Chapter 1

General Introduction

"Fragments of habitat are often viewed as islands and are managed as such; however, habitat fragmentation includes a wide range of spatial patterns of environments that may occur on many spatial scales. Fragments exist in a complex landscape mosaic, and dynamics within a fragment are affected by external factors that vary as the mosaic structure changes. The simple analogy of fragments to islands, therefore, is unsatisfactory."

[Wiens 1994]

An inevitable result of agricultural activities in an area is the reduction in the extent of the original vegetation and the extensive fragmentation of the remainder. The resulting landscape mosaic generally consists of remnants of the original plant communities (remnant vegetation), surrounded by a matrix of agricultural land uses. Fahrig (1997) argued that fragmentation only applied when the number of patches increases due to the breaking apart of habitats. However, this literal, but very restricted use, of the term has rarely been applied in the scientific literature (Saunders *et al.* 1991; Opdam *et al.* 1993; Wiens 1994; Robinson *et al.* 1997). Fragmentation can be viewed as both a pattern and the process that produces such a pattern, and is dependent on the species or process that is being considered (Opdam *et al.* 1993; Wiens 1994). Throughout this thesis I use the definition of Opdam *et al.* (1993) for fragmentation: "... a spatially distributed set of habitat patches, characterised by patch area and shape, by patch configuration and by the resistance of the intermediate land to movements of individuals of a particular species." This definition is not restricted to the changes in a single landscape, but can also be used to compare different landscapes. Fragmentation should be considered a continuous variable (*i.e.* more fragmented or less fragmented) not a categorical one (*i.e.* fragmented *vs* unfragmented).

There are three primary effects of fragmentation on the biota; a reduction of the area of habitat, changes in the biological and physical parameters impinging on that habitat, and changes in the functional level of isolation between patches of habitat (Saunders *et al.* 1991). An understanding of how these processes interact to affect the persistence of species is fundamental to developing sustainable approaches to land use.

There are two disciplines that are central to the study of the effects of landscape fragmentation on the persistence of species, namely Metapopulation Dynamics and Landscape Ecology. The synthesis of these two relatively young sciences has been hindered by their differing views of the landscape. Metapopulation Theory is still strongly linked to the view of the landscape as patches in a featureless matrix (Hanski & Simberloff 1997); while Landscape Ecology, in which landscapes are viewed as heterogeneous mosaics, lacks a theoretical framework that deals with this spatial patterning (Hobbs 1995; Wiens 1997).

Metapopulation Theory

Andrewartha and Birch (1954, 1984) were among the first researchers to formally define the concept of a *Local Population*. They conceived species' populations as being comprised of a series of sub-populations which fluctuated in numbers over time, but which were linked by the dispersal of individuals. A number of different terms have been used in the subsequent literature for the concept of a local population, such as; *Interaction Groups*, defined by the distance that individuals of a species may travel in the non-dispersive period of their life (den Boer 1979); and *Demographic Units*, defined as groups of individuals that have separate dynamic histories (Brown & Ehrlich 1980). All of these terms have two common traits; they define a sub-unit of the population within which factors affecting population parameters are the same, but may differ from those of other sub-units. In addition, these sub-units of the population are linked by some level of dispersal. This system describes the basic concept of a metapopulation.

The term metapopulation was first used by Levins (1969) to describe the concept behind a model he created to explore the population dynamics of a single species, where he observed local populations fluctuating asynchronously in a temporally variable environment. However, it was another 20 years before this concept was developed further

and became central to a new paradigm for conservation biology (Hanski & Simberloff 1997).

Hanski and Gilpin (1991) defined a metapopulation as a "set of local populations which interact via individuals moving among populations." They also argued that the hallmark of genuine metapopulation dynamics was local population turnover. To date, the metapopulation literature is dominated by studies and models measuring metapopulation dynamics in terms of changes in the number of available habitat patches occupied through time (Addicott 1978; Fritz 1979; Thomas & Harrison 1992; Hanski & Thomas 1994; Hanski 1997, 1998; Moilanen *et al.* 1998). These models assume that dispersal between local populations has little effect on the dynamics of those local populations, but observations on real populations indicate that this is not always the case (*e.g.* the *Rescue Effect*, Brown & Kodric-Brown 1977). This led some researchers to incorporate local patch dynamics in their models (Gyllenberg & Hanski 1992; Gyllenberg *et al.* 1997; Stacey *et al.* 1997), but these complex models are deterministic models and the interaction between their predictions and environmental stochasticity remains unknown (Hanski 1998). However, these models did demonstrate that even low levels of immigration allowed populations, which would normally go extinct in a stochastic environment, to persist (Stacey *et al.* 1997).

Harrison (1991; Harrison & Taylor 1997) found that few real populations fit the "classical" metapopulation concept proposed by Levins. She argued that real metapopulations lie along continua the extremes of which can be described by one of four metapopulation types (Fig. 1.1). Alternatively, populations had the structure of a metapopulation, but were not in equilibrium and were declining.

- *Classical* metapopulations have habitat patches with similar probabilities of extinction and the persistence of these metapopulations is dependent on the recolonisation of local populations which go extinct (Fig. 1.1a).

- *Mainland-island* or *Source-sink* metapopulations have a local population which is extinction resistant (*i.e.* Mainland or Source) and other local populations which have much higher extinction probabilities (*i.e.* Island or Sink), but are maintained by dispersal from Mainlands or Sources. The difference between Mainland-Island and Source-Sink metapopulations is that in the former extinction resistance is the result of large population size, while in the latter this resistance is the result of qualitative differences in the habitat (Fig. 1.1b).

- In *Patchy populations* dispersal between habitat patches is so common that individuals from different patches mix freely. Therefore, these patches are effectively a single population. Harrison and Taylor (1997) argued that in patchy populations the distances or rates of movement among patches is less important to population persistence than in true metapopulations (Fig. 1.1c).

- Some species have *mixed metapopulation* structures which contain elements of several different metapopulation types (Fig. 1.1d).
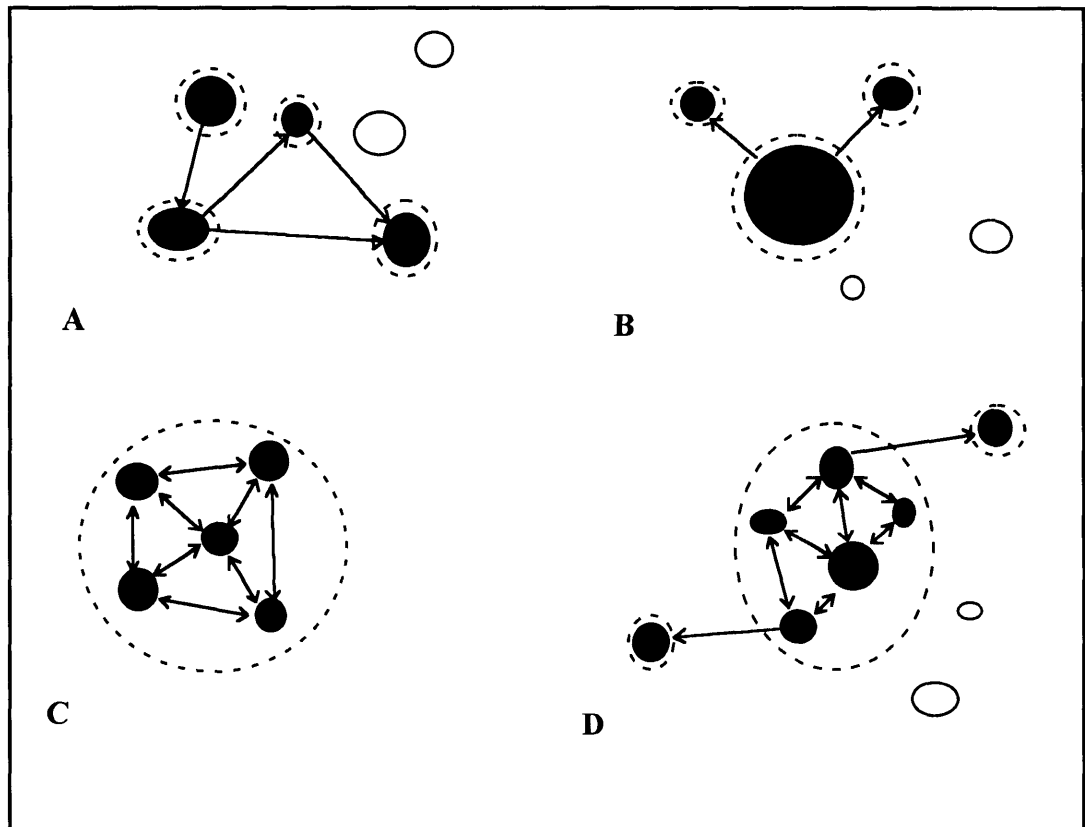

Figure 1.1: Metapopulation types proposed by Harrison and Taylor (1997). Closed circles represent occupied habitat patches, open circles represent unoccupied habitat patches. Dashed circles represent the boundaries of local populations. Arrows represent dispersal. A: Classical model, B: Mainland-Island model, C: Patchy population, D: Mixed metapopulation combining types B and C.

Metapopulation Theory has a strong theoretical base, but development of this theory has been dominated by modelling. It is still strongly focused on the classical view of metapopulation dynamics, despite most real populations failing to fit this model. In

addition, Metapopulation Theory is still based on the patch-matrix view of a landscape. Even when using spatially explicit models, this theory considers inter-patch distances as Euclidean rather than a complex function resulting from the mosaic nature of the landscape (Wiens 1997). This has led some (Doak and Mills 1994; Fahrig & Merriam 1994) to caution against the use of metapopulation models for the management of real populations.

Landscape Ecology

Landscapes are heterogeneous areas consisting of a cluster of interacting ecosystems (Forman & Godron 1986). Landscape Ecology is the study of the structure and function of landscapes and how this changes through time (Forman & Godron 1986; Hobbs 1995; Wiens 1997). The central theme of this science attempts to deal with the heterogeneity of landscapes and it is therefore a spatially explicit discipline.

Much of the work in Landscape Ecology has been descriptive and there has been limited success in generating a theoretical framework for landscape studies (Hobbs 1995; Wiens 1997). However, Wiens (1997) indicated four principle themes which have emerged from Landscape Ecology:

- Patches show spatial and temporal variation in quality. Patch quality should be viewed as a continuous rather than a categorical variable.

- Patch edges may have an important influence on the flows of organisms, nutrients or materials over space. Consequently, they are important to the dynamics both within and between patches.

- The degree of connectivity between landscape elements is an important influence on the interactions between patches and on landscape dynamics. Connectivity is a complex variable which involves much more than corridors.

- The location of a patch within a landscape, or its context, is important to the dynamics within that patch. This means that patches of similar quality may differ, because of features of patches which are adjacent or nearby to them.

Patch edges are an important component of landscape dynamics, because they represent a boundary where there are changes in the flows of organisms or materials between different parts of the landscape (Wiens *et al.* 1985). The dynamics at these boundaries are dependent on the process being considered and the characteristics of the patches involved. Even for a given species the permeability of boundaries will change depending on the structure of adjacent patches (Bach 1988a, b), the geometry of the patch

(Stamps *et al.* 1987), or the density of individuals within the patch (Wiens *et al.* 1985). Boundary permeability may also differ for individuals of the same species which are at different stages of their life cycle and for the two sexes (Wiens *et al.* 1985; Ims 1995).

Patch edges also represent an area of interaction between the components of different patch types. Nest predation levels in birds have often been found to increase at patch edges (Brittingham & Temple 1983; Gibbs 1991; Paton 1994). Andrén (1995) found that the rate of nest predation at edges depended on the types of patches involved. Edges between forest and farmland patches frequently had higher predation rates than core areas of the forest patch, but edges within forest mosaics did not. He argued that this difference was because predators which occupied farmland patches gained access to the edges of forest patches (Andrén 1995).

The movement of individuals through the landscape is fundamental to landscape dynamics and is dependent not only on the characteristics of the species, but also on the landscape in which the movements occur (Wiens *et al.* 1993; Ims 1995; Wiens 1997). Dispersal behaviour may change in different habitat types (Schultz 1998) and with changes in the scale of heterogeneity across the landscape (Wiens *et al.* 1993). Species may also change their dispersal behaviour when landscapes are fragmented (Wiggett & Boag 1989; Matthysen *et al.* 1995). Other aspects of a species' ecology, such as perceptual range and conspecific attraction or repulsion, may also influence movement patterns in landscapes (Lima & Zollner 1996; Yahner & Mahan 1997). Although, these studies demonstrate the complexity of dispersal behaviour at various scales, our understanding of how these changes are reflected in population dynamics is poor (Ims 1995; Wiens 1997).

Frequently the issue of landscape connectivity has been lost in the debate over the value of corridors (Simberloff & Cox 1987; Noss 1987; Simberloff *et al.* 1992; Hobbs 1992). Landscape connectivity refers to the degree to which the landscape facilitates the movement of individuals among patches (Taylor *et al.* 1993) and the issue of corridors is only one small component of this. Important components of landscape connectivity include boundary dynamics, dispersal behaviour, and patch configuration. Andrén (1994) found that when the proportion of suitable habitat in a landscape dropped below 30% patch isolation and size, became the most important determinants of the abundance and distribution of species. Similar findings, based on Percolation Theory, suggest that there is

a critical threshold below which the loss of suitable habitat results in large changes in the connectivity of the landscape (Gardner *et al.* 1987; O'Neill *et al.* 1988; With & Crist 1995). This connectivity threshold is dependent on the spatial patterning of landscape elements (*i.e.* random *vs* aggregated) and the scale at which organisms perceive this landscape pattern (With & Crist 1995; Wiens 1997).

