

Chapter 11

Synthesis

“If we study a system at an inappropriate scale, we may not detect its actual dynamics and patterns but may instead identify patterns that are artifacts of scale. Because we are clever at devising explanations of what we see, we may think we understand the system when we have not even observed it correctly.”

[Wiens 1989]

Population Structure of White-browed Babblers

The population of the White-browed Babbler in the Kellerberrin area was hierarchically structured with four levels of organisation: 1) group (basic breeding unit); 2) social neighbourhood; 3) local population; and 4) metapopulation (Fig. 10.11). This population structure fits the broad definition of a metapopulation, in which a set of local populations are connected by a low level of dispersal (Hanski & Gilpin 1991). However, as with many empirical studies it does not reflect the definition of a metapopulation that has been used to generate most of Metapopulation Theory (Harrison 1991; Harrison & Taylor 1997). Habitat patches used by White-browed Babblers were discrete units in the Kellerberrin landscape and babbler groups within the same patch had greater levels of association than with those groups in other habitat patches. However, each habitat patch did not represent a local population, because most supported too few breeding groups and dispersal between many habitat patches was high. The higher association between groups within the same habitat patch represents social structuring within local populations (*i.e.* social neighbourhood), not local populations themselves. Andrén (1994) has argued that many bird and mammal studies that have used the concept of a metapopulation have done so with habitat patches which are too small to support local populations. This presents a problem, since the processes which are causing extinctions and recolonisations of these

patches may be related more to the dynamics of individuals than populations (Haila 1990; Andrén 1994).

Local populations of White-browed Babblers in the Kellerberrin landscape occurred at a spatial scale larger than that represented by habitat patches, but their boundaries were not discrete. There was a continuous change in the relative rates of dispersal within and between the local population neighbourhoods defined at different scales (Chapter 10). The point along this continuum where local populations should be defined is dependent on that rate of dispersal below which the dynamics of these local populations would still be independent (Harrison & Taylor 1997). It is likely that many real populations are similar to that found for White-browed Babblers, in that they do not have discrete local population structures. Therefore, there is a need for empirical and theoretical investigations of how local population dynamics are affected by varying levels of immigration from other local populations. This would enable a distinction between local populations and single patchy populations to be made.

Another issue that needs to be considered when defining local populations is what temporal scale should the dispersal process be measured at. Generally, dispersal is measured at the scale of a single breeding cycle (*i.e.* from one breeding season to the next). However, in variable environments, such as Australia, population processes are more dependent on the lifetime reproduction of individuals (Rowley & Russell 1991; Haila *et al.* 1993). The current study represents three years in the life of a babbler population. This time period is greater than the breeding cycle of this species (one year). However, it is shorter than the time scale representing the lifetime reproduction of individuals, since first breeding for babblers appeared to be at 2-3 years of age (Chapter 7) and they are long lived birds. Therefore, the annual rate of dispersal between local populations may not need to be as high, because lower levels of dispersal over a longer period may be sufficient to influence the persistence of these local populations.

The distribution of babblers in the Kellerberrin area over a 10 year period (Chapter 4) suggested that no local populations defined by any of the Neighbourhood models had suffered extinction; although, some habitat patches had. However, even this time period is probably too short to assess the likelihood of local population extinction given the long generation time of babblers; and the possible lag in the loss of breeding units, because they

