying Capacity	40	+/- 25
Initial Population sightability factor	5.85	+/- 2.0
Probability of Catastrophe	0.1	+/- 0.1
Percentage of Cells affected by a Catastrophe	0.5	+/- 0.5

Table 6.12 Relative Importance of the parameters in Model 3

Variable	Cost of Omission	% Relative Importance
Juvenile Survival *S(j)*	0.153	100
Adult Survival *S(a)*	0.127	79.0
Female Dispersal to 50% chance survival	0.092	37.6
Probability of a catastrophe	0.093	39.5
Percentage of cells effected	0.093	39.5
Fecundity *M(x)*	0.085	20.2
Carrying Capacity	0.082	0
Initial Population	0.082	0
Male Dispersal to 50% chance survival	0.082	0

In Table 6.12, the carrying capacity is lower than Table 6.10 in Model 2. This is consistent with the effect of letting all sub-adults disperse in Model 1 compared with the 1000 metre model in Section 6.2.2.

In summary, these results show that juvenile survival and adult survival are consistently the most important parameters that influence the probability of extinction and that the influence of other less important parameters depended upon the assumptions one uses in the model. However, two parameters were not altered during theses simulations. Firstly, the Allee parameter was set to three for all simulations and the effect of changing this parameter was not tested. Secondly, in the previous simulations all dispersers were assumed to be active dispersers with this parameter set to ten.

Conversely, a passive disperser moves randomly from cell to cell. In this case, the parameter is set to zero. In a separate set of simulations, passive dispersal strategies were tested along with the assumptions in the previous models. These results have not been reported but again showed that juvenile survival and adult survival remained the most important parameters.

6.2.6 Dispersal and Landscape

The direct (or 'crow flies') distance each dispersing individual has travelled is tracked by the model. This has been coined the 'realised dispersal distance'. The following simulations used the parameter settings in Table 6.3 and the 1000 metre cell model. Figure 6.9 shows the relationship between the mean realised dispersal distance for each simulation and the variance in realised dispersal distance for each simulation. Clearly the mean is proportional to the variance, indicating the data are statistically over-dispersed (i.e. distributed contagiously), resembling a Poisson distribution. The circles represent active dispersers with a search parameter = 10.0. The crosses represent passive dispersers with a search parameter = 0.0 from a separate 10,000 simulations. Passive dispersal is when individuals do not actively choose their habitats during dispersal but move in random directions. The passive dispersal strategy exhibits larger variances for the same mean.

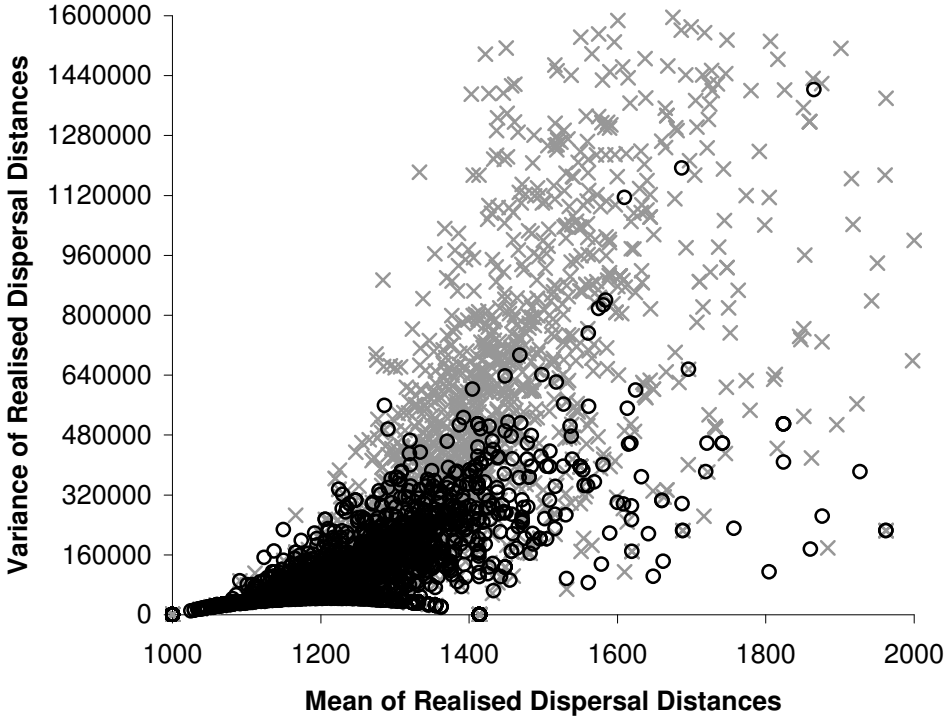


Figure 6.9 Relationship between the mean realised dispersal distance and the variance in realised dispersal distance.

The circles represent active dispersers (search parameter = 10.0) and the crosses represent passive dispersers (search parameter = 0.0).

Figure 6.10 shows the relationship between average realised dispersal distances and abundance after 60 years for passive and active dispersers.

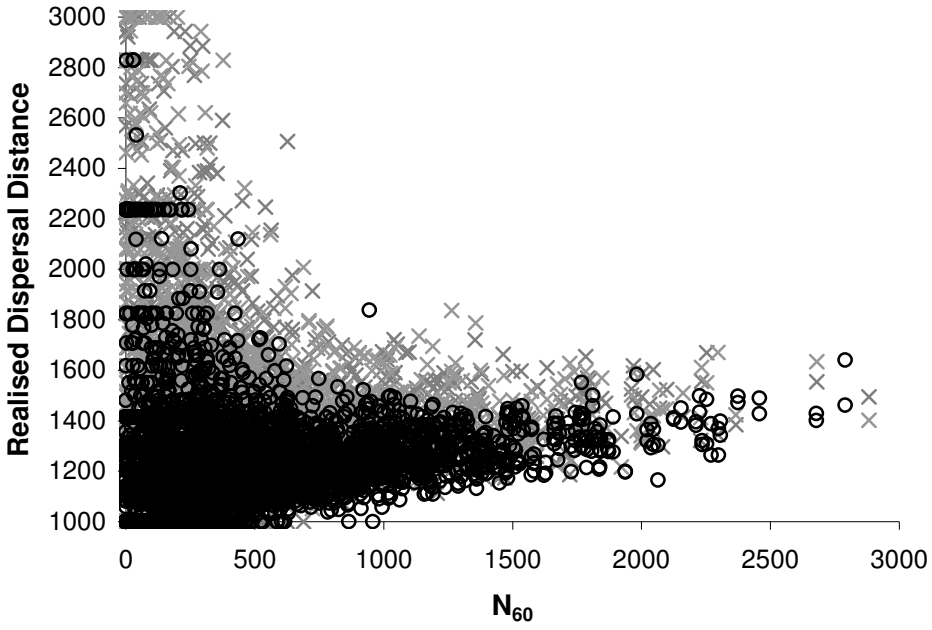


Figure 6.10 The final abundance N at year 60 versus the average realised dispersal distance (metres) over the entire period.

Here the dots represent passive dispersal (dispersal search parameter =0) and the circles are from Figure 5.12 where dispersal is active (dispersal search parameter =10).

Not surprisingly, the passive dispersal distances (depicted as crosses) in Figures 6.9 and 6.10 are more scattered than the active dispersal distances (depicted as circles). This shows that random dispersers can potentially travel further before they settle in suitable habitat.

6.2.7 Inbreeding Potential

The inbreeding potential in the area around Mt Stuart (Figure 6.5) was simulated using Wright's Equation and separately by using pedigrees. Simulating pedigrees is computer intensive and to reduce processing time, these simulations were limited to a 32 year period and 2000 simulations. Figure 6.11 shows the accumulated inbreeding F from a 32 year simulation where the maximum carrying capacity of the cell, $K = 40$. The dispersal search parameter was set at 10 to indicate active dispersal, and sub-adults only dispersed when the population in each cell approached carrying capacity. Table 6.13 lists all of the other parameter settings. No individuals were found to have immigrated into this site in 2000 simulations. The dashed line in Figure 6.11 represents the

accumulation of inbreeding at Mt Stuart simulated using Wright's equation (Equation 5.8). The primary assumption of this equation is that mating is random. Clearly this approach overestimates F when compared with the solid line representing the accumulation of inbreeding using simulated pedigree data.

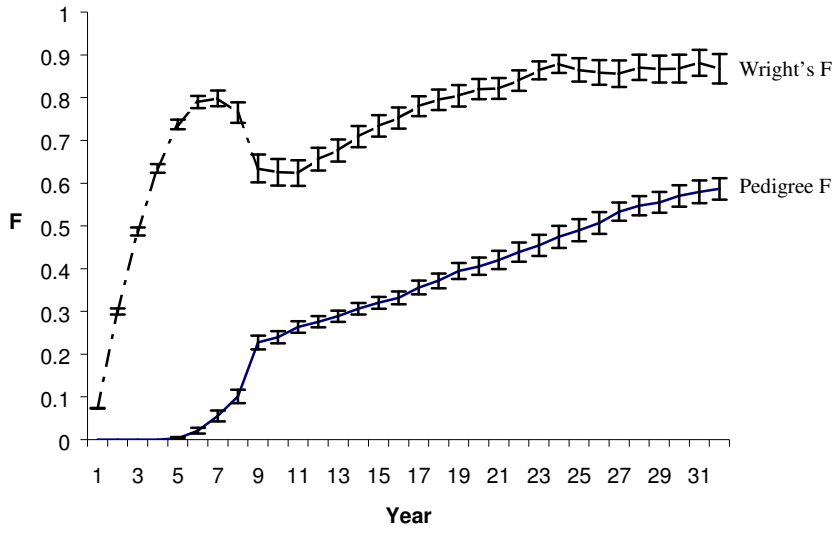


Figure 6.11 Inbreeding coefficient (F) over 32 years with no immigration and K =40 for Mt Stuart

The dashed line and 95% confidence bars represents the accumulation of inbreeding estimated using Wrights Equation (Equation 5.8). The solid line represents inbreeding estimated from pedigree simulations.