The location of a patch within a landscape (*i.e.* context) is important to the dynamics within that patch (Wiens 1997). The existence of higher nest predation rates at patch edges is dependent on the configuration of landscapes (Donovan *et al.* 1997; Hartley & Hunter 1998). The landscape context of patches has been found to have a major influence on the abundance of some bird species, while for other species it had little influence (Pearson 1993). The importance of context is especially prevalent in landscapes which have been fragmented by extensive agriculture, where new patch types can differ substantially from the original landscape (Saunders *et al.* 1991). The loss of Carnaby's Cockatoo *Calyptorhynchus latirostris* from areas of the Western Australian wheatbelt is an example of the effect of such changes (Saunders 1977; 1980). Saunders found that clearing for agriculture caused a change in the habitat mosaic, isolating patches used for nesting (woodland) from those used for foraging (heath). This change in the context of nesting patches resulted in a decline in breeding success due to food shortages, despite the presence of suitable foraging patches. Pairing success of Ovenbirds *Seiurus aurocapillus* is lower in patches from highly fragmented landscapes compared to those in less fragmented landscapes. This was probably due to changes in dispersal dynamics, or the habitat selection patterns of females (Gibbs & Faaborg 1990; Villard *et al.* 1993). These studies illustrate how patch quality may alter with changes in patch context.

Scale

Levin (1992) described the issue of scale as "... the fundamental conceptual problem in ecology." Yet most ecological theories fail to deal adequately, if at all, with scaling issues (Meentemeyer & Box 1987; Wiens 1989). One of the major reasons for this is that there is no correct scale at which an object or process should be described. The appropriate scale to use is dependent on the question being asked (Wiens 1989; Levin 1992).

Most ecological studies use *absolute* scales (*i.e.* actual distances or time periods). However, objects or processes can also be considered at *relative* scales, where absolute distances or time periods are transformed to relative values based on some functional relationship (*e.g.* the relative distance between two places based on the effort required by an organism to move between them) (Meentemeyer & Box 1987; Turner *et al.* 1989). The scale of an investigation is characterised by its *grain* and *extent*. *Grain* is the finest resolution (*i.e.* size of the individual units of observation) possible in the investigation, while *extent* is the overall size or duration of the study (Turner *et al.* 1989; Wiens 1989).

Increasing the grain of an investigation generally results in a decrease in variability and consequently an increase in predictability (Wiens 1989). Levin (1992) argued that this was the principal technique of scientific inquiry. Increasing the scale of description allows greater generalisation by ignoring the variability of finer scale entities, but it suffers from the loss of this detail. Hierarchy Theory deals with this problem by emphasising the functional links between scales and incorporating them into the resultant description (Allen & Starr 1982; Urban *et al.* 1987; Allen & Hoekstra 1992). Hierarchy Theory identifies the problems of considering processes at only one scale. Processes observed at any one level in a hierarchy are set within the context of the level above and are driven by the processes operating at the level below. If all of these levels are not considered together then important information about the processes being studied will be lost (Allen & Hoekstra 1992).

Rolstad (1991) indicated the importance of considering the scale at which parameters occurred relative to the scale of the species, when assessing the importance of habitat configuration. The configuration of habitat patches can be considered to have a fine or coarse grain, or it can be a combination of these which he called hierarchical patch configuration. A patch configuration is considered fine grained if the home range of an individual encompasses a number of patches. A configuration in which patches are large enough to encompass the home ranges of several individuals is considered coarse grained. The hierarchical patch configuration contains patches which are smaller than the home ranges of individuals, but which are clustered into units that support the home ranges of a number of individuals.

Rolstad (1991) argued that, depending on the degree of isolation between patches, coarse and hierarchical patch configurations were most likely to result in populations with

a metapopulation structure. However, these patch configurations were determined at the scale of an individual's home range, but it is at the larger scale of a group of individuals' home ranges at which population structure is defined. Whether the coarse and hierarchical patch configurations result in either single populations or a metapopulation depends on their configurations at this larger scale. This hierarchical nature of patch scales was outlined by Kotliar and Wiens (1990). They argued that to understand the effect of heterogeneity on any process it was essential to determine the appropriate scale of patchiness for the process being investigated. Some of the inconsistencies found by Harrison (1991) between metapopulation models and real populations may be a consequence of this use of inappropriate scales. For example, Hailia (1990) and Andrén (1994) argued that many of the empirical studies investigating metapopulation dynamics in fragmented landscapes dealt with small fragments (<100 ha) which were unlikely to hold local populations of the species studied.

Aim

This thesis is an empirical study of aspects of the spatial dynamics of a single bird species in a fragmented agricultural landscape. The aim of this project was to investigate how landscape fragmentation and other associated processes affect the spatial dynamics of a species. I used the principles generated by Metapopulation Theory and Landscape Ecology to define the population structure of the White-browed Babbler in the Kellerberrin landscape and to identify the scales at which it operates.

Chapter 2 provides a context for this study, describing the area where the study was conducted and the changes which have occurred to the landscape and to the associated bird communities. Chapter 3 describes the study species, the White-browed Babbler, and my methods for sexing this species. Chapter 4 outlines the spatial distribution of White-browed Babblers in the study area, and provides a description of the study sites and my selection criteria. This chapter then proposes a conceptual model identifying spatial scales at which population structure might be defined.

An issue central to understanding the population dynamics of a species is the quality of the habitat occupied by individuals. This issue is dealt with in Chapters 5 and 6 which deal with two aspects of habitat quality (vegetation structure and food availability) and

how they change with different levels of grazing by domestic stock. Chapter 8 defines habitat quality with respect to reproductive success, and discusses how it is affected by vegetation structure and landscape configuration. The effect White-browed Babbler group size has on the definition of this aspect of habitat quality is also discussed.

The social structure of a bird species has an important influence on many aspects of its population dynamics, especially dispersal. A model of the social structure of White-browed Babblers is proposed in Chapter 7 and is used in Chapter 9 to explain the dispersal behaviour of White-browed Babblers. Chapter 9 also describes other aspects of the spatial dynamics of this species. In Chapter 10 a model of the population structure of the White-browed Babbler in the Kellerberrin landscape is formulated, using the data described in the previous chapters and a spatially explicit dispersal model developed by Brooker *et al.* (1999; Appendix I). Chapter 11 provides a synthesis of this work identifying the effects of landscape fragmentation on the population dynamics of this species, and discussing these findings in relation to the principles of Metapopulation Theory and Landscape Ecology. The implications these finding have for conservation management in agricultural landscapes is also discussed.

Chapter 2

The central wheatbelt of Western Australia

*"The southwest of Western Australia is a classic example of our failure
to follow the principles of ecologically sustainable development. The
region is rich biologically, and over the past 165 years has been
subjected to development for intensive agriculture which has imposed
extensive changes upon the landscape. Widespread, rapid and selective
clearing of native vegetation for the development of agriculture, together
with the introduction of exotic species have seen the disappearance of
many species of native plants and animals."*

[Saunders & Ingram 1995]

This study was carried out in three locations within a 1680 km² area just north of the town of Kellerberrin, which is approximately 200 km east of Perth. This area is part of the central wheatbelt of Western Australia and has been the subject of an extensive collaborative research program run by CSIRO Wildlife and Ecology. This research commenced in 1985 and investigates the integration of nature conservation and sustainable agriculture (Hobbs & Saunders 1993; Saunders *et al.* 1993).

Vegetation

The Kellerberrin district is part of the Mount Caroline vegetation system described by Beard (1980). The vegetation of this district is broadly associated with soil and landform patterns, as described by Bettenay and Hingston (1964) and Bettenay (1984). However, it is typical of much of the wheatbelt region in that it shows an intricate mosaic of vegetation types mingled together to form broad divisions (McArthur 1993).

Eight landform types have been identified in the district. The Ulva unit supports a number of sandplain heaths (Kwongan). These vary from highly diverse communities dominated by a shrub layer which includes *Melaleuca* spp., *Acacia* spp., and *Grevillea* spp. and sometimes containing taller shrubs and mallees; to heaths dominated by single

species such as *Allocasuarina campestris*. The Collgar unit generally supports a mallee vegetation with or without an understorey. The understorey varies, but is often dominated by *Melaleuca* spp., or *Acacia* spp. Four landform units, Booraan, Merredin, Belka and Nangeenan support varying types of woodland communities dominated by *Eucalyptus salmonophloia, E. capillosa,* and *E. salubris*. These communities have varying types of understorey. Rock outcrops are generally associated with the Danberrin unit and have two major vegetation communities associated with them; an *Acacia acuminata/Eucalyptus loxophleba* community, or dense shrubland of *Allocasuarina* spp. The final landform unit, Baandee, represents the ancient drainage zones which are now occupied by lakes and playas, most of which are saline. The vegetation associated with this landform depends on its salinity. Saline areas generally support samphire communities, while less saline areas support halophytes such as *Atriplex* spp. and *Maireana* spp. (McArthur 1993).

The Ulva, Booraan, Merredin, and Danberrin landforms are the most common in the study area. The Collgar unit is almost as common, while the Belka, Nangeenan, and Baandee units are rare (Arnold & Weeldenburg 1991). However, clearing patterns have altered the relative amounts of the remnant vegetation supported by these landforms. Remnant vegetation is under-represented on the Merredin, Belka and Collgar landforms, while the vegetation types associated with rock outcrops (Danberrin) is over-represented (Arnold & Weeldenburg 1991). This results in an under-representation of woodland and mallee communities in the study area.

Climate

Kellerberrin has an mean annual rainfall of 330 mm most of which falls between May and September (Table 2.1). The district has between 3 and 4 months of the year when average rainfall exceeds effective rainfall (Beard 1980). The mean daily maximum temperature varies from a high of 34.1°C in January to a low of 16.3°C in July, while the mean daily minimum varies from 17.6°C in February to 5.8°C in August (Table 2.1).

The seasons in the Kellerberrin area are unreliable due mainly to variability in rainfall patterns. Summer extends from November to March and is hot and dry. During this period rain is very unreliable and generally results from thunderstorms (*i.e.* localised, heavy rain for short periods) generated by cyclonic activity in the north. Autumn is short (April and

May), but defines the start of rains generated by south-westerly cold fronts. This "break of season" is unreliable, being strongly influenced by *El Niño* events. This means that dry conditions can frequently last for six to seven months of the year. Winter is the most reliable season for rain and these three months are the coolest of the year. Spring (September to October) represents a period of mild but increasing temperatures and decreasing rainfall. This is the most active breeding period for birds in this region.

Table 2.1: The mean monthly rainfall and mean monthly maximum and minimum temperatures for Kellerberrin (31° 38' S, 117° 43' E). Rainfall data is based on records from 1892 to 1999. Temperature data is based on records from 1962 to 1992 (from the Bureau of Meteorology, Perth).

	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Mean monthly Rainfall (mm)	11	14	21	22	42	57	53	41	26	18	12	13
Median monthly Rainfall (mm)	3	5	11	14	37	54	48	39	23	14	7	4
Mean monthly Max. Temp. (°C)	34.1	33.3	30.2	25.2	20.7	17.5	16.3	17.4	20.3	24.7	28.6	32.1
Mean monthly Min. Temp. (°C)	17.5	17.6	15.6	12.2	8.8	7.3	6.1	5.8	6.7	9.3	12.7	15.6

This study commenced in 1994 which was an exceptionally dry year (annual rainfall of 168 mm), and was preceded by a year of below average rainfall (278 mm). In 1995 annual rainfall was above average (413 mm) and in the final year of the study the annual rainfall was about average (318 mm).

Clearing History

The Kellerberrin area was settled in the early 1860s, with the initial settlement consisting of a number of sheep pastoral leases of a minimum of approximately 20 000 acres (8000 ha). This pastoral occupation of the area continued until the railway was extended from Northam to Southern Cross in the early 1890s (Leake 1962). The establishment of the railway opened up the area for more intensive settlement, and the

clearing of the native vegetation increased greatly; with approximately 36% of the area having been cleared by 1920, and a further 40% by 1940. The next 20 years saw another 11% of the area cleared and by 1984 93% of the area had been cleared for agriculture (Fig. 2.1). Since then only 70 ha of the area has been cleared and revegetation programs have commenced.

The current state of the native vegetation in the district is that 7.3% remains in remnants, excluding road verge vegetation and linear strips of vegetation along fencelines. Of this area only 23% is publicly owned land and 65% of this is vested for conservation of flora and fauna (approx. 1660 ha). Of the remaining remnants, both publicly and privately owned, 77% are less than 20 ha in size and only 4% are larger than 100 ha (Arnold & Weeldenburg 1991).

Human activities have also modified vegetation communities, mainly through grazing by domestic stock, but also through the introduction of rabbits and weeds. Arnold and Weeldenburg (1991) ascertained that at the end of 1990 only 61 remnants were protected from grazing and of these only 30 had not been subject to grazing in the last 70 years. The effect of grazing by domestic stock has been shown to reduce the abundance of trees and shrubs, and alter the relative cover of exotic and native annuals to the detriment of the native species (Scougall et al. 1993).

Road verge vegetation now represents a significant amount of the remaining native vegetation in the district. There are approximately 600 km of road in the district many of which still have verges of the original vegetation of the area (Saunders et al. 1987). These road reserves vary in width from 20 m to 60 m (this includes the 10m wide road surface). Sometimes their width is increased by vegetation strips on private property, producing road verges up to 100 m wide. The vegetation on these road verges is typical of the district, but generally suffers a greater degree of disturbance compared to remnant vegetation (Cale & Hobbs 1991; van Schagen et al. 1992). Road verges are a valuable habitat resource for many species of birds, with 88% of the avifauna of the district having been recorded on them (Cale 1990). Though for most species this use is only temporary, for some species road verges can represent a substantial contribution to their available habitat.