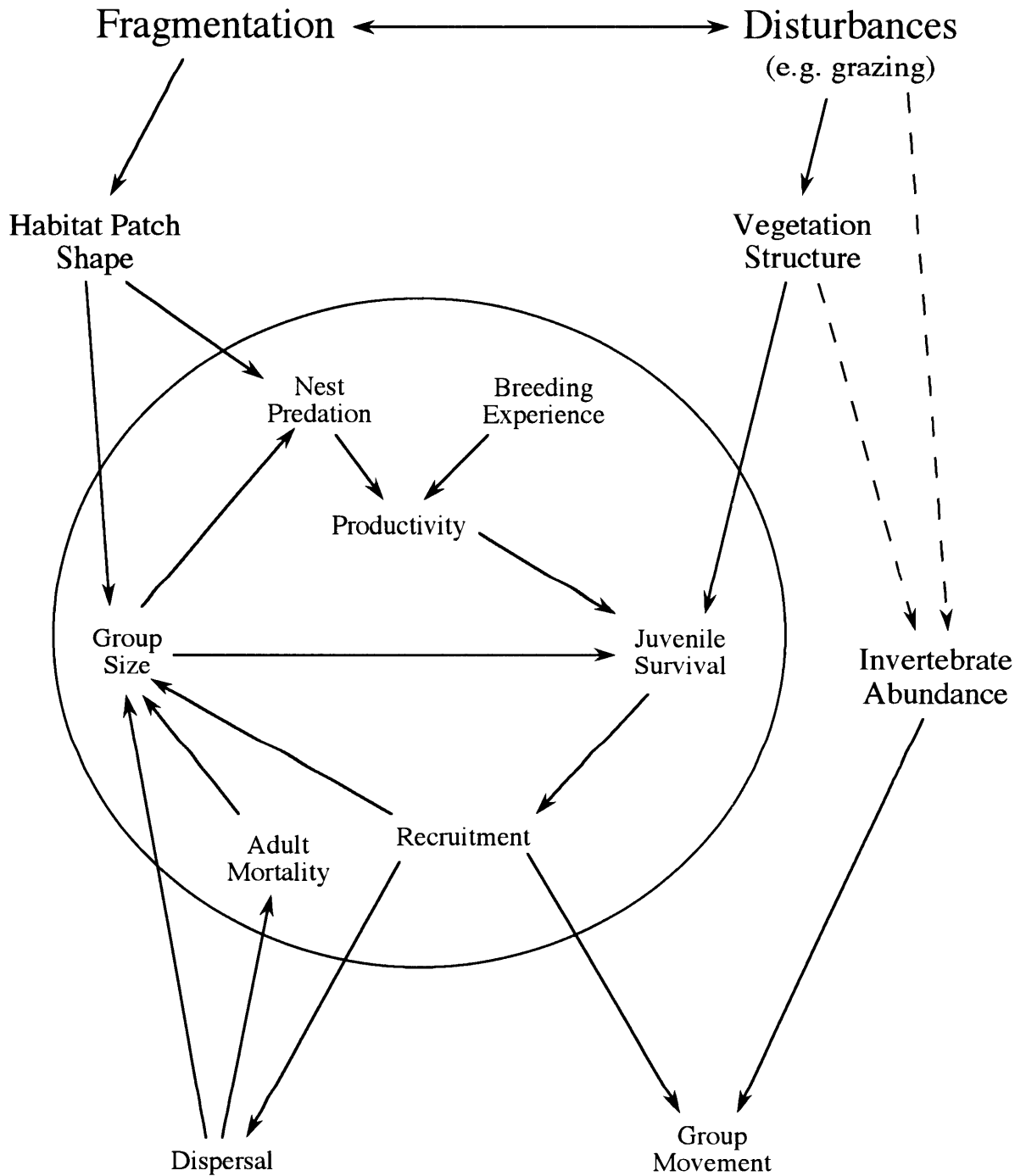
live in groups. This comparison highlights the problem of identifying local populations at inappropriate scales. Problems in the use of inappropriate scales when determining the status of species have been demonstrated by Hecnar and M'Closkey (1997). They found that data collected at four different spatial scales resulted in very different interpretations of the status of the Green Frog *Rana clamitans*. If habitat patches were equated to local populations for White-browed Babblers, turnover of local populations would be considered relatively common (*i.e.* 6% of patches suffered patch extinction and 3% were colonised over no more than 10 years). The short time scale of this analysis would suggest that local populations defined by the Neighbourhood models were stable and had a relatively low risk of extinction. The dynamics of these local populations suggest that neither of these interpretations is likely to be true.

The Effects of Landscape Modification on Population Dynamics

White-browed Babblers are one of the few sedentary, ground foraging insectivores that have been able to persist in the modified landscapes of the Western Australian wheatbelt (Cale 1994; Saunders & Ingram 1995). However, this does not mean that the changes in these landscapes have not adversely affected White-browed Babblers. Habitat loss and fragmentation, and changing disturbance regimes (*e.g.* the introduction of grazing by domestic stock) have had adverse effects on the demography and social dynamics of babbler groups and on the population dynamics of this species.

The reproductive success of individual babbler groups (group dynamics) was influenced primarily by differences in the shape and vegetation structure of habitat patches, which altered the level of nest predation and the survival of juveniles (Fig. 11.1). However, the effects of these habitat differences on nest predation and juvenile survival were modified by differences in group size (Chapter 8). The level of nest predation was the primary determinant of group productivity, though breeding experience may also have had some influence. Nest predation was influenced by the shape of the habitat which comprised a group's home range. Groups living in linear strips of habitat, which were a consequence of the fragmentation process, had substantially higher levels of nest predation than those living in patches. Small groups living in linear strips had little success in producing young.