Table 6.13 Parameters varied for inbreeding tests

Parameter	Value	Random Variation
Juvenile Survival *S(j)*	0.85	+/- 0.15
Adult Survival *S(a)*	0.85	+/- 0.15
Fecundity *M(x)*	0.85	+/- 0.15
Male Dispersal to chance survival (50%)	3000	3000
Female Dispersal to chance survival (50%)	3000	3000
Carrying Capacity	40	+/- 25
Initial Population sightability factor	5.85	+/- 2.0

Similarly Figure 6.12 is an example of a 32 year simulation having the same parameter settings but where the maximum carrying capacity of the cell was set to K = 80. Again, no individuals were found to have immigrated into this site in 2000 simulations.

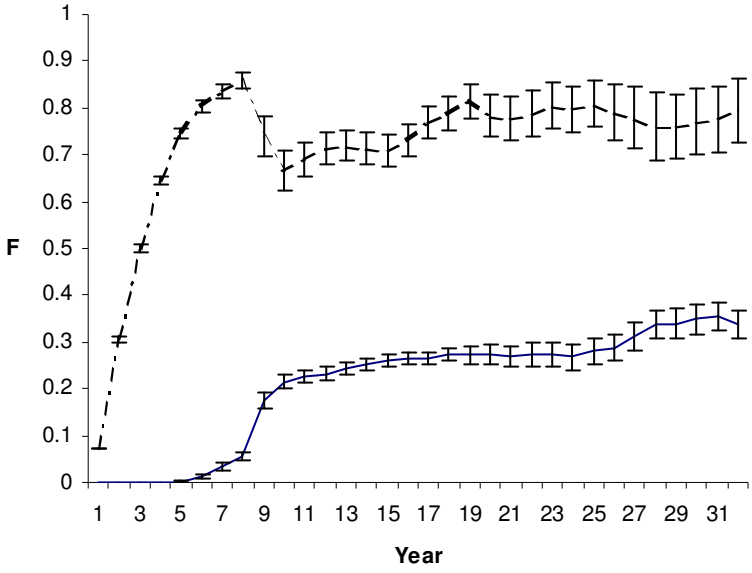


Figure 6.12 Inbreeding coefficient (F) over 32 years with no immigration and K =80 for Mt Stuart

The dashed line and 95% confidence bars represents the accumulation of inbreeding estimated using Wrights Equation (Equation 5.8). The solid line represents inbreeding estimated from pedigree simulations.

The dispersal search parameter was then set to zero. This simulates the individual randomly moving from cell to cell. The results were almost identical to Figures 6.11 and 6.12 using the pedigree method and the Wright equation. Consequently, these graphs have not been shown. In all cases, estimates of F after 32 years are consistently higher than estimates using the pedigree simulations. Interestingly, in all cases there were significant differences in the first ten years in the shape of these two curves. This is likely to be due to the age and sex structure in the population taking some time to stabilise. The random mating model ignores these effects.

Table 6.14 summarises a repeated number of model simulations that were conducted using a range of assumptions related to the way in which individuals select habitat, carrying capacity and the level of fragmentation in the landscape. In all cases active dispersers have a dispersal search parameter of ten and passive dispersers have a search parameter of zero. The results in Table 6.15 are from models that assume sub-adults disperse as the population exceeds 90% of the carrying capacity.

Table 6.14 Mean inbreeding estimates (F) after 32 years under different assumptions.

Dispersal Search Effort	Maximum carrying capacity	Habitat	Mean F_{32} from pedigree simulations	Mean F_{32} using Wright's equation
Active (10.0)	K=40	Default model	0.586	0.858
Active (10.0)	K=80	Default model	0.326	0.762
Passive (0.0)	K=40	Default model	0.531	0.860
Passive (0.0)	K=80	Default model	0.522	0.745
Active (10.0)	K=40	Fragmented	0.592	0.857
Active (10.0)	K=80	Fragmented	0.351	0.759
Passive (0.0)	K=40	Fragmented	0.565	0.852
Passive (0.0)	K=80	Fragmented	0.486	0.722

The mean values of F in Table 6.14 are calculated from all 2000 simulations after 32 years. These are the result of varying the parameters according the ranges specified in Table 6.13. Inbreeding depression will be lower when there are a larger number of animals in the area or a sufficient number of immigrants. Both immigration and population abundance in the area are highly correlated because they are both regulated by vital rates *S(j), S(a)* and *M(x)*. In order to be able to tease out these interactions, graphs relating immigration to the vital rates, F to dispersal realized distance and F to immigration have been analysed.

As previously mentioned, tracking pedigree information significantly increased the computer processing time. Conversely, calculating the cumulative effects on F using Wright's approach (Equation 5.8) incurs no noticeable delays in computer processing time. As such, 10,000 simulations were repeated for each scenario in Table 6.14 using only Wright's random mating model (Equation 5.8). Only the final estimate of F after 32 years was noted. For simplicity, the vital rates *S(j), S(a)* and *M(x)* are also pooled as one statistic, calculated as their joint probability. Having dramatically reduced processing time, it was also possible to test the effects of the assumption that all sub-adults disperse independently of population density.

Figure 6.13 shows the result of simulations where sub-adults are allowed to disperse only when the population in each cell approached carrying capacity. Here dispersers actively select from the surrounding cells in each move (i.e. the search parameter was set to ten). No immigrants were found to enter the area. At first glance, the decrease in F appears to decrease as the average realised dispersal distances increases in Figure 6.13. However given that there were no immigrants, this is not the result of a causal relationship, it is because both the realised dispersal distance and the abundance of the population independently increase with the joint probability of S(j), S(a) and M(x) increases. Inbreeding is therefore decreasing as the abundance in the area increases not immigration.

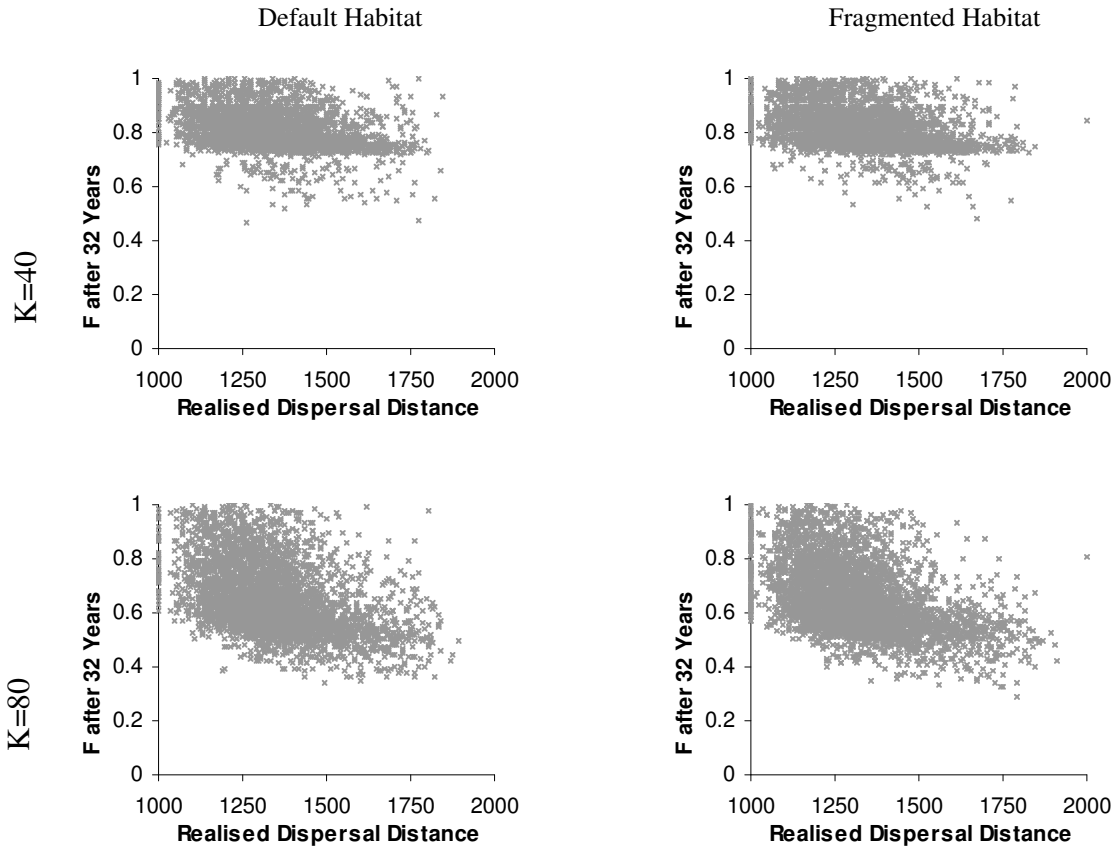


Figure 6.13 Estimate of Wright's inbreeding coefficient in the area versus average realised dispersal distance.