Fig. 2.1: The clearing history of the Kellerberrin district (from Arnold & Weeldenburg 1991). The black areas represent uncleared native vegetation.
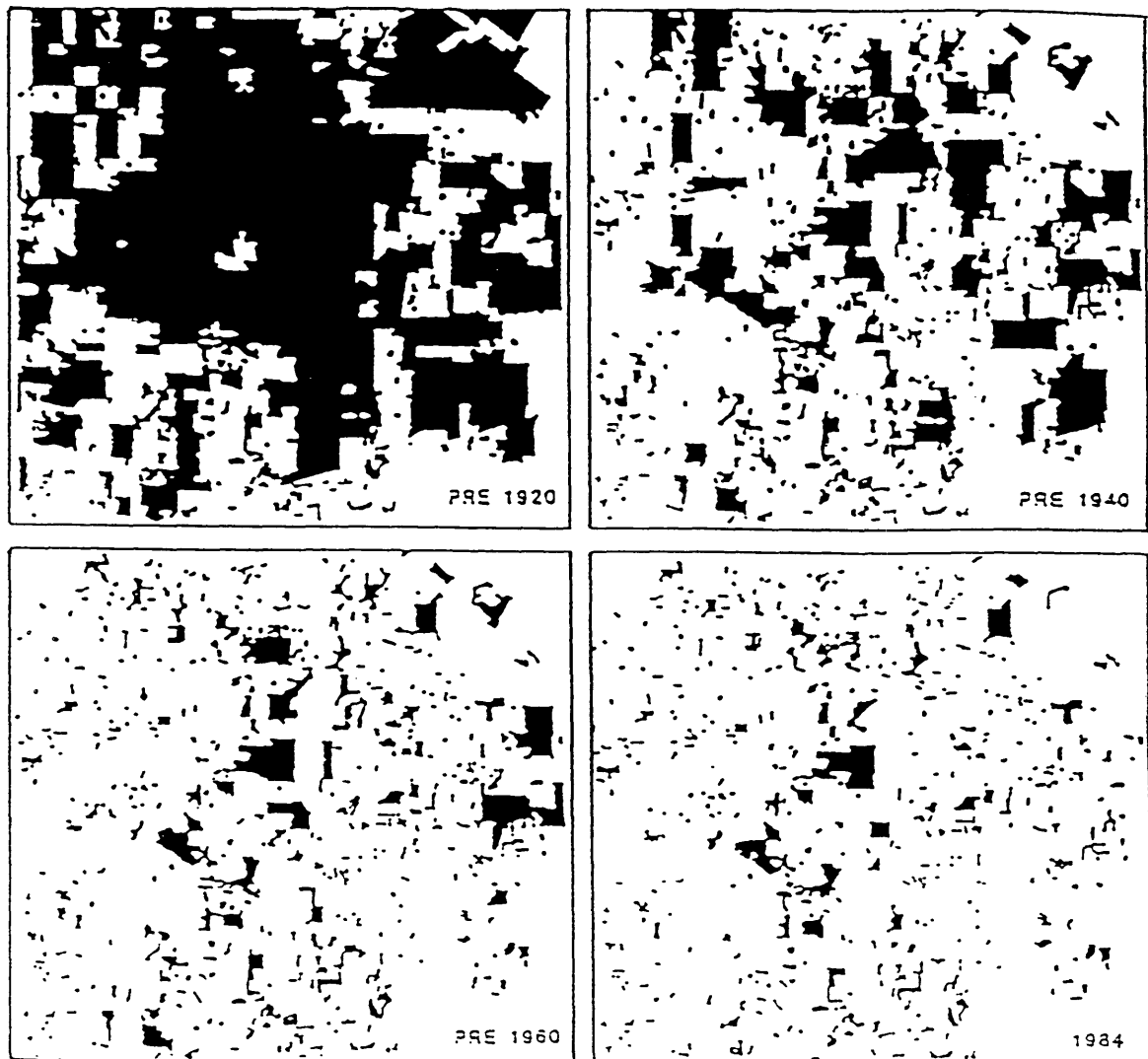
The Effect of Changes due to Agriculture on the Avifauna

The central wheatbelt of Western Australia has undergone extensive changes to its landscape, resulting from clearing for agriculture. The new landscape is one dominated by agricultural land use with many small remnants of the original vegetation scattered throughout. These changes to the landscape and the corresponding modification of the remnant vegetation, caused by agriculture and introduced animals, has had a dramatic impact on the avifauna of the region (Saunders 1989; Hobbs *et al.* 1993; Saunders & Ingram 1995). One hundred and ninety five species of bird have been recorded in the Western Australian wheatbelt since the start of European settlement. Of these, 49% have declined in range and/or abundance and only 17% have increased (Saunders & Ingram 1995). When a high percentage of the land has been cleared there is expected to be a decline in the population sizes of species due to a loss of habitat. However, many of these species have declined in abundance beyond the levels which would be expected from the loss of habitat alone. Of the 76 species analysed in the Kellerberrin district, 20% were considered to have become locally extinct and a further 13% had declined in abundance since European settlement (Cale 1994).

The analysis of the changes in the Kellerberrin avifauna also indicated that some groups of ecologically similar species were more likely to have declined than others (Cale 1994). The majority of the avifauna in this area are insectivorous, but only 29% (15 species) of these have declined or become locally extinct, whereas 62% of granivores (5 species) and 50% of nectarivores (5 species) have declined. The majority of the granivorous and nectarivorous species are nomadic and consequently a high proportion (62%) of nomadic species have declined. Of the insectivorous species that have become locally extinct or declined, 80% are ground foragers (representing 41% of ground foragers) and no foliage foragers have become locally extinct or declined in abundance. Of the 25 species that have declined or become locally extinct 20 used specific vegetation types, such as woodland or heath.

Chapter 3

The White-browed Babbler
(*Pomatostomus superciliosus*)

"... moves about in small troops of from six to ten in
number, and is without exception the most restless, noisy,
querulous bird I ever observed."
[Gould 1865]

Taxonomy and distribution

The White-browed Babbler is a member of the genus *Pomatostomus*, which is represented by five species restricted to Australia and New Guinea. Three species *P. superciliosus*, *P. ruficeps* and *P. halli*, are found only in Australia. One species, *P. temporalis*, occurs in both Australia and New Guinea, and one species, *P. isidori*, is restricted to New Guinea (Boles 1988; Sibley & Ahlquist 1990).

The genus *Pomatostomus* was once considered part of the family Timaliidae, the "true" babblers. Sibley and Ahlquist (1985, 1990) reviewed the taxonomy of the Australo-Papuan passerines and placed the genus *Pomatostomus* in its own family, the Pomatostomidae, which was not closely related to the family Sylviidae where the "true" babblers were placed. The members of this family are part of the Australian "old endemics" a parv-order that originated and radiated in Australia and New Guinea (Sibley & Ahlquist 1985). Though the techniques used by Sibley and Ahlquist have been criticised their classification of the babblers has been maintained (Christidis & Boles 1994).

The members of the genus *Pomatostomus* have an Australia-wide distribution. Only the south-eastern coast plus the adjacent highlands, the south-western coast, and Tasmania lack a representative of this genus. The White-browed Babbler is distributed across southern Australia from the west coast to the Great Dividing Range in the east (Fig. 3.1). Its distribution overlaps with the Grey-crowned Babbler (*P. temporalis*) in the northern parts of Western Australia and with all three Australian species of *Pomatostomus* in the central region of eastern Australia (Blakers *et al.* 1984).

Figure 3.1: The distribution of the White-browed Babbler (solid black area). Modified from Blakers *et al.* (1984).

The ecology of the White-browed Babbler

White-browed Babblers are cooperative breeders (Chandler 1920; Counsilman & King 1977; Brooker *et al.* 1979), living in groups of up to ten or more individuals (Gould 1865; Lynch *et al.* 1995). Groups build a number of nests in their home range, some of which are only used for night roosts (Beruldsen 1980). Nests are large dome structures made from sticks and lined with fine grass, fur and feathers. Nests made for night roosts generally have less lining (Beruldsen 1980). Both night roosts and breeding nests generally persist for many years after they have been abandoned by the group (*pers. obs.*).

White-browed Babblers appear to be sedentary (Saunders & de Rebeira 1991; Lynch *et al.* 1995), though Baldwin (1975) claimed that after breeding they became nomadic in the Inverell district of NSW. At Kellerberrin, Saunders and de Rebeira (1991) banded 133 White-browed Babblers over a period of five years and had a retrapping rate of 21%. Of these retraps 89% were caught in the same location and the largest recorded movement by an individual was 1.5 km. Lynch *et al.* (1995) found home ranges during the breeding season were on average 2.6 to 4.7 ha in size, depending on the configuration of the remnant vegetation. They found that six of seven individuals that they radio-tagged in two consecutive years used the same home range in both breeding seasons.

White-browed Babblers are generally ground foragers, but they also forage on the bark of the trunks and branches of shrubs (Cale 1994; Recher & Davis 1997; Brooker 1998). Their diet is predominantly invertebrates, although seeds have been found in both stomach content and scat analyses (Lea & Gray 1935; Brooker 1998). They take a wide range of invertebrate prey and occasionally feed nestlings small skinks (Brooker 1998). Boles (1988) claimed that White-browed Babblers predate the nests of other birds. He quoted Samuel White as having recorded this species predating the nests of the introduced House Sparrow *Passer domesticus*, but provided no reference for this quote. I have observed one instance of a White-browed Babbler group predating young nestlings of the Red-capped Robin *Petroica goodenovii* in the Kellerberrin area.

White-browed Babblers occupied mainly shrubland vegetation types in the Kellerberrin area, but were also found in other vegetation which had a good shrub layer (Lynch & Saunders 1991). They were found to be dependent on this remnant vegetation for both foraging and breeding (Saunders & de Rebeira 1991; Cale 1994). However, unlike

many remnant-dependent bird species, they used the interior and edges of remnants, and linear strips of remnant vegetation along roads with equal frequency (Lynch & Saunders 1991). White-browed Babblers rarely use agricultural land (*i.e.* pasture and crops) except within 20 m of remnant edges where they sometimes forage (Cale 1994; Lynch *et al.* 1995).

In the central wheatbelt of Western Australia the pattern of declines in bird species caused by clearing the land for agriculture was correlated with a number of ecological characteristics (Cale 1994). One of the groups which appeared most sensitive to these changes in the landscape were sedentary, ground-foraging insectivores which were dependent on remnant vegetation. The White-browed Babbler is a member of this guild, but is unique in that it appears to have been able to deal with the changes that have occurred in the Western Australian wheatbelt. This was one of the major reasons for choosing the White-browed Babbler for this study.

Sexing and aging White-browed Babblers

Morphological measurements have been used to sex individuals of species for which the sexes have similar plumage (Green 1982; Rogers *et al.* 1986; Green & Theobald 1989; Pyke & Armstrong 1993; Rogers 1995; Rogers & Rogers 1995; Sweeney & Tatner 1996). These studies have used a wide range of techniques which vary in sophistication. Some estimated graphically the location of the internodal trough of a bimodal frequency histogram (Pyke & Armstrong 1993). Others use univariate analytical procedures that derive estimates of the location and shape of frequency distributions from birds of unknown sex (Rogers *et al.* 1986; Rogers 1995; Rogers & Rogers 1995). The final group of techniques use a multivariate approach (*e.g.* discriminant analysis) on birds of known sex (Green 1982; Green & Theobald 1989; Sweeney & Tatner 1996).

Rogers *et al.* (1986) developed a model for sexing the White-browed Babbler using univariate procedures. Their model was based on the measurements of 78 birds mainly from Victoria. They found that females were smaller than males and they sexed birds using differences in head-bill length.

Iris colour has been found to be a reliable method of aging some bird species in Australia (Rowley 1974, 1978; Counsilman & King 1977). In the White-winged Chough iris colour changes gradually for five years (Rowley 1974, 1978). For the Grey-crowned

Babbler four age categories could be identified which enabled aging up to three to four years of age (Counsilman & King 1977). Rogers *et al.* (1986) suggested that immature White-browed Babblers could be identified in their first autumn by differences in gape and palate colour, but found no other characteristics that could be used to age this species. Boles (1988) records that juvenile White-browed Babblers had a buff wash to their throat, underparts and eyebrow. However, he did not indicate the source of this information.

This chapter provides a general description of the White-browed Babbler and details of the morphometric data used to sex individuals. In addition, it discusses morphological differences between adult and juvenile birds.

Methods

From 1994 to 1996 I caught and banded 357 White-browed Babblers. Most were caught using mist nets, by attracting the group to the nets with the taped call of a fledgling. I also banded nestlings before they fledged and occasionally I caught newly fledged young by hand. I also found six birds in my study groups which had been banded as part of another study, but were never caught by me (Saunders & de Rebeira 1991).

I tried to band all of the birds found in Sites A and B throughout the study (see Figure 4.1). In Site C birds were only banded during 1994. All babblers caught were uniquely colour banded. Colour band combinations consisted of a metal and one colour band on one leg, and two colour bands on the other leg. Whenever possible all members of the same group were given the same colour band on the leg with a metal band, while adjacent groups were given a different colour. The double colour band combinations for individuals in the same group were made as different as possible to enhance identification of group members.

Morphometrics

Of the 363 babblers banded, 90 were only caught as nestlings (47) or juveniles (43). Of the remaining 273 birds, 267 were weighed (to the nearest 0.1 g) and two measures of body size were made. The head-bill measurement, which is the widest point from the back of the skull to the tip of the bill (Lowe 1989), was measured to the nearest 0.1 mm with

vernier callipers. The wing length was measured with a flattened, unstraightened wing chord to the nearest 1 mm, using a butted steel rule (Lowe 1989).

Four characteristics; gape size and colour, eye colour, and plumage colour were observed for all known aged birds. This was done in an attempt to assess their value as indicators of age. Palate colour was also observed in some birds.

The aging notation used throughout this thesis is similar to that used by Rowley (1978). The year starts in July when breeding begins. Nestlings are aged in days with day one being their estimated hatching day. Fledglings are young that have recently (1-2 weeks) left the nest. After this short period they are considered to be juveniles until the next July when they become 1 year old. This means that individuals are considered to be 1 year old during the first breeding season following their birth. The age of birds then increases after each subsequent July. The addition of a '+' to the age notation indicates that a bird is at least that many years old (*e.g.* 2+ years old means the bird is 2 or more years old).

A group of known females was collated on the basis of the presence of a brood patch and observations of incubation at nests. Known males were determined by behaviour at observed nests (see Chapter 7), and from other observations made throughout the year (*e.g.* copulations with breeding female).

Discriminant analysis was used to develop a model based on the group characteristics of the birds of known sex. These models were developed so that the sex of unknown birds could be determined. Models were generated using head-bill alone and in combination with wing length. These models were compared on the basis of which best predicted group membership for birds of known sex. Birds which were only measured when they were known to be less than one year old were excluded from these analyses. Weight was not included in the analyses as some birds had not been weighed and this reduced sample sizes.

A *t*-test was used to determine if differences in measures of body size, between adult male and female babblers were significant. An ANOVA was used for similar comparisons between fledgling, 3-4 month old juvenile and 1 year old babblers. I then used Scheffe's test to determine which between group comparisons contributed significantly to observed differences (Zar 1996). All analyses were done using the SAS statistical program (SAS Institute Inc., 1989).

Results

There are no discernible differences in the plumage of male and female White-browed Babblers. This species is predominantly a grey-brown bird with a white throat and breast shading into a brown belly and flanks (Plate 3.1). The species' most prominent feature is the white eyebrow that extends from the bill to the back of the head. The tail is grey-brown with all but the central two feathers broadly tipped in white. This results in a white tip to the tail which is only visible from the ventral view, or when the bird is in flight and the tail is spread.

Sexing individuals

The distribution of head-bill and wing length measurements for all adults measured were not obviously bimodal (Fig. 3.2). However, the distributions of both of these measurements differed for known males and females (Fig. 3.3). The mean values of the head-bill, wing length and weight measurements were significantly smaller for females than males (Table 3.1).

Table 3.1: Morphometric data for adult birds of known sex. The number of individuals measured is indicated in parentheses. Head-bill and wing length were measured in mm and weight was measured in g

	Minimum	Maximum	Mean	S.E.	*t* test	
Head-Bill length						
Female (42)	44.9	49.5	47.1	0.1	7.93	p<0.001
Male (15)	47.7	51.8	49.4	0.3		
Wing length						
Female (42)	77	85	80.0	0.2	4.18	p<0.001
Male (15)	79	85	82.0	0.4		
Weight						
Female (35)	37.5	50.2	42.0	0.5	2.80	p<0.01
Male (13)	42.0	49.2	44.4	0.5		

Figure 3.2: Frequency distribution histograms for a) head-bill length and b) wing length of all adult White-browed Babblers measured. The maximum value for classes is shown.
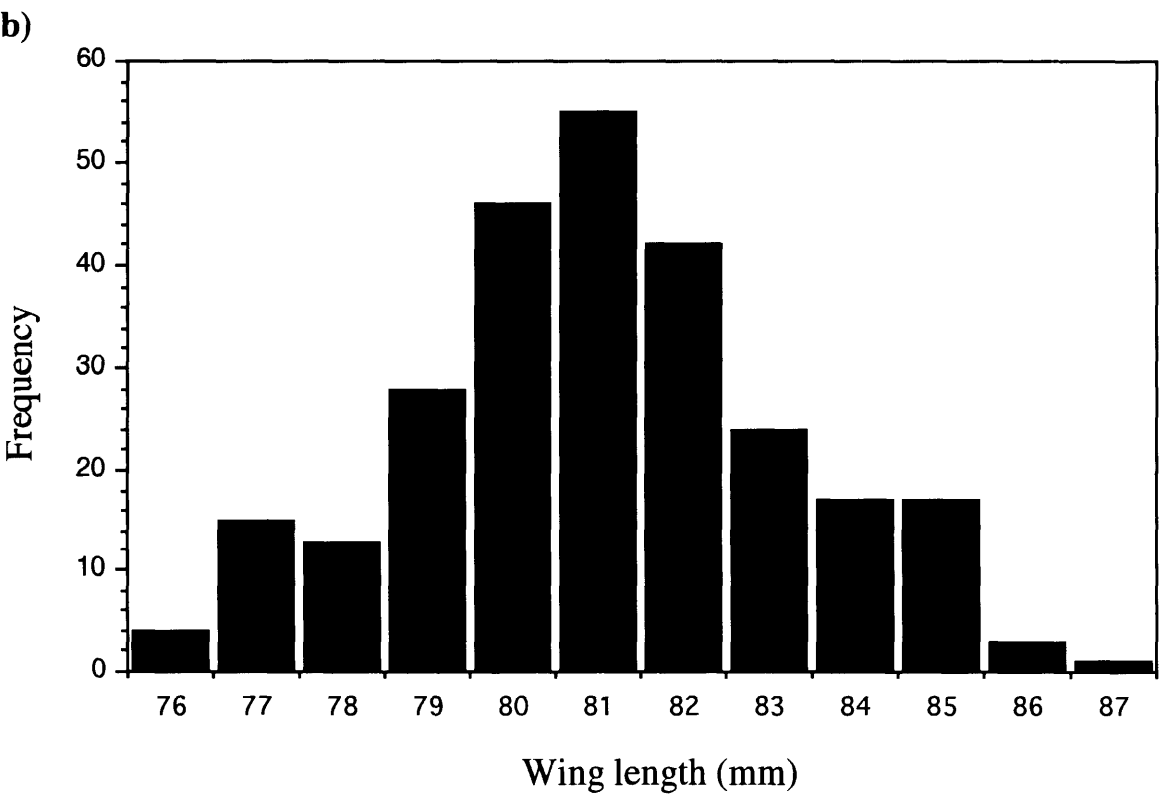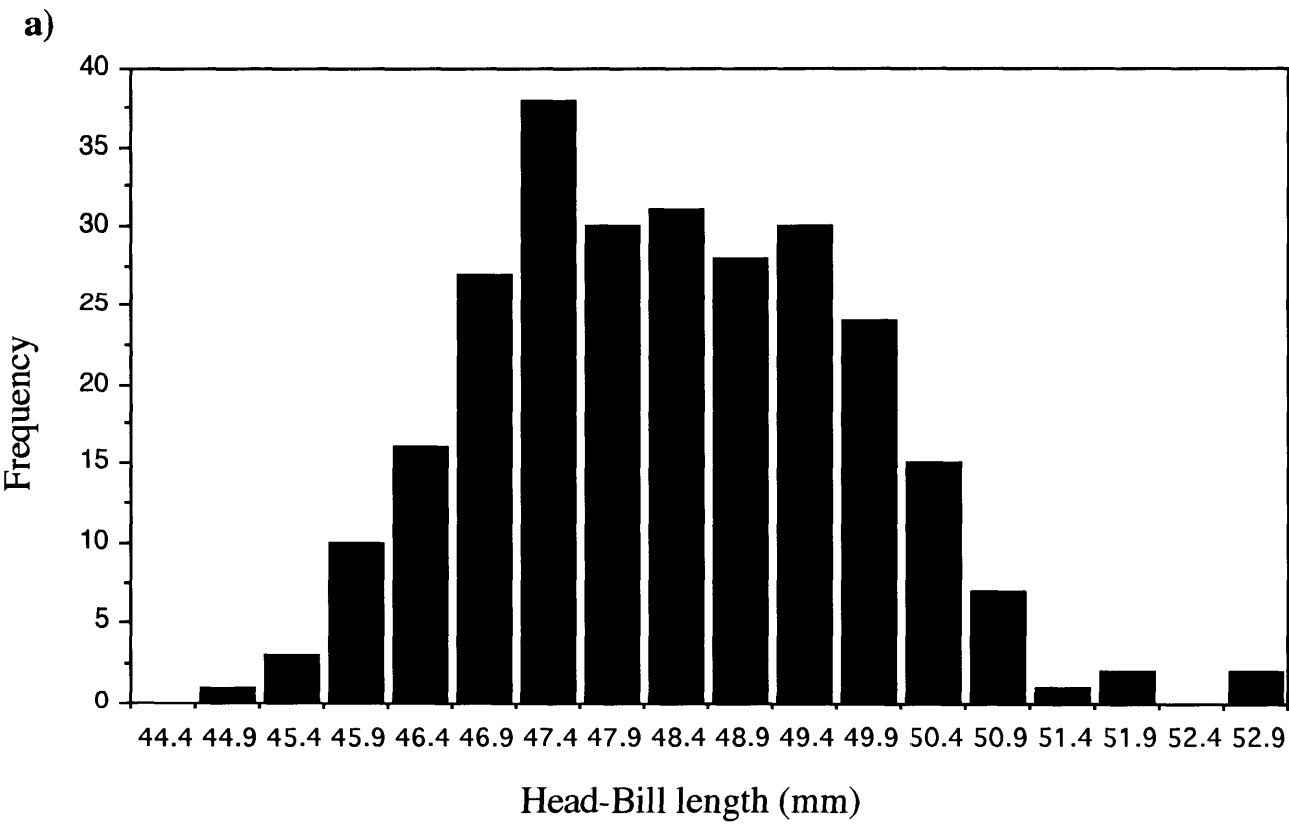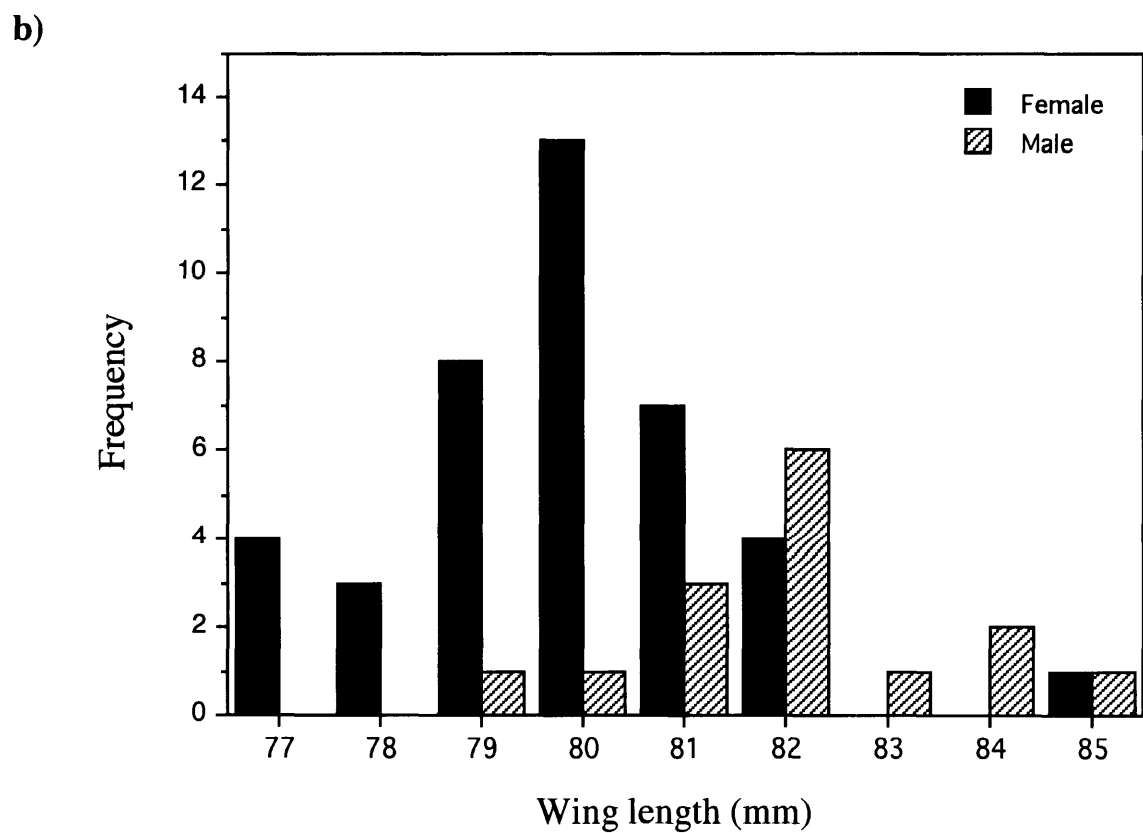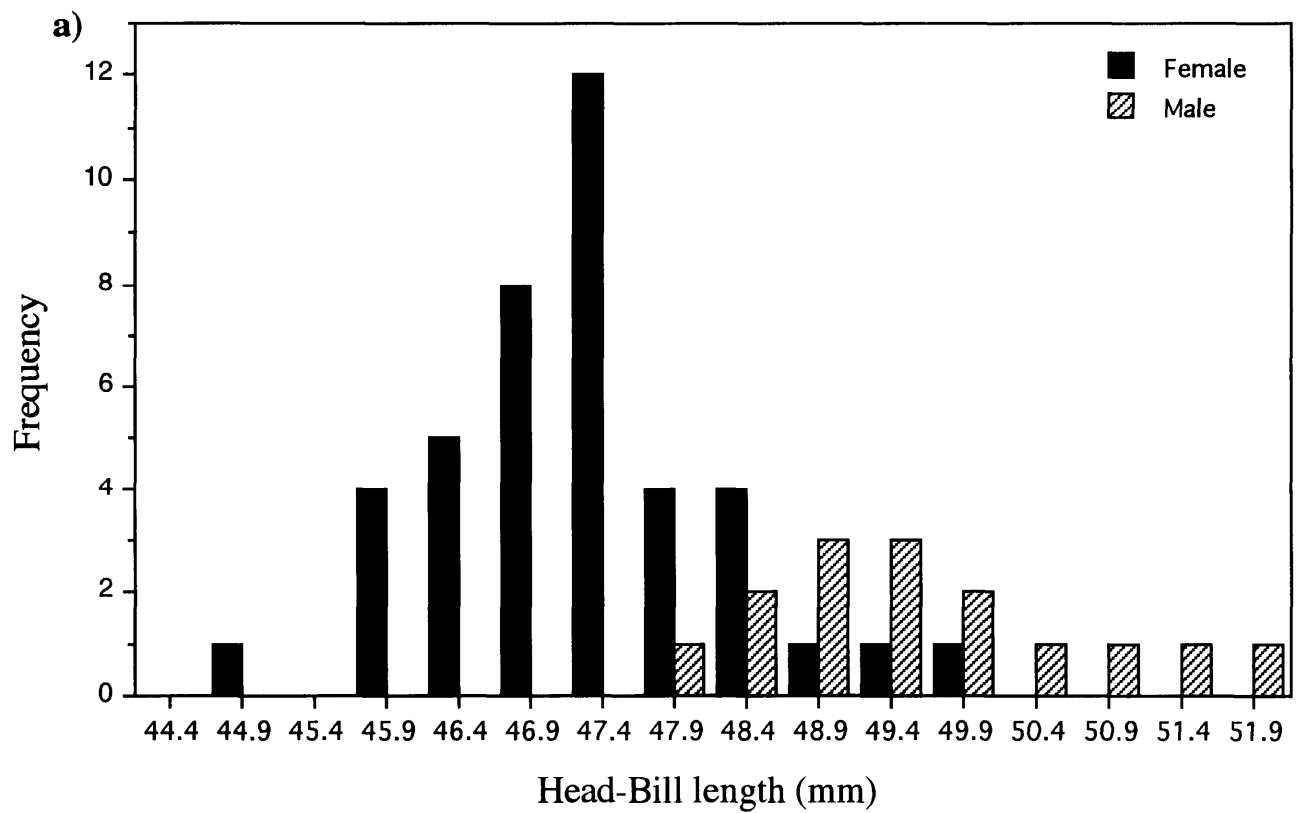
a)