K represents the maximum carrying capacity attainable for habitats scoring 1.0. Individuals actively select habitat = 10. Sub-adults only dispersed when the population in each cell approaches carrying capacity.

The Figure 6.13 results are based upon the assumption that dispersers actively search for better habitat. Figures 6.14 and 6.16 describe the results when dispersal is passive and each individual moves randomly through the landscape (i.e. dispersal parameter = 0.0). Figure 6.14 shows a significant increase in the number of immigrants moving into the quarantined area under passive dispersal strategy. This suggests that a substantial number of individuals are now crossing marginal habitats. Figure 6.14 also indicates that there is little difference between the number of individuals immigrating in the default habitat compared with the fragmented habitat. Carrying capacity appears to limit the number of immigrants.

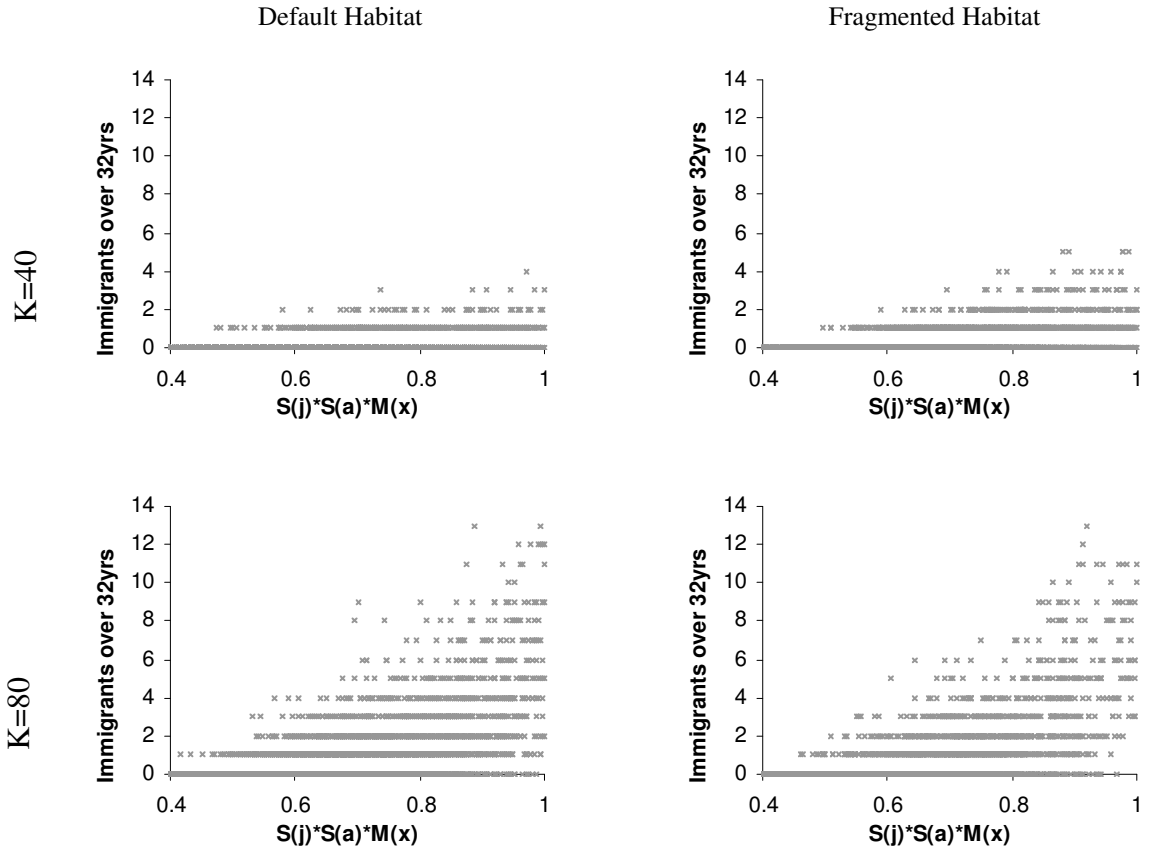


Figure 6.14 Number of immigrants verses the joint probability of S(j), S(a) and M(x).

K represents the maximum carrying capacity attainable for habitats scoring 1.0. Search parameter =0. Sub-adults only dispersed when the population in each cell approaches carrying capacity.

Figure 6.15 appears to show more strength in the relationship than the result of an active dispersal strategy. Again there is little difference between the distribution of data in the fragmented and default landscapes.

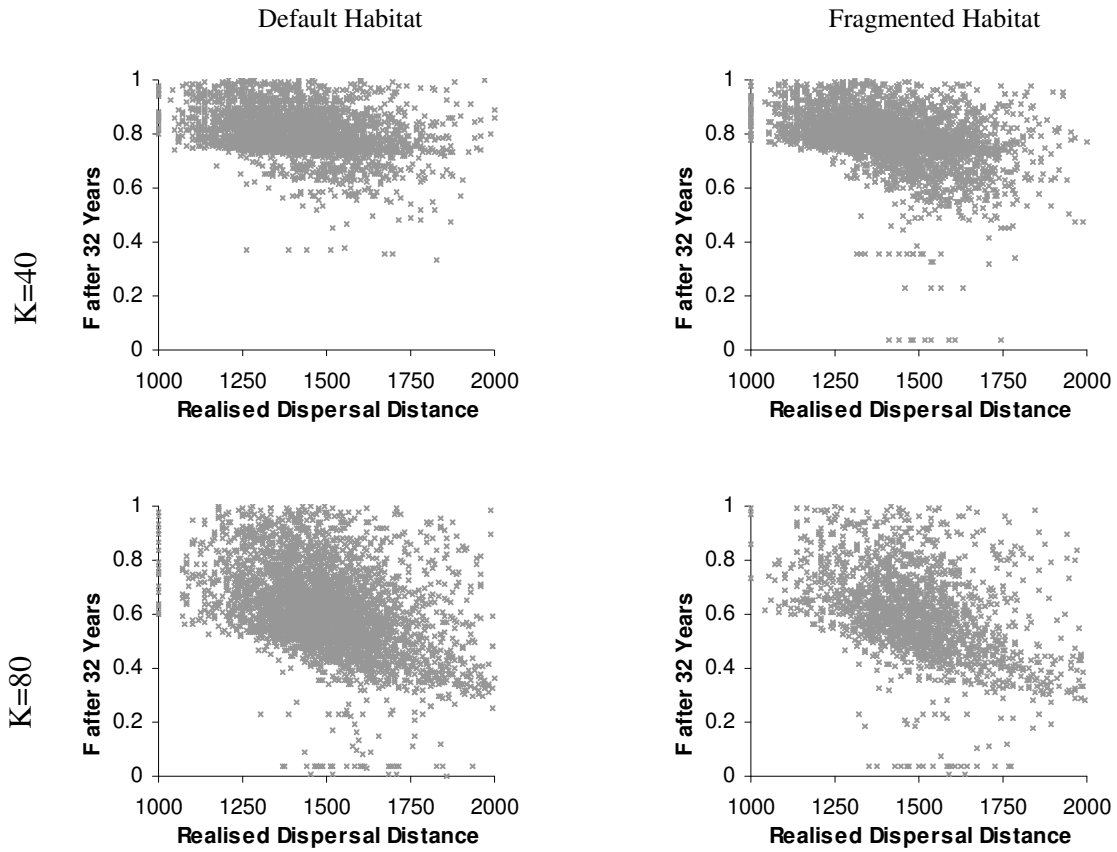


Figure 6.15 Estimate of Wright's inbreeding coefficient in the area verses average realised dispersal distance.

K represents the maximum carrying capacity attainable for habitats scoring 1.0. Search parameter =0. Sub-adults only dispersed when the population in each cell approaches carrying capacity.

Increasing the carrying capacity now appears to have some impact on the inbreeding estimates in the area.