Head-Bill length (mm)

b)

Wing length (mm)

Figure 3.3: Frequency distribution histograms for a) head-bill length and b) wing length of adult White-browed Babblers of known sex. The maximum value for classes is shown.

The discriminant analysis model using head-bill measurements correctly identified 93.0% (53 of 57) of individuals, while the model using a combination of head-bill and wing length, correctly identified 89.5% (51 of 57) of individuals. Therefore, the head-bill model was chosen to sex unknown birds.

The preferred model predicted that an individual with a head-bill measurement of $\leq$48.2 mm was female. However, birds with head-bill measurements of 48.1 to 48.4 mm inclusive were classified as male or female with a probability of $\leq$60%. Of the four individuals of known sex that were incorrectly classified three were females. All had head-bill measurements greater than 48.4 mm (48.8, 49.1, and 49.5 mm). The one male that was incorrectly classified had a head-bill of 47.7 mm.

Birds of unknown sex were classified as male or female if they were identified by the model as belonging to that sex with a probability estimate of greater than 60%. Therefore, all birds with a head-bill of $\leq$48.0 mm are considered to be females and those with a head-bill of $\geq$48.5 mm are considered to be males. This resulted in 247 (93%) of the 267 birds measured being sexed. The remaining 20 birds were classified as unknown sex.

Aging individuals

The head-bill length, wing length and weight of young White-browed Babblers increased with age up to 1 year old (Table 3.2). These differences were statistically significant and Scheffe's test for multiple comparisons indicated that all between group comparisons for all three body size measures were significant with $p<0.05$.

Fledgling babblers differed from adults in a number of ways. Apart from a difference in size, fledglings had a swollen, yellow gape, orange palate and much broader areas of white on the tail. In addition, the bill is shorter and less decurved (Plate 3.2).

Juvenile babblers had similar plumage to adults with the exception of more rufous wing coverts. This characteristic became less obvious as the feathers aged and was generally impossible to distinguish in the field by 4-6 months of age. Juveniles also had a lighter coloured gape, which was slightly swollen. For birds in the hand this characteristic was distinguishable up to an age of approximately 4-6 months. The palate colour of juvenile babblers did not appear to be consistently different from adults after about 3-4 months.

Table 3.2:   Morphometric data for fledgling, juvenile (approximately 3-4 months old) and 1 year old White-browed Babblers. The number of individuals measured is indicated in parentheses. Head-bill and wing length were measured in mm and weight was measured in g

	Minimum	Maximum	Mean	S.E.	F test
Head-Bill length					
Fledglings (18)	33.1	37.3	35.8	0.3	171.96 p<0.001
Juveniles (40)	44.5	48.7	44.8	0.4	
1 year old (17)	45.6	51.7	47.8	0.4	
Wing length					
Fledglings (18)	58	65	61.4	0.6	345.0 p<0.001
Juveniles (40)	75	82	77.8	0.4	
1 year old (17)	77	85	80.2	0.5	
Weight					
Fledglings (11)	29.0	33.4	31.1	0.5	47.10 p<0.001
Juveniles (39)	30.9	41.1	37.2	0.5	
1 year old (13)	36.6	44.4	40.1	0.7	

Discussion

Ford (1971), using museum specimens, found that White-browed Babblers increased in size from southern to northern Western Australia. Wooller and Richardson (1986) confirmed this north-south cline in size using measurements from live birds. They found a strong relationship between the size (measured by weight) of White-browed Babblers and the potential evapotranspiration in the areas they lived. White-browed Babblers were smaller in more mesic areas (Wooller & Richardson 1986). Rogers *et al.* (1986) measured 78 White-browed Babblers mainly from Victoria, and they recorded weights ranging from 35.1g to 46.0g, which are lower than those found in the current study (37.5-50.2g). In addition, they recorded a mean head-bill length for males of 48.9 mm and for females of 46.0 mm. Both of these measurements are smaller than those recorded in the current study. Since Victoria is generally more mesic than Kellerberrin, this data suggests that the relationship found by Wooller and Richardson (1986) also applies to birds in eastern Australia.

Because of the size differences between Kellerberrin and Victoria, the model generated by Rogers *et al.* (1986), which sexed White-browed Babblers on head-bill length, was not considered appropriate for the current study. Although their model criteria would not result in any misclassification of the known sexed birds, it would have classified only 10 (24%) of the known females and 5 (33%) of the known males.

Sexing individuals

The separation of measurements between male and female White-browed Babblers was greatest in the head-bill measurement and least in the measure of weight. The high overlap in weight is possibly due to the different times of year when weights were taken for individual birds. It is possible that females have higher weight early in the breeding season (when carrying eggs), and this may have increased the overlap between the sexes. Sweeney and Tatner (1996) found that weight was not a very repeatable measure. They argued that this was due to actual changes in weight and not measurement error. This suggests that weight would not be a reliable measure for sexing many bird species.

Discriminant analysis showed that head-bill alone was a better predictor of sex than in combination with wing length. The problem with the model containing both variables was an increase in the error of sexing females (the error increased from 7% to 11%). This was due to a number of females with very large wing length measurements. Sweeney and Tatner (1996) found that measures of wing length were less repeatable than measures of head-bill length. They argued that because of this, wing length was a less reliable measure for sexing birds. The lower repeatability for wing length is due to both seasonal changes (old feathers are shorter than new ones, due to abrasion of the tips) and measurement error. In addition, the wing can be measured in a number of ways; unflattened chord, flattened chord with unstraightened wing, and flattened chord with straightened wing (Lowe 1989). These methods give slightly different results. Even if one method is used consistently, as in this study, the degree to which the wing is flattened and/or straightened can vary slightly.

Models based on discriminant analysis provide a probability that an individual with a given value of the model parameters (*i.e.* head-bill length) belongs to a given category (*i.e.* male or female) (Tabachnick & Fidell 1996). Since the head-bill measurements of known males and females overlap there is a range of values for which the probability of belonging

to either sex is similar. Therefore, an arbitrary decision needs to be made as to what level of reliability is required in sexing birds. A probability of 60% was chosen in this study. This was a compromise between a reasonable level of confidence in the sexes of birds and the need to sex as many individuals as possible. The result is that a sex could be allocated to 93% of the individuals caught in this study.

Aging individuals

Rogers *et al*. (1986) reported that juvenile White-browed Babblers could be identified in their first autumn (*i.e.* approximately 6 months old) by their pale pink/buff gape and orange/yellow palate. The findings from the current study are consistent with their observations. However, for juveniles seen in the field the difference in gape colour was only reliable for approximately 3 to 4 months. A better characteristic for identifying free ranging juveniles, was their rufous wing coverts. However, this characteristic disappeared with time, and was unreliable by the time juveniles had reached 4 to 6 months old. Boles' (1988) claim that juveniles had a buff wash to their throat, underparts and eyebrow, was not consistent with the findings of this study.

Measures of body size showed that fledgling White-browed Babblers were considerably smaller than adults and had a shorter bill. These size differences were still significant at 3-4 months of age. At this age these size differences were large enough to be discernible in free ranging juveniles. It was not possible to statistically test whether 1 year old birds were smaller than 2+ year old birds, because sexes differed in size and there were insufficient 1 year olds of known sex. However, the sample of 1 year old birds had a similar range of head-bill and wing length measurements to those of adult birds.

The combination of a smaller body size, a shorter less decurved bill and more rufous wing coverts enabled me to distinguish juveniles from adults in their first 4 to 6 months. After this they could not be reliably distinguished from adults birds. Because of this the age of birds in this thesis has been allocated in the following way. Any bird of unknown age caught between July and January that did not show juvenile characteristics was considered to be 2+ years old as of the next July. Those caught between February and June were considered to be 1+ years old as of the next July. This means that the age of adult birds caught between February and June could have been underestimated.

Plate 3.1:   An adult White-browed Babbler from the Kellerberrin area of Western Australia.

Plate 3.2:   A fledgling White-browed Babbler from the Kellerberrin area of Western Australia. This individual fledged on the same day the photograph was taken.

Chapter 4

The distribution of the White-browed Babbler in the Kellerberrin area.

*"A landscape is a mosaic of patches, the
components of pattern."*
[Urban *et al.* 1987]

Introduction

This chapter describes the distribution of White-browed Babblers in the Kellerberrin area, based on a survey of the area in 1994 and data collected by other scientists working in the area. The major aims of this survey were to determine the distribution of White-browed Babblers in relation to vegetation and landscape variables and to provide the data required for the selection of the study sites for this project. The landscape characteristics of these sites are described here, while the structure of the vegetation used by babblers in these sites is described in Chapter 5. Based on the spatial distribution of White-browed Babbler groups in the survey area, I propose a conceptual model which identifies a set of spatial scales at which population structure might be defined by changes in the rates of dispersal.

Methods

The Survey

During April and May 1994 I conducted a survey of remnant and road verge vegetation in 620 km² of the Kellerberrin area (Fig. 4.1). Prior to this survey I collated existing information on the location of White-browed Babbler groups. This information, which included published and unpublished data, came from work conducted on birds in the area, from 1985 to 1994, as part of a collaborative research program run by CSIRO Wildlife and Ecology (Saunders 1989; Cale 1990, 1994; Lynch & Saunders 1991; Saunders & de Rebeira 1991; Lynch *et al.* 1995; G. Arnold, M. Brooker, D. Saunders, G. Smith *pers.*

comm.). I used these existing data to maximise my search effort in areas where little was known about the distribution of White-browed Babblers, although most areas covered by this data were also searched during my survey.

The survey involved the systematic searching of the majority of remnants greater than five hectares in size and some smaller remnants. Searches were also conducted in most of the road verges that still contained remnant vegetation. Searches covered all vegetation types, but concentrated on those which were most likely to support White-browed Babblers (*i.e.* those containing a good cover of shrubs). The persistence of babbler groups in areas where previous work had located them was checked, but searches concentrated on adjacent locations to determine if any new groups had formed.

Since this survey was conducted in April and May, when groups sometimes aggregate (see Chapter 9), the number of groups in a patch was not always easy to determine. Therefore, my estimates of the number of groups are conservative. In some locations no birds were found during the survey, but I had evidence of previous occupation (*i.e.* old roosting and breeding nests were found, or previous work had recorded their presence). In these cases the locations were recorded as vacant home ranges.

Spatial Distribution

For all babbler groups found in the survey area a *Habitat Patch* was defined, based on the distribution of vegetation considered suitable for the permanent occupation of a group (see Chapter 5 for description of vegetation). The boundaries of these habitat patches were determined from a hardcopy of the 1994 Landsat image (summer scene using spectral bands 2, 4 and 5), which was enhanced to maximise the differences between major vegetation types. These boundaries were then verified by extensive ground 'truthing'. Areas of suitable vegetation were considered to be discrete habitat patches if they were separated by more than 100 m of unsuitable vegetation.

The distances between habitat patches were measured to the nearest 100 m from the hardcopy of the Landsat image. These distances indicated that habitat patches tended to be aggregated across the survey area. *Patch Clusters* were defined as all habitat patches which were associated at a given spatial scale. The boundaries of these clusters represent patches

which are all further than a given distance from all other habitat patches. Patch Clusters were measured at two spatial scales, inter-patch distances of ≤1 km and ≤2 km.

The Study Sites

Three sites were initially chosen for this project. My primary criteria for choosing the two major sites (Sites A & B) were the differences in the configuration of suitable habitat patches, and their spatial association with other areas occupied by White-browed Babblers. However, I also tried to ensure that these sites had a sufficient number of babbler groups in them to generate the sample sizes necessary for an analysis of population structure. Site C was chosen because it was a small cluster of habitat patches close to Site B, but the two areas appeared to be poorly connected by remnant vegetation. The purpose of Site C was to increase the number of habitat patches in this area, because Site B contained only eight. Site C was abandoned after the first year of this study, because the logistics of adequately monitoring three areas were too high for one person.

All of the habitat patches in the study sites were mapped on the landsat image of the area, using the GIS system GRASS. Using these maps the total area of remnant vegetation and the area of each habitat patch used by White-browed Babblers were measured to the nearest 0.1 ha. The distances between habitat patches were measured, from patch edge to patch edge, to the nearest 100 m.

Two indices of patch configuration were calculated for Sites A and B. *Habitat Patch Isolation* was used to measure the degree of spatial isolation between patches. This index is the mean distance to the two nearest neighbouring habitat patches. The mean of the values for each habitat patch in the two study sites was used to compare these landscapes.

Habitat Grain is a measure of the likelihood of encountering suitable habitat in the area immediately adjacent to a given area of suitable habitat. It was measured by placing a standard-sized grid over the landscape. For each grid cell containing suitable habitat the number of adjacent cells (range 0-8) which contained suitable habitat was determined. The Index of Habitat Grain was the mean value for the cells in a landscape. A grid with a cell size of 500 x 500 m was used, as this represented the approximate size of White-browed Babbler home ranges (Lynch *et al.* 1995). The value for Habitat Grain increases as habitat patch size increases and/or the distance between habitat patches decreases. This index is

also affected by the spatial pattern of habitat patches. A landscape that has patches distributed in narrow linear clusters will have a lower value of habitat grain than one in which clusters of patches are more circular in shape.

Results

Ninety three White-browed Babbler groups were found during the 1994 survey (Fig 4.1). An additional seven groups were found, during the first year of this study, in patches not searched during the survey. These groups were assumed to be present at the time of the survey. No babbler groups were found during the survey in six locations where babblers had been recorded previously. There were also a further eight locations where babbler groups formed during the period of this study (not recorded on Fig. 4.1). Therefore, 14 (14%) home ranges known to have contained babblers at sometime during the period 1985 to 1996 were unoccupied at the time of the 1994 survey.

Seventy three patches of vegetation believed to be suitable for White-browed Babbler groups were found in the survey area (Fig 4.1). Of these, 58 (79%) had at least one group in them; four (6%) had contained a group recently (i.e. since 1985), but were currently unoccupied (patch extinction); two (3%) contained no groups, but were occupied during this study; and nine (12%) showed no signs of having been occupied by White-browed Babblers.

Spatial Distribution

At a fine spatial scale (i.e. inter-patch distances of ≤1 km) the survey area was extensively fragmented with 25 different patch clusters (Fig 4.2). However, when the spatial scale was increased to inter-patch distances of ≤2 km the number of clusters was significantly reduced (8 patch clusters).

Site A contained two patch clusters at the fine scale, but all habitat patches in this site became part of an extensive patch cluster at the larger spatial scale. Site B was more fragmented than Site A at the fine spatial scale (3 patch clusters), but all patches within this site became part of a single patch cluster at the larger spatial scale. Site C was a single patch cluster and this group of habitat patches was spatially isolated from other habitat patches (Fig. 4.2).

Figure 4.1: The distribution of White-browed Babbler groups in the Kellerberrin area and the location of the Study Sites. The distribution of babbler groups is based on a 1994 survey of the area, but includes seven additional groups, found in the first year of this study, which were assumed to have been present during the survey period. Those babbler locations marked as vacant home ranges are based on records from other scientists working in the area from 1985 to 1994 or evidence such as the presence of old roosting and breeding nests. Habitat Patches represent areas of vegetation considered to be suitable habitat for White-browed Babblers. Remnant vegetation represents all areas of native vegetation not suitable for White-browed Babblers. All other areas are dominated by agricultural land uses (*e.g.* pasture or cereal/legume cropping).

- ● Occupied home ranges
- ○ Vacant home ranges
- ▣ Habitat Patches
- ☐ Remnant Vegetation

0 ————————— 5

Scale (km)

Site A

Site B

Site C

Figure 4.2: The spatial association between habitat patches in the Kellerberrin area at two spatial scales, inter-patch distances for habitat patches of ≤ 1 km and ≤ 2 km. Habitat Patches represent areas of vegetation considered to be suitable habitat for White-browed Babblers. Remnant vegetation represents all areas of native vegetation not suitable for White-browed Babblers. All other areas are dominated by agricultural land uses (*e.g.* pasture or cereal/legume cropping).
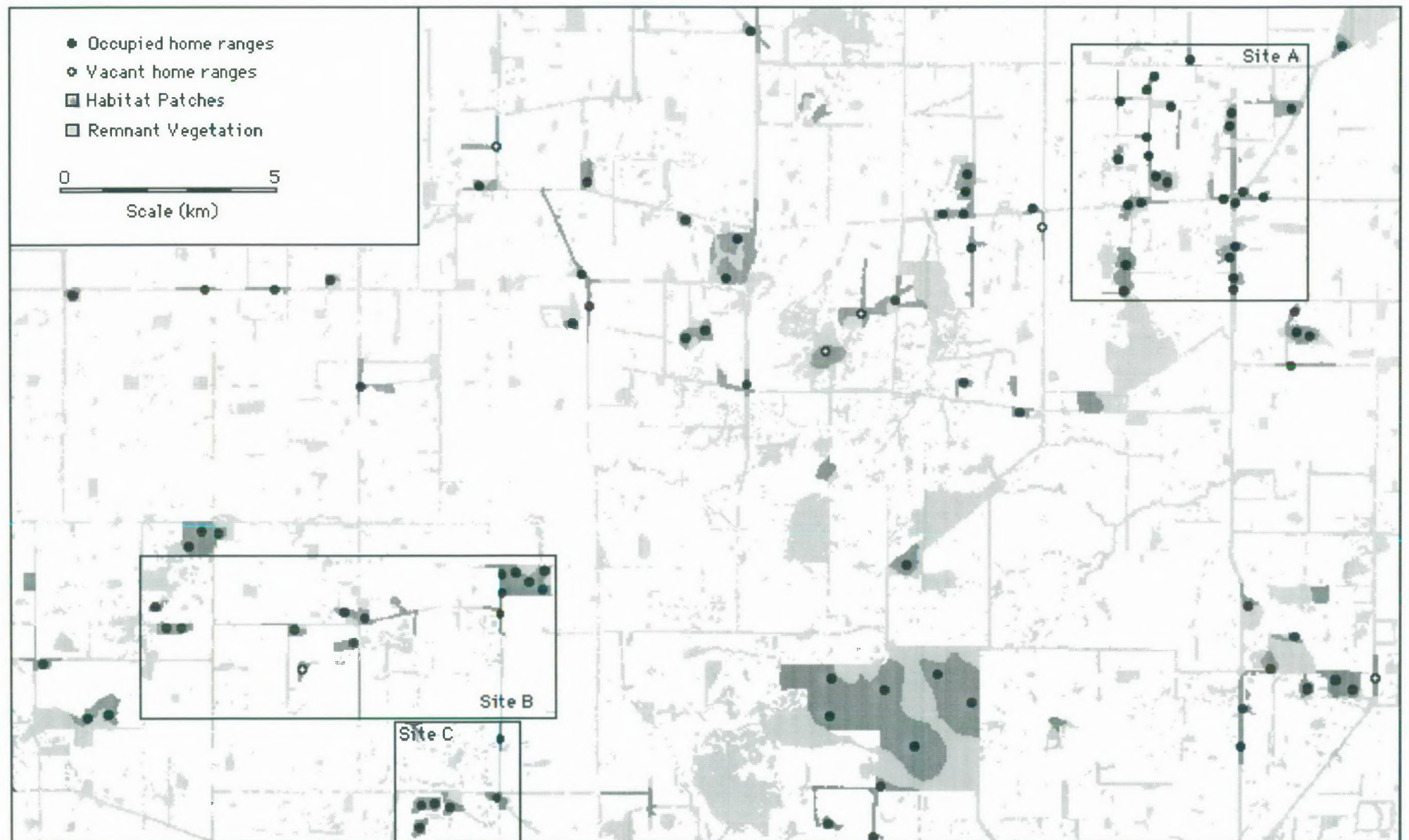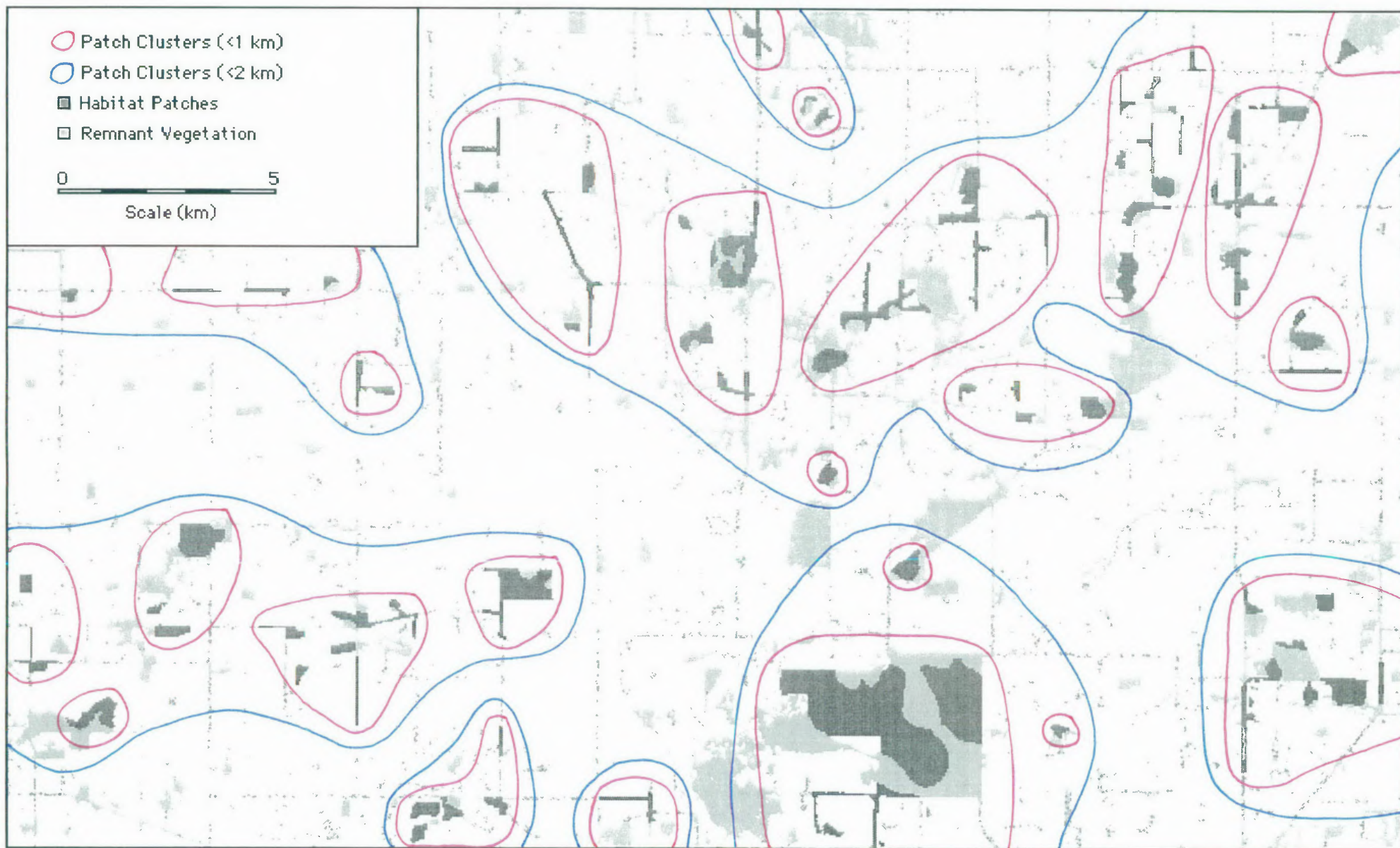
Legend:
- Patch Clusters (<1 km)
- Patch Clusters (<2 km)
- Habitat Patches
- Remnant Vegetation

0 — 5

Scale (km)

Site Characteristics

The area analysed in Sites A and B were similar (3739 ha and 3769 ha, respectively). Both study sites were dominated by agricultural land use, but Site A had slightly more remnant vegetation than Site B (17% and 12%, respectively). Approximately the same proportion of the remnant vegetation in these two sites was considered suitable habitat for White-browed Babblers (27% and 31% respectively). This meant that the total area of suitable habitat in Site A was slightly higher than in Site B (Table 4.1).