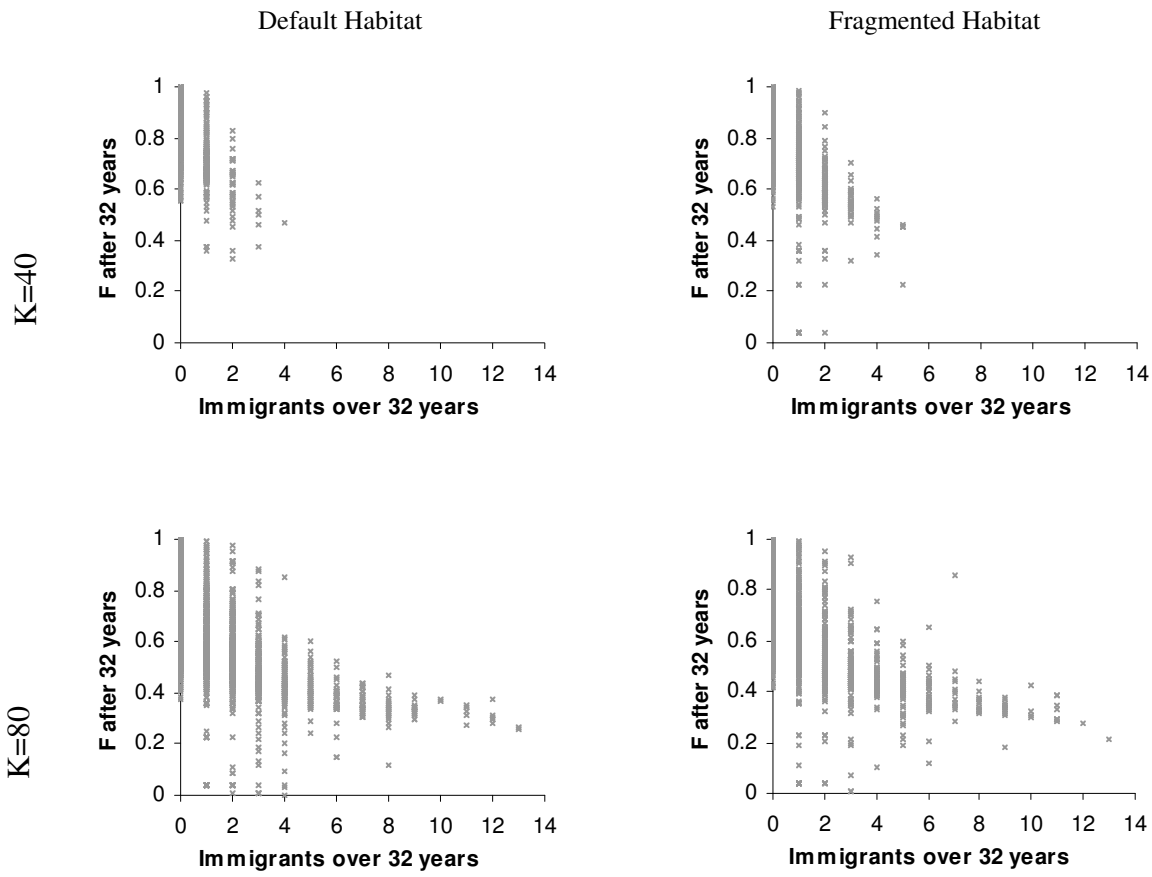


Figure 6.16 Estimate of Wright's inbreeding coefficient in the area verses the number of immigrants entering the area for passive dispersers.

K represents the maximum carrying capacity attainable for habitats scoring 1.0. Search parameter =0. Sub-adults only dispersed when the population in each cell approaches carrying capacity.

Here dispersers actively search the landscape but all sub-adults disperse regardless of the population density. This has little effect on the number of immigrants. Figure 6.17 now shows the number of immigrants entering the area in the default habitat configuration. Almost no immigration is evident when the landscape is fragmented.

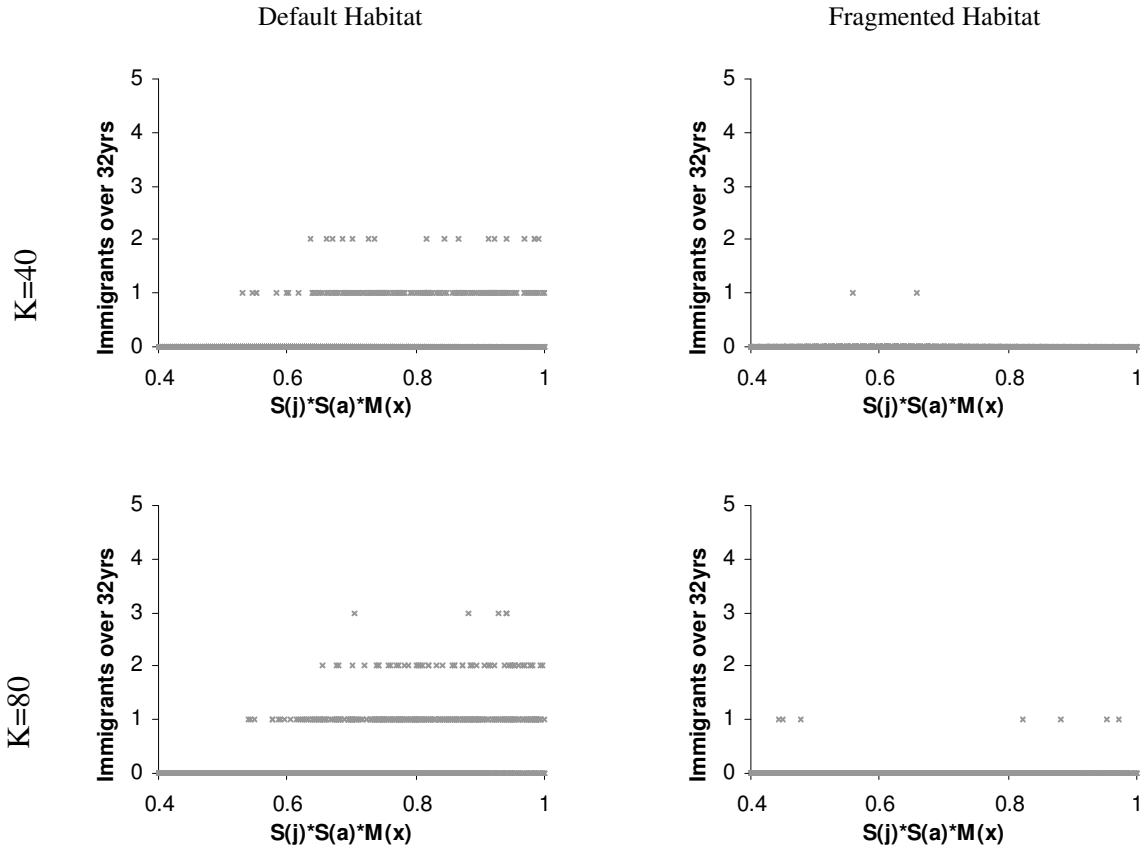


Figure 6.17 Number of immigrants versus the joint probability of S(j), S(a) and M(x).

K represents the maximum carrying capacity attainable for habitats scoring 1.0. Individuals actively select habitat = 10. All sub-adults disperse regardless of the population density in relation to carrying capacity.

The final model assumes that all sub-adults disperse regardless of the current carrying capacity and that dispersal is passive. In Figure 6.19, there is a strong exponential relationship between the number of immigrants and the joint probability of vital rates.

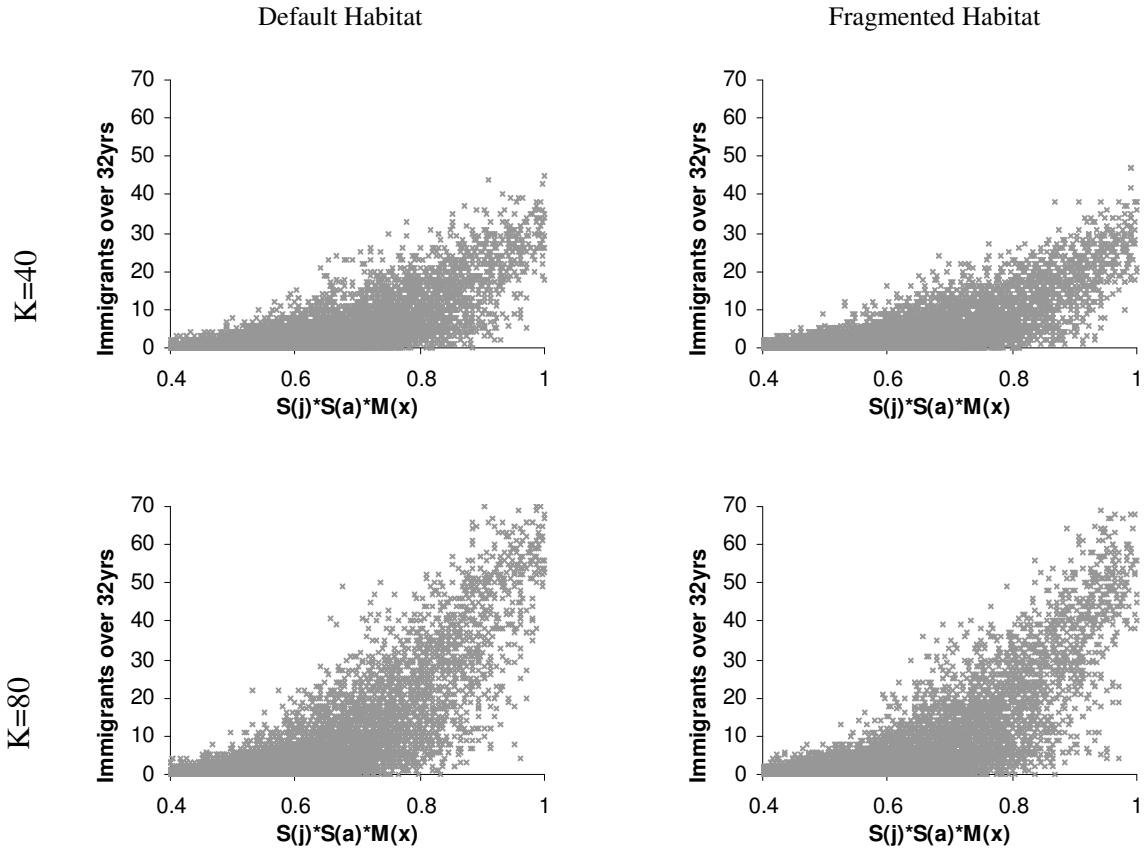


Figure 6.19 Number of immigrants versus the joint probability of S(j), S(a) and M(x).

K represents the maximum carrying capacity attainable for habitats scoring 1.0. Search parameter =0. All sub-adults disperse regardless of the population density in relation to carrying capacity.

Figure 6.20 also shows a strong relationship between F and the number of immigrants.

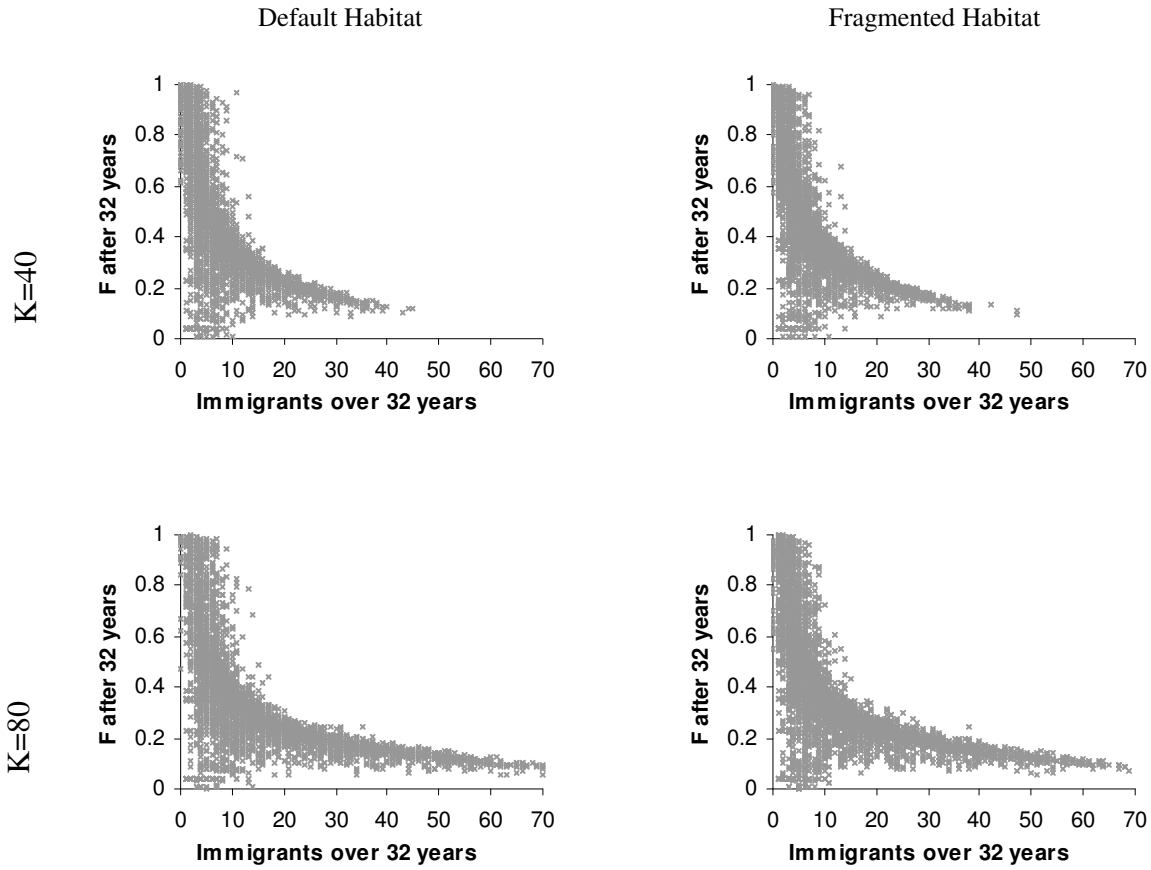


Figure 6.20 Estimate of Wright's inbreeding coefficient in the area versus the number of immigrants entering the area for passive dispersers.

K represents the maximum carrying capacity attainable for habitats scoring 1.0. Search parameter =0.

All sub-adults disperse regardless of the population density in relation to carrying capacity.

6.3 Discussion and Summary

This chapter presented the application of a new PVA programme to help answer three questions related to the population dynamics of *P. x. xanthopus*. The first question related to the apparently insignificant differences found between the survival estimates from mark recapture data. Here a closed population was simulated to ascertain the effect of these differences on the probability of extinction. The strength of the relationship between survival and rainfall was also analysed to ascertain the effect this has on extinction.

Spatially explicit PVAs employing a habitat quality layer enable one to test the effects of the landscape configuration and dispersal on the population's viability. Following a series of tests related to the effect of different cell sizes, three models were tested to assess the relative importance of key parameters on the viability of *P. x. xanthopus* in the Flinders Ranges, South Australia in order to help guide the future management of the metapopulation in this area.

A unique feature of the PVA described in Chapter 5, is its ability to test the relative effects of different landscape configurations and dispersal strategies on inbreeding depression. While little is known about how this species moves through the landscape, inbreeding simulations provided some insights about the effects of different dispersal strategies. This is meant to help prioritise further research.

6.3.1 Local Population Survival

These simulations focused on a hypothetical local population. To isolate the effect that demographic processes have on the probability of extinction, movement was ignored. Survival was the most important parameter that influenced the probability of extinction.

The survival estimates from Sharp (2002) and Chapter 3 are confounded by animals emigrating from these sites and in the absence of other information, the fate of these individuals is unknown. However, Pope et al (1996) and Sharp (2002) have suggested that the movement of this species is limited and in Chapter 3 it was reported that only two individuals were assigned as having moved between Wilkawillina North and South using genetic data (see Section 3.6.3).

It is therefore temping to assume that there is little movement. If this is the case, the comparisons in Figure 6.5 indicate that Sharp's (2002) population has a 55% chance of extinction whereas the Eregunda Creek population has less than a 10% chance of extinction. On this assumption, the

Wilkawillina South estimate has a high probability of extinction. However, in Chapter 2, the aerial estimates did not indicate a declining population over the entire Wilkawillina Gorge of several kilometres (see Figures 2.9 and 2.10 in Chapter 2), which contradicts the results above.

One explanation is that there is transient movement within Wilkawillina Gorge. This is partially evident in Figure 2.13 of Chapter 2. Here a univariate kernel density smoothing technique was used to describe the univariate densities recorded along the flight line each year over five years. While noisy, there is some evidence of transient movement over the period of the mark recapture sampling within the Wilkawillina Gorge. This movement could account for the lower estimates of survival at the Wilkawillina South trap site.

The shift in the univariate densities also coincides with a drought, when Park staff reported much activity from other herbivores around the water holes near the Wilkawillina South trap site. This may have driven some animals away from this site, lowering the mark recapture estimates of survival. Regardless of whether individuals may have died or departed from the site during this time, there is some cause for concern about the conditions that have influenced mortality or emigration given that Sharp's (2002) site and the Eregunda Creek site were not subject to fox control and the Eregunda Creek site has only limited goat control. Unfortunately, pest abundances were not measured at Eregunda Creek and hence the evidence of goat and fox pressure is qualitative. Moreover, these results highlight the need to narrow the uncertainty of survival estimates and, given the relatively small number of animals sampled, attempt to measure movement.

Varying parameters a_s and a_f was intended to simulate different microclimate characteristics. For example, in a complex rock formation the microclimate afforded by the rocks will maintain resource availability throughout a dry period and may have less of an influence on survival and fecundity. This is indicated in Figure 6.7, which shows the population is particularly vulnerable at sites where there is little or no microclimate and where the resources fluctuate strongly with rainfall. Table 6.2 also shows that the effect of microclimate on survival a_s, is more important than *S(j), S(a), M(x)*, carrying capacity and the fecundity microclimate parameter a_f . Hence highly variable environmental conditions will decrease population persistence (Lande, 1993; Shaffer, 1987; White, 2000). This finding suggests that future monitoring and management of this species should pay closer attention to the microclimate afforded in different habitats and monitor survival in relation to rainfall. The effects of rainfall are only anecdotal so it is vitally important that resource abundance surveys are conducted in conjunction with mark recapture studies.

6.3.2 Scale Effects

To test the relative effect of different cell sizes on the spatially explicit predictions, a sensitivity analysis was conducted of the parameters in Table 6.3 for three different cell sizes, 500 x 500 metres, 1000 x 1000 metres and 1500 x 1500 metres. Noticeably different results were found between these three models. These differences are also evident in Table 6.7, which shows the average dispersal distances and number of extinctions for each model.

As previously mentioned, the original habitat grid cell size in Chapter 4 was 30 metres. This was progressively aggregated to the cell sizes used in the PVA. Much of difference in the results obtained for the three cell sizes can be explained by mathematical round-off errors. For example, four 500 metre cells each having a habitat quality each of 0.4 with K_{500} = 4, would each support 1.6 individuals (0.4 x 4). However, this would be rounded down by the model to one individual in each cell giving a total of four individuals. However the equivalent 1000 metre cell with an average quality of 0.4 supporting K_{1000}=16 (4 cells x K_{500}) individuals would support 6.4 individuals, which rounds down to six.