Table 4.1: The landscape characteristics of Sites A and B. Differences between sites were tested with the Mann-Whitney U-test; NS represents no significant difference, * represents a significant difference at $p<0.05$.

Landscape Characteristic	Site A	Site B
Total Area of Habitat Patches (ha)	172	141
Number of Habitat Patches	13	8
Mean Habitat Patch Size (ha)	13.2 NS	17.5
Mean Habitat Patch Isolation (m)	500 *	900
Index of Habitat Grain	3.7 *	2.9

Site A had more habitat patches than Site B and the average area of these patches was slightly lower, but this difference was not significant ($U_{(8,13)}$ = 53.5 $p>0.5$) (Table 4.1). The average level of spatial isolation between habitat patches in Site A was almost half that found in Site B ($U_{(8,13)}$ = 77.5 $p<0.05$). The Index of Habitat Grain for Site A was significantly higher than for Site B ($U_{(30,36)}$ = 730.5 $p<0.05$). The values for Habitat Patch Isolation and Habitat Grain indices indicate that the habitat patches in Site A were spatially more closely associated with each other than those in Site B. This is reflected in the number of patch clusters (based on patches ≤ 1 km apart) found in the sites (Fig 4.2).

The number of groups occupying the study sites changed during the period of this study (see Appendix 9.1). Twelve of the 13 habitat patches in Site A contained groups of White-browed Babblers and a total of 24 groups were found (including three groups found shortly after the survey which were assumed to have been present at the time of the

survey). The one empty patch in Site A was occupied for one of the three years of this study. In Site B, two of the eight habitat patches did not contain babbler groups at the time of the survey. One of these was occupied in 1995, while the other was never occupied during this study. A total of 12 groups were found during the survey, with an additional group being found during the breeding season of 1994. All of the five habitat patches in Site C were found to contain groups during the survey and a total of six groups were found.

Discussion

The majority of vegetation patches considered suitable for White-browed Babblers (habitat patches) were occupied by this species at the time of the survey. Only four of those that were unoccupied had been occupied at some time in the past decade. This suggests that there have not been major changes in the distribution of White-browed Babblers in this area for at least ten years.

Study Sites

The habitat patches in the study sites varied in size, shape and the number of babbler groups they supported, but on average the size of the patches in Sites A and B were similar. Site A contained more habitat patches, but the spatial association (*i.e.* isolation and patch grain) between these patches was higher than for those in Site B. In part, this was due to the more linear distribution of habitat patches in Site B. In addition, Site A supported more groups than Site B, though the number of groups in both sites changed throughout the study period. These differences in spatial configuration and the abundance of groups means that White-browed Babbler groups from different patches might be more likely to associate in Site A than in Site B.

Spatial Distribution

White-browed Babblers were not evenly distributed across the survey area. Groups aggregated within habitat patches and at larger scales these habitat patches were spatially aggregated across the landscape (*i.e.* patch clusters). This patchy distribution of White-browed Babbler groups suggests that the population structure of this species might fit the concept of a Metapopulation (Hanski & Simberloff 1997).

The local populations within a Metapopulation can occur in a range of configurations (Harrison 1991; Harrison & Taylor 1997). Local populations can be contained within habitat patches (Moilanen *et al.* 1998), or closely associated habitat patches may represent patchy local populations (Hill *et al.* 1996). Which of these spatial structures occurs is dependent on the relative rates of dispersal between landscape elements. This is the concept of an *Ecological Neighbourhood* (Addicott *et al.* 1987). Ecological neighbourhoods are defined by an ecological process, a time scale appropriate to that process, and the activity or influence of the species during that time period. For the population process the scale of the ecological neighbourhood would be defined by dispersal. Therefore, the *Local Population Neighbourhood* (LPN) would be that region of a landscape in which dispersal between elements within the neighbourhood was equally likely, but dispersal between neighbourhoods was less frequent.

Given the distribution of White-browed Babbler groups in the survey area, I propose a simple conceptual model of the possible scales at which interactions between these groups might occur (Fig. 4.3). The purpose of this model is to provide a framework for determining local population neighbourhoods for White-browed Babblers. Therefore, dispersal is the process that would define interactions. Dispersals can occur between groups occupying the same habitat patch (D_w), between groups occupying different habitat patches in the same patch cluster (D_b), or between groups occupying habitat patches in different patch clusters (D_{PC}). At one of these scales a change in the rate of dispersal might occur and this would define the local population neighbourhood. For example, if $D_w > D_b = D_{PC}$ then habitat patches would represent local population neighbourhoods. However, if $D_w = D_b > D_{PC}$ then patch clusters would represent local population neighbourhoods. The spatial scale associated with D_w is determined by the distribution of the vegetation in the landscape, but patch clusters, which define D_b and D_{PC}, can be defined at any spatial scale. The comparison of the two scales used here demonstrated that significant changes in landscape pattern can result. Therefore, some means of determining a biologically meaningful scale is required. This process is attempted in Chapter 10, where a spatially explicit dispersal model is used to define a set of patch clusters based on relative rates of dispersal.

Figure 4.3: A conceptual model of the scales which might be important in determining the population structure of White-browed Babblers in the Kellerberin landscape. There are three scales at which interactions (dispersals) might change: D_w between groups (solid circles) within habitat patches (fine ellipses), D_b between habitat patches within patch clusters (thick ellipses), and D_{PC} between patch clusters.
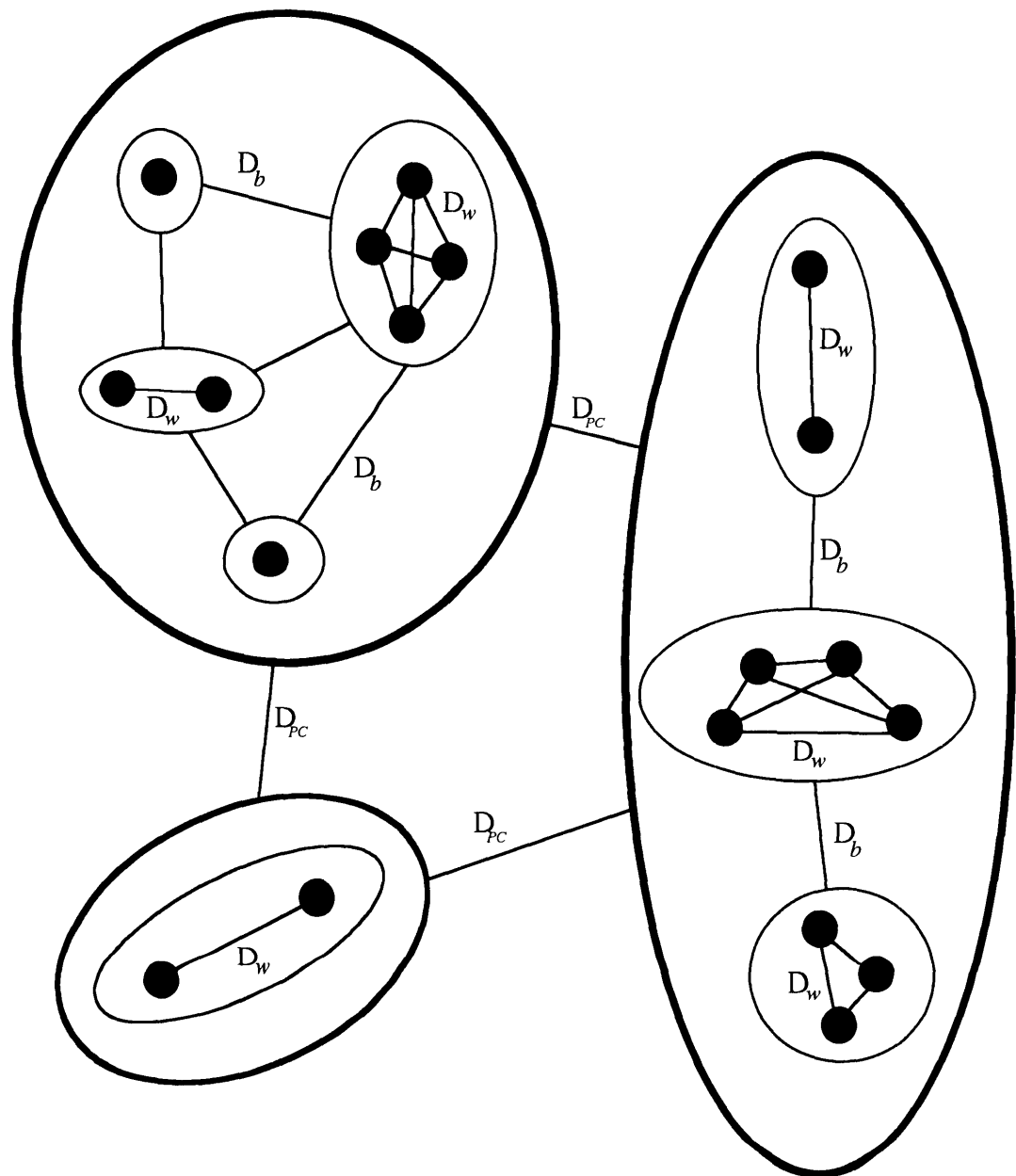
Chapter 5

Description of the vegetation in White-browed Babbler habitat patches

Introduction

The White-browed Babbler has been found occupying a range of vegetation types throughout its distribution. These vegetation types vary from shrublands (Ford 1977; Brooker et al. 1979; Cody 1994; Recher & Davis 1997) through eucalypt woodland (Baldwin 1975) to wet sclerophyll forest (Wooller & Calver 1981). However, their use of eucalypt woodland and forest communities appears to be restricted to the more mesic areas of their distribution. In the Kellerberrin area, White-browed Babblers are generally associated with the Ulva and Danderrin landforms, which support a range of heath and shrubland communities (see Chapter 2). The White-browed Babbler was generally associated with the taller shrubland communities in these areas (Cale 1994; Lynch et al. 1995).

In landscapes dominated by agriculture, remnant vegetation is often modified by the disturbance of livestock grazing (Hobbs & Hopkins 1990). Grazing by sheep has a wide range of effects on the structure and floristics of vegetation communities. These effects may include the selective removal of plant biomass, disturbance of the soil structure and litter layer, and/or indirect effects such as changes in the cycling of nutrients (King & Hutchinson 1983; Hobbs & Hopkins 1990; McIvor & Gardener 1990; Wilson 1990).

This chapter reanalyses vegetation data collected by Noack (1996) in ten of the habitat patches in my study sites. With this data I describe the structural and floristic characteristic of the three major vegetation types used by White-browed Babblers. I also describe the structural changes that occur in these vegetation types when they are subject to grazing by sheep. The importance of the structural and floristic characteristics of these vegetation types to the foraging requirements of White-browed Babblers is then discussed in Chapter 6.

Methods

Sampling for the vegetation survey was done in March 1996, except for estimates of weed cover which were done during September 1996. The survey was conducted in ten of the habitat patches in the study sites (5 in each site) (Fig 4.1). Five, 100 m long transects were sampled in the home range of each White-browed Babbler group within these habitat patches. Each transect was randomly located in one of three vegetation types; *Allocasuarina* shrubland, Mixed shrubland, and *Callitris* woodland. *Allocasuarina* shrubland was distinguished from Mixed shrubland by the fact that the shrub layer was dominated by one or more *Allocasuarina* spp.

All plant species encountered during this survey were identified to species level in the field, or a specimen was taken and later identified as far as possible (to at least genus) in the laboratory.

Canopy Substrates

The number of touches by each plant species was recorded within each 25 cm interval along a 2 m high levy pole. The presence of vegetation over 2 m high was also recorded at each levy pole. These levy pole samples were taken every 5 m along each transect (*i.e.* 20 levy poles/transect). An index of the percentage cover of vegetation in each height class was determined by dividing the number of levy poles touched in that height class by 20 (the number of levy poles/transect). An index of the total shrub canopy cover, was determined from the number of levy poles that were touched by vegetation anywhere along their length. This index included the presence of vegetation over 2 m high, but excluded perennial grasses, ground covers and annuals. An index of foliage density was calculated by dividing the total number of touches in a height class by the number of levy poles touched in that height class. The relative frequency of plant species was calculated as the proportion of the total vegetation cover contributed by that species.

Standing Stems

The density of standing stems was estimated at 5 m intervals along each transect by counting the number within a 2 m radius. They were recorded as stems/100 m^2. Standing stems were distinguished by their bark structure and whether they were alive or dead.

Rough barked trunks had either fibrous bark or in the case of *Eucalyptus* spp. had exfoliating bark strips. All other standing stems were classified as smooth barked. Only standing stems with a basal diameter of at least 5 cm were included and these were divided into two size classes, 5-10 cm and >10 cm basal diameter. Shrubs with many stems coming from a single base were included when the basal diameter of all stems combined was estimated to fit into one of the size classes.

Ground Substrates

The ground substrate characteristics were sampled within 1 m^2 quadrats, placed every 20 m along each transect. Within each quadrat the percentage cover of litter, bare ground and native tussock grasses was estimated. During the spring these quadrats were re-sampled to obtain an estimate of weed cover. Four estimates of the litter depth (to the nearest mm) were made in each quadrat. If the litter was too thin to measure it was given a depth of 1 mm. The litter was classified as needle leaved (cylindrical phyllodes, *e.g. Allocasuarina* spp.), broad leaved (flat, wide phyllodes, *e.g. Acacia neurophylla*), or macro litter, depending on what types of leaves dominated it. Macro litter was defined as any litter that contained larger debris like exfoliated bark strips.