The difference in the dispersal results for each cell size is also likely to be the result of an artificial reduction in the level of fragmentation. As the cells are increased in size the habitat quality indexes become more aggregated. Figure 6.8 illustrates this phenomenon. For example, using the 500 metre cell landscape, an individual dispersing from a high quality habitat that encounters a very low quality habitat adjacent its natal cell, would have to disperse further to find suitable habitat. In smoother landscapes this effect is reduced. As the lower quality scoring cells less than or equal to 0.2 were reduced to zero, this compounds the effect of fragmentation. However, as the cells sizes become larger, the average dispersal distance is also forced upward because an individual cannot disperse a distance less than the cell size. These two competing forces are evident in Table 6.7 where individuals in the 1000 metre cell landscape have, on average, dispersed shorter distances than both the 500 metre and 1500 metre cell landscapes.

Sharp (2002) calculated an average home range for this species of 18 to 20 hectares. He found a 64% overlap of 18 individuals for a colony home range of approximately 117 hectares. This is the equivalent of approximately four animals in a 500 metre cell, 15 animals in a 1000m cell, and 35 animals in a 1500 metre cell. Other individuals not trapped or radio-collared may have also shared this area. Carrying capacity is difficult to measure. Consequently, these was no attempt to calculate

it in this study or by Sharp (2002). Hence the carrying capacity in the 117 hectares in Sharp's study may have been higher than 18 individuals.

The structure of this model allows a population to occupy each cell as opposed to models specifically designed to allow only one individual to occupy each cell. Sharp's figures therefore suggest that it is unlikely that a cell size close to an individual's home range is suitable for this model. Conversely, the 1500 metre cells significantly smoothed the landscape and artificially increased the dispersal distance. On the weight of this evidence and the results from Table 6.7, it was decided that the 1000 metre cell landscape would be more suitable than both the 500 metre and 1500 metre landscapes in any further simulations.

6.3.3 Spatially Explicit Models

The clearest generalisation that emerged here is that despite the models having different assumptions, juvenile survival and adult survival were consistently the most important parameters that influenced the probability of extinction. Ranking parameter importance helps set priorities for the future management of the species. These findings show that the factors that directly affect individual survival (*S(j)* and *S(a)*), particularly juvenile survival, should be a priority for management. Given that juvenile survival is known to be affected by predation intensity (Hornsby, 1995; Lim, 1983; Lim and Giles, 1987; Sharp, 2002; Sharp and Norton, 2000), fox control is likely to be an important management priority. However, the multipliers, *S(j)* and *S(a)* also represent the effects of competition for resources, suggesting that further monitoring needs to focus on the effects of both predation and competition (e.g. introduced herbivores) on survival.

The importance of all other parameters were found to vary according to the assumptions that underpinned each model. Not surprisingly, an increase in the severity of catastrophes in Model 2, increased their level of importance above fecundity and dispersal (see Table 6.10). Interestingly, all model variations revealed a relatively low contribution to the viability of population from male dispersal. This may be because males do not have to move out quite as far out as females for a new cell to have a positive growth rate. Assume a given male disperses from the same natal cell and moves in the same direction as a given female. Assuming the Allee parameter is set to three cells, if the male disperses a shorter distance than a female by one cell, this is still sufficiently close to the female for her to breed. Given that dispersal in macropods is likely to be male biased (Johnson, 1989; Sharp 1997), these simulations appear contradictory. This is because they fail to indicate the other role of dispersal: gene flow.

6.3.4 Dispersal and Inbreeding

Inbreeding usually leads to "phenotypic abnormalities, resulting in a loss of fitness through lower viability or fertility" (Perrin and Goudet, 2001 p125). Unfortunately, few spatially explicit PVAs model inbreeding. This relatively new approach has the potential of closing the gap between the disciplines of genetic science and population ecology. Dispersal in this study was confined to natal dispersal. This is defined here as a complete departure from in the natal cell (or patch) by sub-adults. The realised dispersal distance is the direct (or 'crow flies') distance from the source to destination cell for each individual.

Figures 6.9 and 6.10 provide an indirect measure of the spatial distribution of dispersers in relation to their source patches. In both figures there is a greater spread of realised dispersal distances for passive dispersers. This indicates that passive dispersers potentially move further in the landscape across less favourable habitats.

In attempting to better understand the effect of dispersal on inbreeding more specifically, a small zone in the landscape was windowed to study the effects of immigration on the inbreeding coefficient (F) in this area. No additional restrictions were placed on the individuals in this zone and they were allowed to immigrate and emigrate in and out of the zone.

Two distinctly different inbreeding models were compared. The first approach tracked individual mating pairs in the zone over the simulation period. This approach follows the work carried out by Daniels et al (2000). The rules governing mating pairs were outlined in Section 5.5.6. Falconer and Mackay (1996) suggest that although the rate of inbreeding will be reduced if close relatives do not mate, this only delays the first increment of inbreeding and does little for reducing subsequent rates of inbreeding. In light of their findings and in the absence of empirical information, siblings were allowed to mate when there were no other individuals available because some of these habitats are known to support very few animals and, in light of no other evidence, under these conditions they may be forced to mate. There is also no evidence to support or deny parent-child mating when numbers are low. While this was prevented from occurring in the model it is not likely to have made much difference to the result.

The second approach assumed mating was random and used Wright's (1931; 1951) equation (Equation 5.8) to calculate an average inbreeding coefficient. Like the pedigree approach, founders and immigrants are assumed to be unrelated. Both the pedigree and random approaches effectively calculate a relative measure of inbreeding with F starting at zero in year one.

The results from Figures 6.11 and 6.12 in Section 5.7.3 showed that the random mating model significantly overestimates the inbreeding coefficient in the quarantined area. This is because of the breeding constraints in the pedigree simulations. For example, females cannot mate with a father or son in the pedigree model. So a limited membership of males (other than the dominant male) in breeding pool is likely to reduce the average relatedness in the population. One major flaw in both approaches is that they assume any immigrants are unrelated to the resident population (Ball, 2000).

There was no direct correlation between the estimates of F derived from pedigree simulations and F calculated from Equation 5.8. Nevertheless there was some agreement between the two techniques. For example, lower carrying capacities are generally associated with a higher estimate of F using both methods. This is because higher carrying capacities generally increase the population sizes depending upon the vital rates. Consequently, inbreeding is reduced as the population size increases and the estimate of F is always higher for K=80 as compared with K=40 across the range of vital rates (in these models, *S(x), S(a) and M(x)*) specified in Table 6.13.

Inbreeding depression is affected by immigration into the quarantined area and the number of residents in the quarantined area. Given that immigration and population abundance are both likely to be controlled by other parameters such as dispersal distance and vital rates, they are also highly correlated. To better understand these interactions, graphs relating immigration with the vital rates (*S(j), S(a)* and *M(x)*), F and realised dispersal distance and F and immigration were analysed. These were compared using Wright's random mating model.

Four scenarios were tested. The active and passive disperser assumptions were modelled with the two dispersal trigger assumptions (subadults dispersing when the population exceeded 90% of the carrying capacity and subadults always dispersing). Only when dispersal was passive and all sub-adults dispersed, was there a significant increase in the number of immigrants and reducing in inbreeding. However, Figures 6.11 and 6.12 indicate that if a pedigree model had been used in these tests, the estimates of inbreeding might have been even lower because Wright's random breeding model over-estimated inbreeding when compared with the pedigree simulations.

Little is known about the factors that trigger dispersal in this species and yet the inbreeding simulations show that these factors and the extent to which the individuals search the habitat, has a large effect on inbreeding in an isolated population. Measuring these two factors is an important direction for future research. Conversely, the probability that an individual survives a given dispersal distance was not an important factor in the inbreeding simulations, although this did increase in

importance 'marginally' under the assumption that all sub-adults disperse despite the population density.

6.3.6 Assumptions and Limitations

Brook et al (2002) suggest PVA helps set priorities and provides a framework that ensures an internal consistency of arguments that reduces subjective and intuitive interpretations. PVA is also provides a framework in which theoretical assumptions can be explored and their management implications can be better understood.

In this study, PVA was used to rank the relative contribution of parameters to the viability of the population. This is more robust to model and input data uncertainty than absolute predictions of extinction times (Akçakaya and Raphael, 1998; Lindenmayer and Possingham, 1996; McCarthy et al., 2003; Possingham et al., 1993). However, despite the emphasis on relative parameter contribution, there remain two primary sources of error. The first source of error relates to the data that underpin the model. The second source of error relates to the construction of the model and the assumptions upon which it rests. Firstly, the central values around which the input parameters were varied and the range of these variations may have been inappropriate. For example, the juveniles survival multiplier *S(j)* was varied from 0.7 to 1.0. If these ranges were set at, say 0.6 to 0.9, this may yield slightly different results and shift the relative importance of this parameter.

Other variables including the landscape data were also assumed to be correct. For example, the parameter *K* stipulates carrying capacity. This is the number of animals that can live in a 1.0 quality habitat cell. When multiplied by the habitat quality index in each cell, this figure defines the maximum number of animals allowed in that cell. However, the habitat quality grid cell values have been derived from presence and absence data, and the habitat quality may not be a true reflection of the population density likely to be supported by the habitat. Moreover, the habitat model in Chapter 4 is a probability distribution model not a habitat quality model.

Models are purpose built. Unfortunately, this can create a 'self fulfilling prophecy' and assumptions may bias the results according to what the researcher believes to be true (Funke, 1995). To avoid the risk of presenting PVA as a 'truism' based upon a predetermined position, Burgman and Possingham (2000) stress the importance of clearly and thoroughly communicating the uncertainties, assumptions and limitations of any model. This includes identifying sources of contention, critical assumptions and constraints. Some of the system constraints and assumptions of the model have been raised in Chapter 5. However, some of the constraints and assumptions relate directly to *P. x. xanthopus*.

Firstly, density dependence in this study follows the algorithm in ALEX (Possingham and Davies, 1995) where the population is capped randomly back to the carrying capacity for each cell. This is a relatively coarse representation of density dependence because survival is not influenced by population density until the population reaches carrying capacity. The advantage of this approach is it is based upon fewer assumptions and requires less computer processing. Nevertheless, little is known about the exact way in which density dependence influences *P. x. xanthopus* and alternative approaches were not explored. This may have affected the level of importance of carrying capacity on the probability of extinction.

Burgman et al (1993) suggest that a major limitation of single species models is that they ignore interactions with other species including predation, mutualism and competition (Burgman et al., 1993). This was not considered. However, Sharp (2002) suggests there is some evidence of a complicated predator-prey dynamic between foxes (*Vulpes vulpes)* and *P. x. xanthopus*.

The PVA model also ignored individual variation in the vital rates. White (2000) calls this 'individual heterogeneity'. This variation may have its roots in genetic variation or environmental conditions in early stages of the individual's development. White (2000) demonstrated that this may have a positive affect on the population. This is because a few individuals with exceptionally high reproductive potential or survival may carry the population during bad times. The difficulty is having a sufficient sample size in the mark recapture samples to measure this heterogeneity. Using the weight, or animal condition data from mark recapture sampling may have been a way of incorporating individual heterogeneity into a PVA.

6.3.7 Further questions to be explored

It is clear from this study that there is a need to better understand movement. The estimates of survival from mark recapture will also improve if the number of individuals leaving the sampled population can be ascertained.

There is evidence to suggest seasonally biased sex ratios in some macropods may be linked to sex-bias in dispersal (Johnson, 1989). Indeed sex-biased dispersal is often recognised as being an inbreeding avoidance strategy (Johnson and Gains, 1990). Unfortunately, there is little data in this study, or other studies of the *Petrogale* genus, to support sex bias dispersal. However, in a study conducted by Lethbridge et al (2001), sex-biased dispersal in *P. x. xanthopus* was simulated in a PVA and explored in relation to the probability of extinction. The most interesting result of this study was that when both males and females disperse longer distances, the probability of extinction increased. Conversely, when the one of the sexes was relatively philopatric, particularly females, the probability

of extinction was lowered. This is because the potential distance between breeding partners increases as the dispersal distances of both sexes increases. In reality this would also depend upon the landscape configuration. Unfortunately, the relationship between sex-biased dispersal and sex ratio was not explored by Lethbridge et al (2001), nor were the effects of these strategies on inbreeding. These relationships are worth investigating in future empirical studies and simulation models.

It is also important to better understand how the population breeds and the interplay between the demographic and genetic structure (Peacock and Ray, 2001). For example, little is known about how female *P. x. xanthopus* select males, particularly immigrant males over resident males. Furthermore, Falconer and Mackay (1996) show that the variation in the number of breeding offspring for a given individual and sex bias in the breeding pool have the greatest affect on N_e, the effective number breeding individuals. While, pedigree data can be derived from genetic samples, this is a technique that continues to be expensive. However, as genetic testing becomes more rapid and more markers become available, future analyses of these samples may be sufficiently cost effective to sample pedigree trees from wild populations.

Long-term empirical studies need to focus on the conditions that trigger dispersal. This requires a careful consideration of the spatial scale of the environmental conditions at which condition-dependent dispersal is measured (Imms and Hjermann, 2001). The PVA simulations in this study were confined to active and passive search strategies and yet the way in which individuals choose their habitats is likely to lie somewhere between these two extremes. This stresses the need for studies that investigate how individuals choose suitable patches. Moreover, Stamps (2001) stresses the need to look at the differences in the choice of habitat in relation to what an individual has learnt in its source patch. This is also requires careful consideration of spatial scale (Stamps, 2001).

The relationship between PVA predictions based upon mark recapture data and trends in the aerial data was not compared in this study. However, it is feasible that future work could look at linking these two distinctly different and scale dependent monitoring strategies. For example, an average population growth rate can be derived from the PVA simulations. Using the rainfall deviates generated in the PVA simulations, it may be productive to compare the Ivlev (1961) equations derived from the PVA with the observed data. If microclimate does affect the link between survival and rainfall, these simulations would somehow need to accommodate the wide variety of different microclimates afforded in the landscape.

CHAPTER 7

Conclusions

7.1 Overview of Findings

This study consisted of a collection of three interrelated empirical studies and a PVA of *P. x. xanthopus*. In Chapter 2, a range of summary population parameters were explored that were derived from aerial census data. In semi-arid environments, rainfall patterns directly affect the herbivory. This is often described as environmental stochasticity. In the face of environmental stochasticity, the mean exponential rate of increase $\bar{r}$, inadequately describes the population trends and fails to reveal the interaction of ecological and environmental processes.

In fluctuating environments, it is more appropriate to adopt an indirect approach and model the rate of growth against resource availability (McCallum, 2000). Following Sharp and Norton (2000), the Ivlev (1961) equation was tested. This is a nonlinear inverted exponential equation that enables rainfall, a surrogate of resource availability, to be modelled with population growth. The parameters derived from the Ivlev (1961) model indicated that the population's capacity to grow at Wilkawillina Gorge in the northern Flinders Ranges and Plumbago Station in the Olary Hills is significantly higher than the Depot Flat and Hawker areas, both in the central Flinders Ranges. Wilkawillina Gorge and Plumbago Station have well-established fox and goat control programmes in place. Despite this, the Wilkawillina Gorge data indicates that the limited availability resources may be lowering the intrinsic rate of growth of the population.

Unfortunately, these summary parameters do not describe the biological processes that underpin them, and without supporting data, it is difficult to ascertain the likely causes of these differences. The utility of the aerial census data depends upon the management objectives. For example, if the underpinning objective to maintain a viable metapopulation, population trend analysis alone fails to indicate the viability of a population. Conversely, mark recapture sampling has the potential to be able to sample many of the biological processes that underpin summary population trends and

provide a better understanding of the causes and effects. However, mark recapture sampling is limited in its application because it is specific to a particular land system and environment. This means it may not be appropriate to generalise the findings without a sufficient number of sample sites.

Chapter 3 described a mark recapture methodology that estimated survival and fecundity at two populations. The only problem with estimating survival is that an individual captured, and subsequently not seen, may have died or emigrated from the population. Recognising this, survival was replaced by the term χ, the probability of an individual remaining in a population. Most of the mark recapture models tested indicated that χ at the Eregunda Creek trap site was higher than Wilkawillina South trap site by approximately 15%. This evidence suggests that either more animals are leaving the Wilkawillina South site or dying. Given that the physical condition of sub-adults and adults at Wilkawillina South was also found to be lower than Eregunda Creek, these findings concur with the aerial data that resources are limited at Wilkawillina Gorge. While there were too few data, fecundity also appeared to be lower at Wilkawillina Gorge. Predation has been discounted because there is little evidence of foxes in and around Gorge (De Prue, 2000) and there are no apparent differences (although not measured) in Wedge-tailed Eagles (*Aquila audax*) numbers between the sites.

Following Sharp's (2002) hypothesis, another explanation is that predation may have a balancing effect, and the foxes at Eregunda Creek prevent the population from reaching a level where density dependent processes lead to population decline. However, the high abundance of Euros (*Macropus robustus*) competing for resources in the Gorge (De Prue, 2000), particularly around the attractive permanent waterholes during dry periods, is a more likely explanation. This suggests that conservation managers need to monitor herbivore abundance and vegetation more closely in the Gorge.

Interestingly, the aerial data did indicate some evidence of transient movement (although not conclusive) in Wilkawillina Gorge when conditions are harsh. Presumably, if adults range more widely when conditions deteriorate, then it is feasible that male and female sub-adult dispersal is also higher in this area when conditions deteriorate. Hence the estimates of χ at Wilkawillina Gorge may instead be indicating condition-dependent dispersal. This requires more empirically testing.

There are also wider implications of these finding. The problems of managing permanent water points in semi-arid areas are not new. However, most of the work to date has focussed on managing stock water and reducing the impacts at these sites. The findings in this study also stress the importance of managing natural permanent water sites, on and off reserves, and particularly when one or more or species are threatened. It is also suggested that long-term vegetation monitoring in Wilkawillina Gorge and Eregunda Creek take place, together with continued mark recapture sampling, in order to be able to establish a definitive link between available food resources, survival, fecundity and condition. The installation of a local rainfall gauge around these sites will also provide a more direct relationship between the food resources and rainfall.

Apart from providing relative measures of isolation, genetic sampling provides an indirect measure of movement in recent ecological time (Moritz and Lavery, 1996; Sherwin and Moritz, 2000). Assignment tests measure movement by providing a probabilistic assignment of each individual to its source population (Sherwin and Moritz, 2000). This requires more than one site to be sampled. Having a better understanding of movement also helps to differentiate emigration from mortality in mark recapture sampling. However, in order to be able to have sufficient statistical power in genetic assignment tests, more mark recapture sites would probably need to be installed in and around Wilkawillina Gorge. Radio tracking can also be employed but this is likely to have less statistical power than genetic sampling because it only captures emigration for the duration of the study. Conversely, genetic sampling captures past and present movement.