Ground debris was divided into 2 categories, fallen branches and logs. Logs were at least 5 cm in diameter at their narrowest end. Fallen branches were any items smaller than this. The number of fallen branches and logs were counted in a 1 m wide strip running the length of each transect. An item was included if some part of it was within this strip. Fallen branches were recorded as the number/100 m^2. All logs were measured (diameter and length), and an index of log volume was calculated, using the formula: Volume Index = (π x radius^2 x length)/4. This index was recorded in units of m^3/100 m^2.

Effects of Grazing

All of the study area has been subject to some level of grazing over the past century (Arnold & Weeldenburg 1991), but the distinction made in this analysis was between historical grazing and current grazing. Each White-browed Babbler home range was classified as grazed if sheep had access to the area during the period of this study. This was determined from discussions with the landholders and direct observations of sheep activity

in the study sites. Most of the currently grazed habitat patches were grazed at low levels, but there were several which were periodically, very heavily grazed. A total of 14 of 35 *Allocasuarina* shrubland sites, 26 of 55 Mixed shrubland sites and all four of the *Callitris* woodland sites were classified as grazed.

Results and Discussion

Floristic Characteristics

Mixed shrublands were distinguished from *Allocasuarina* shrublands by their higher plant diversity (Table 5.1) (Plate 5.1a, b). *Allocasuarina acutivalvis* was a common canopy species in both shrubland types, but Mixed shrublands contained more *Acacia neurophylla*, *Hakea* spp., *Eucalyptus leptopoda*, and *Melaleuca uncinata*. The differences in composition between these shrublands correspond to changes in soil type. *A. acutivalvis* dominates the Ulva landform where the soil is shallow and lateritic and overlays a hard cemented layer, while Mixed shrublands occur on deeper sands of various types (Frost & Bennett 1990). All of these shrublands would be classified as mixed Kwongan by Beard (1980).

Callitris woodland is floristically very different from the shrubland communities (Table 5.1). *Callitris* woodland had low plant species diversity and was dominated by a single species *Callitris glaucophylla* (Plate 5.1c). This vegetation type is found on the Booraan landform (shallow loamy sands), where the soil overlays kaolinized rock (Frost & Bennett 1990). These soils can be so shallow that the underlying rock is exposed. This was not a common vegetation type in the study sites and was generally restricted to narrow strips often closely associated with Wandoo (*Eucalyptus capillosa*) woodland.

Grazed and ungrazed shrublands did not differ greatly in their floristic composition. The major differences were a decline in the relative frequency of native grasses (*Amphipogan carcinus* and *Stipa* sp.) and native annuals (*Lawencella lindleyii*) in grazed *Allocasuarina* shrublands (Table 5.1).

Structural Characteristics

Allocasuarina and Mixed shrublands were generally 3-4 m high, but often had a few taller elements which could be 5-6 m high. The total canopy cover in *Allocasuarina* and

Mixed shrublands were similar, but their vegetation profiles differed. *Allocasuarina* shrubland had a higher canopy cover above 2 m, while the canopy cover of Mixed shrubland was higher near the ground (0-1 m high) (Table 5.2). The foliage density in ungrazed Mixed shrubland tended to be higher than that in ungrazed *Allocasuarina* shrubland, but these differences were not significant. *Callitris* woodland was generally taller than the shrubland communities (6-8 m high). This vegetation type had little vegetation cover below 1 m, due to the growth form of *C. glaucophylla* and probably the effects of grazing (Table 5.3). The foliage density was also slightly lower than in the shrublands.

The vegetation cover and foliage density in grazed shrublands was lower than their ungrazed counterparts, especially up to 1 m in height (Table 5.2). This was due, in part, to declines in the abundance of native grasses and annuals (*e.g. Amphipogan carcinus*, *Stipa* sp. and *Lawencella lindleyii*), but in some sites the foliage of shrubs had been completely removed to this height. This is the major level at which sheep graze and consequently suffers the greatest grazing effects.

Both shrubland types were dominated by species with rough bark. However, *Allocasuarina* shrubland had a higher density of alive and dead standing stems (Table 5.2). The density of standing stems in the smaller size class was lower in grazed compared to ungrazed *Allocasuarina* shrubland. A similar pattern was found in Mixed shrublands, but the difference was not significant. This may reflect a decline in the recruitment of shrubs in these grazed sites. *Callitris* woodland had comparable stem densities to *Allocasuarina* shrubland and was also dominated by rough barked stems. *C. glaucophylla* showed no signs of recruitment in the areas sampled and the high density of dead trees suggests that grazing in these areas is causing a decline in this vegetation.

The cover of litter was significantly higher in ungrazed *Allocasuarina* shrubland compared to all Mixed shrubland sites (Table 5.2). Litter volume showed a similar trend, but it was not significant. The litter in *Allocasuarina* shrublands is dominated by the needle-like phyllodes of this genus (83% needle and 17% broad litter). In Mixed shrublands there is a greater diversity in litter structure, with needle leaved (64%), broad leaved (30%) and macro (6%) litter being present. Litter dominated by needle leaves tended to form a dense mat and this structure resulted in it occupying a smaller volume. There is a

moderately high cover of litter in *Callitris* woodland (Table 5.3), the majority of which is needle leaved (78%). This is predominantly that of *C. glaucophylla* and due to the fine, needle shape of these leaves it produced low litter volumes. There were no significant differences in the quantity of ground debris in the two shrubland types, but *Callitris* woodland had much higher log volumes than those found in shrublands.

Grazing had little observable effect on the quantity of litter and ground debris in either shrubland type (Table 5.2). The lack of any decline in the litter volume or cover with grazing is possibly a consequence of the periodic nature of most of the grazing in the study sites. This would allow the accumulation of new litter between periods of stock grazing.

The abundance of weeds was generally higher in grazed shrublands compared to ungrazed ones, but the difference was much greater in Mixed shrubland than *Allocasuarina* shrubland (Table 5.2). *Callitris* woodland had very low levels of weed invasion (Table 5.3). Weed invasion in the wheatbelt is limited by soil nutrient levels (Hobbs & Atkins 1988). Therefore, the greater level of weed invasion in grazed Mixed shrublands may reflect higher nutrient levels in the soils this vegetation grows on.

The major structural differences in the vegetation types used by White-browed Babblers in the Kellerberrin area were associated with grazing and not different vegetation types. The vegetation changes observed in these grazed shrublands were mainly associated with the shrub layer with little change in the structure of the ground substrates. One of the major effects of grazing was a decrease in the differences in the vegetation structure between the two shrubland types. Since all of the study area has been subjected to grazing in the past, this may have resulted in the structure of these shrubland communities becoming more homogeneous.

One effect of grazing which is not dealt with by structural and floristic data is changes in the nutrient cycles. Such changes might influence the suitability of the vegetation for White-browed Babblers, though their effect on the availability of invertebrates. This could be especially important in the shrubland communities, because of the naturally low nutrient levels in the soils which support them (Bettenay 1984).

Table 5.1:   The relative frequency of plant species in grazed and ungrazed *Allocasuarina* and Mixed shrublands, and in grazed *Callitris* woodland. Values are mean frequencies from all transects in each vegetation type. Only species with relative frequencies ≥0.01 are included. Those values ≥ 0.1 are in **bold** type.

Plant species	*Allocasuarina* shrubland		Mixed shrubland		*Callitris* woodland
	Ungrazed	Grazed	Ungrazed	Grazed	Grazed
	n = 21	n = 14	n = 29	n = 26	n = 4
Acacia sp. A	0.04	0.01	0.02	0.01	0.06
Acacia neurophylla	0.05	0.09	**0.14**	**0.11**	-
Allocasuarina acutivalvis	**0.41**	**0.39**	**0.18**	**0.19**	0.09
Allocasuarina campestris	**0.12**	**0.14**	0.05	**0.10**	0.06
Allocasuarina corniculata	0.05	**0.12**	0.02	0.04	-
Amphipogan caricinus	0.07	0.01	0.08	0.07	-
Baeckea behrii	-	-	0.03	0.02	-
Borya sp.	-	0.02	0.01	-	-
Callitris glaucophylla	-	-	-	-	**0.72**
Calothamnus sp.	-	-	-	-	0.03
Ecdeiocolea sp.	-	0.06	0.04	0.05	-
Eucalyptus leptopoda	-	-	0.02	0.07	-
Eucalyptus capillosa	-	-	-	-	0.03
Grevillea paradoxa	0.05	0.03	0.08	0.05	-
Hakea coriacea	-	-	0.01	-	-
Hakea erecta	-	-	0.01	-	-
Hakea invaginata/scoparia	-	-	0.05	0.02	-
Lawrencella lindleyii	**0.14**	0.01	**0.13**	**0.11**	-
Melaleuca conothamnoides	0.01	-	0.03	0.04	-
Melaleuca eleuterostachya	-	-	-	0.03	-
Melaleuca radula	-	0.07	0.01	0.01	-
Melaleuca uncinata	-	-	0.04	0.02	-
Micromyrtus sp.	0.02	0.02	0.03	0.01	-
Santalum acuminatum	-	-	0.01	-	-
Stipa sp.	0.02	-	0.03	0.02	-
Species richness	11	12	21	18	6
Diversity	0.9	0.9	1.2	1.2	0.4

Table 5.2: A comparison of the structural characteristics of ungrazed and grazed sites in *Allocasuarina* (n = 21,14) and mixed (n = 29,26) shrublands. ANOVAs showed significant differences at p<0.05 between columns with the same letters for each structural variable.

Structural Variables	*Allocasuarina* shrubland Ungrazed Mean	S.E.	Grazed Mean	S.E.	Mixed shrublands Ungrazed Mean	S.E.	Grazed Mean	S.E.
CANOPY COVER								
Total Canopy Cover	0.71 [ab]	0.03	0.55 [ac]	0.06	0.66 [cd]	0.02	0.50 [bd]	0.03
2.01 m+	0.59 [abc]	0.04	0.39 [a]	0.06	0.46 [b]	0.03	0.37 [c]	0.04
1.51-2.0 m	0.24	0.02	0.22	0.02	0.19	0.02	0.19	0.02
1.01-1.5 m	0.10	0.01	0.11	0.02	0.13	0.01	0.10	0.02
0.51-1.0 m	0.06 [a]	0.01	0.04 [c]	0.02	0.11 [abc]	0.02	0.05 [b]	0.02
0.0-0.5 m	0.09 [a]	0.02	0.06 [c]	0.04	0.15 [abc]	0.02	0.08 [b]	0.02
FOLIAGE DENSITY								
1.51-2.0 m	4.6	0.3	5.4	0.8	4.9	0.4	4.6	0.3
1.01-1.5 m	4.1	0.4	3.7	0.7	4.9	0.4	4.2	0.4
0.51-1.0 m	3.3 [a]	0.9	1.2 [ab]	0.4	3.9 [bc]	0.4	2.1 [c]	0.5
0.0-0.5 m	3.0	0.6	1.5 [a]	0.6	4.1 [ab]	0.6	2.3 [b]	0.5
Smooth Bark 5-10 cm (#/100m²)	22 [ab]	5	9 [a]	3	20 [c]	4	9 [bc]	2
>10 cm	0.4	0.4	0.6	0.6	0.3	0.3	1.8	1.3
Rough Bark 5-10 cm	210 [abc]	23	118 [a]	21	113 [b]	9.71	88 [c]	10
>10 cm	172 [ab]	16	134	15	119 [a]	10	114 [b]	12
Standing Dead 5-10 cm	69	15	32	10	40	8	40	10
>10 cm	35 [ab]	4	16 [a]	8	24	4	21 [b]	4
Litter Volume (m³/100m²)	1.2	0.3	0.9	0.3	0.6	0.1	0.9	0.3
% Litter Cover	69 [ab]	5	53	8	49 [a]	5	48 [b]	4
% Weed Cover	10 [a]	6	16 [c]	7	12 [b]	4	35 [abc]	7
% Native Grass Cover	3	1	2	2	4	1	3	1
Fallen Branches (#/100m²)	101	7	81	11	79	8	73	8
Log Volume (m³/100m²)	9.7	2.2	3.4	1.1	11.0	2.4	7.9	2.3

Table 5.3: The structural characteristics of *Callitris* woodland (n = 4).

Structural Variables	*Callitris* woodland Mean	S.E.
CANOPY COVER		
Total Canopy Cover	0.49	0.13
2.01 m+	0.41	0.14
1.51-2.0 m	0.22	0.06
1.01-1.5 m	0.09	0.04
0.51-1.0 m	0.03	0.01
0.0-0.5 m	0.00	0.00
FOLIAGE DENSITY		
1.51-2.0 m	3.0	1.0
1.01-1.5 m	2.2	0.9
0.51-1.0 m	2.0	0.8
0.0-0.5 m	0	0
Smooth Bark 5-10 cm (#/100m^2)	-	-
>10 cm	4	4
Rough Bark 5-10 cm	209	88
>10 cm	125	33
Standing Dead 5-10 cm	84	17
>10 cm	32	16
Litter Volume (m^3/100m^2)	0.4	0.2
% Litter Cover	56	13
% Weed Cover	2	1
% Native Grass Cover	-	-
Fallen Branches (#/100m^2)	74	18
Log Volume (m^3/100m^2)	19.4	11.5

Plate 5.1:   The major vegetation types used by White-browed Babblers in the Kellerberrin area; a) *Allocasuarina* shrubland, b) Mixed shrubland and c) *Callitris* woodland.