The aim of Chapter 4 was to gain an understanding of the current habitat preferences of *P. x. xanthopus* and produce a spatially explicit habitat model. Two distinctly different habitat modelling approaches at two different scales were presented. The first approach was an aspatial approach based upon presence-absence data of this species and habitat characteristics observed at 150 sites from 2000 to 2002 in the Flinders Ranges, South Australia. This provided important information about the habitat associations of this species at a microhabitat scale. The second approach involved constructing a spatially explicit habitat model using a Geographical Information System (GIS). This used presence and absence data based upon five years of aerial survey data, all available ground survey data of *P. x. xanthopus*, climate, vegetation community and topographical data.

Three spatial models were tested. The first was a Generalised Additive Model (GAM). This was hybridised with a regression tree in order to be able to separate the continuous explanatory

variables from the vegetation categorical variable. This hybrid approach combines the strengths of these two distinctly different modelling approaches. The second approach, Multivariate Adaptive Regression Splines (MARS - Friedman, 1991) uses multidimensional piecewise linear basis functions to fit the data. The third approach, using the software PolyMARS (Stone et al, 1997) is a robust logistical framework that better models presence-absence responses and unlike MARS, employs continuous polynomial regression splines (Hastie et al, 2001). The strength of both of these approaches lies in their ability to find interactions in the explanatory variables and, like GAMS, deal with non-linear responses. Despite their capacity to find interactive effects, no explanatory variable interactions were found. The application of MARS and PolyMARS to habitat modelling is novel as they have traditionally been confined to database mining (Hastie et al, 2001).

Spatial autocorrelation was also modelled. If the observation data are spatially dependant, part of the variation in the model may be explained by neighbourhood values (Overmars et al, 2003). To their detriment, most spatially explicit predictive models assume observation data to be independent and rarely investigate the neighbourhood relationship between the observation data (Guisan and Zimmermann, 2000). By way of comparison, two raster GIS prediction surfaces were built with one of these incorporating an autocorrelation term. Extrinsic tests of these two surfaces using independent data revealed a minor difference between these surfaces. In more isolated, marginal areas or where there has been no recorded presence of the species, the inclusion of the autocorrelation term lowered the prediction probability. However in areas where there was either a high concentration of large prediction probabilities or a high concentration of recorded presences, the inclusion of the autocorrelation term lifted the prediction probability.

The influence of the explanatory variables also provided a better understanding of the habitat preferences of *P. x. xanthopus*. For example, a higher probability of presence was predicted in dense vegetation, particularly on higher slopes, and vegetation communities known to be in the diet range of this species (Lapidge, 1997).

Chapter 5 described a new spatially explicit individual-based PVA model written in the C++ programming language and interfaced with a GIS. This software provides a seamless and robust interface between the GIS and the PVA simulation engine, which more easily enables one to alter landscapes and initiate the PVA tool rather than importing new landscapes. Many spatially explicit PVA do not adequately represent continuously varying and heterogeneous landscape (Wiegand et al, 1999; Weins, 2001). For this reason a GIS raster grid was chosen to represent

landscape habitat quality. Other unique characteristics of this model include its ability to model both sexes, simulate inbreeding and the facility to set a distance threshold between breeding partners (Allee, 1949). The PVA model structure described in Chapter 5 was then applied to this species in Chapter 6. This was not intended to provide definitive results related to expected extinction times but highlight the gaps in knowledge about this species and set priorites for its future management.

First, a sensitivity analysis was conducted over a single population to rank the importance of several demographic parameters on the probability of extinction. Specifically, the effect of rainfall and survival were tested. Assuming no animals move in and out of the population, these comparisons indicated that Sharp's (2002) NSW population has a 55% chance of extinction whereas the Eregunda Creek population has under a 10% chance of extinction. Interestingly, the Wilkawillina South trap site would almost certainly become extinct according to this model if χ does not incorporate emigration. Even if emigration accounts for the lower estimates of χ, this site is a likely sink (Pulliam, 1998) over the study period.

While there is much debate about density-dependence, most populations probably fall along a continuum of density-dependent and density-independent processes (Wilson, 2003). For example, in semi-arid environments, rainfall may be a particularly important density-independent process. The influence of these two these process on the population depends upon the life history strategies and environmental conditions such as habitat (Wilson, 2003). These simulations indicate that local populations may be particularly vulnerable at sites where there is little or no microclimate and survival fluctuates strongly with rainfall. This was found to be less severe when the carrying capacity is higher. For example, sites with a dense vegetation overstorey or complex rock formations may ameliorate the effects of infrequent rainfall and high temperatures on survival by providing a more stable environment. This finding does have some merit given the higher correlation found between dense vegetation (e.g. Mallee) in steep terrain and presence of this species in Chapter 4. These findings suggest that wildlife managers should more closely monitor and manage open sites with little protection afforded in the habitat.

However, the clearest finding in this study was that extinction was most sensitive to juvenile survival and adult survival. Given that juvenile survival is thought to be directly affected by predation intensity (Hornsby, 1995; Lim, 1983; Lim and Giles, 1987; Sharp, 2002; Sharp and Norton, 2000), further monitoring needs to focus on the effectiveness of different predator control strategies on survival. As the survival parameters also indirectly reflect competition, it is also

important to understand the affect of goat abundance on resource availability and survival. Both of these threats may affect the population differently in areas where there is little protection afforded by the habitat.

Few spatially explicit PVAs have modelled inbreeding. Incorporating genetic models in PVA is a therefore a relatively new and exciting development. These models have the capacity to model the interaction of movement and landscape and their effects on inbreeding (Daniels et al, 2000). In this study, an area in the landscape was windowed to study the effects of immigration and abundance on the inbreeding coefficient F. Two distinctly different inbreeding models were compared, following the work carried out by Daniels et al (2000). The first approach tracked pedigrees. The second approach assumed mating was random and used Wright's (1931; 1951) equation to estimate F. The results showed that the random mating model significantly overestimated the inbreeding. However, due to the significant increase in computer processing time to simulate the pedigrees, Wright's (1931; 1951) equation was more useful in testing a large range of assumptions related to movement.

These simulations suggest that if dispersal is passive (i.e. animals move randomly through the landscape) and all sub-adults disperse regardless of population density, there are notable reductions in the inbreeding estimates. An important insight revealed in these findings is that when individuals actively choose habitat, the occupancy remained confined to higher quality habitats, indicating a "fence effect" (Krebs, 1992). While, there was some evidence that there is transient movement within Wilkawillina Gorge, there was little or no movement evident in or out of the Gorge from 1996 to 2002. This evidence also supports the "fence effect" idea. If this is the case, there are important implications for management because many isolated populations of this species will become inbred and consequently extinct. Long-term studies therefore need to focus on how an individual chooses suitable patches.

The population at Mt Stuart was chosen because it is relatively isolated and has been of particular interest to DEH and the local property manager. However, the relative isolation of this population suggests the simulations will reveal high levels inbreeding depression. While there are many other colonies in the Flinders Ranges that are also isolated, this population may be more atypical than typical. Obviously it would be fruitful to conducted further simulations on a less isolated population and compared the results, however the results do suggest that unless there is some immigration into the Mt Stuart population over the next few years, artificial translocations may be necessary.

7.2 Final Comments

As previously mentioned, Active Adaptive Management (AAM) involves varying management actions and monitoring the performance of these actions in order to make better management decisions (Possingham, 2001). Limited resources usually means conservation biology involves the setting of management priorities (Burgman and Lindenmayer, 1998). However, a well-designed monitoring system needs to effectively influence management actions and assess conservation management performance (Possingham, 2001). Effective management therefore requires that efficient and effective monitoring strategies are chosen and this study has demonstrated the value of using PVA to help chose more effective monitoring strategies.

To this end, three important findings emerged from the PVA modelling. Firstly, the miroclimate afforded in some habitats may ameliorate the effects of infrequent rainfall and high temperatures and theses habitats may support more viable populations. This requires conservation managers to manage these populations differently to populations found in less protected habitats.

Secondly, the viability of this species was most sensitive to survival, particularly juvenile survival. This requires closer attention to be paid to the processes that affect survival. As juvenile survival is likely to be directly affected by fox predation, fox control should be a priority in threat abatement programmes. However, this does not dismiss the need to better understand the effect of competition from other herbivores. The latter is likely to be particularly important in areas where there is permanent water, which requires more careful management and monitoring.

Finally, there is a need to better understand movement. Source-sink theory and metapopulation theory place a great deal of importance on dispersal in the role of ecological rescue. The ecological rescue affects described by Merriam (1995) are distinct from genetic processes associated with movement (Merriam et al, 1989; Turchin, 1998). In this study, the PVA simulations suggest that dispersal had a greater influence on inbreeding. These simulations also showed that altering the assumptions related to what triggers dispersal and how individuals move had a large effect on the inbreeding estimations.

This has highlighted the need to better understand three components of dispersal and breeding. These are:

1. what triggers dispersal,
2. how individuals move through the landscape and select patches,
3. how individuals select mates.

The challenge for future research is the application of population models that link scale-dependent sampling and monitoring strategies. For example, the PVA model described in this study could be used to predict the rate of growth of a population in relation to simulated rainfall patterns using mark recapture demographic parameters and compare this with aerial census data. Finally, this study has also demonstrated a relatively new and yet challenging direction for population modelling that links the genetic and demographic processes in a population to help guide the future management of threatened species.

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