Figure 11.1: The effects of landscape fragmentation and changes in disturbance regimes on the group dynamics of the White-browed Babbler in the Kellerberrin landscape. Parameters within the circle represent the dynamics of individual babbler groups. Effects occur in the direction of the arrows. Dashed arrows represent effects which were likely, based on the literature, but were not clearly identified in this study.

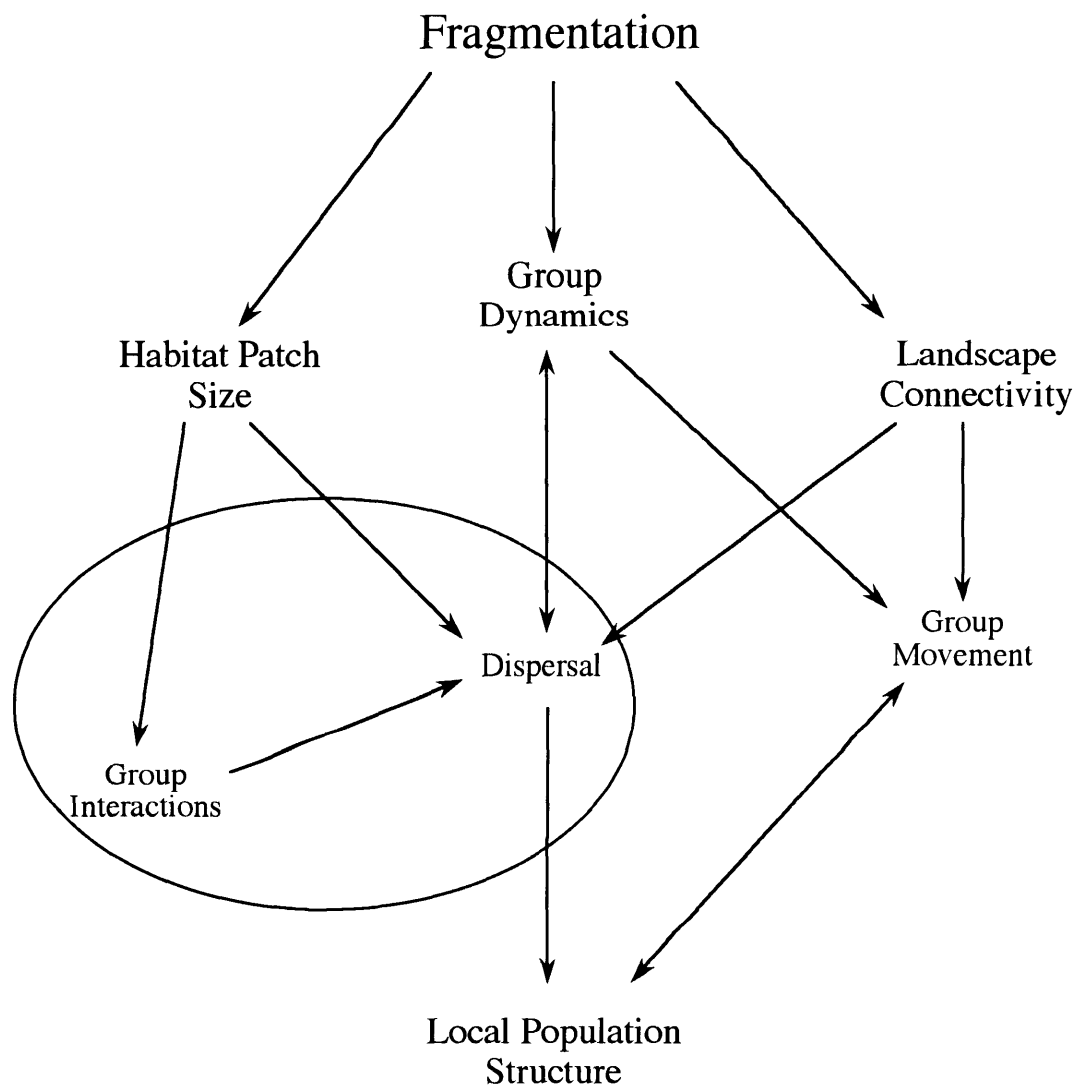


Juvenile survival was low in groups which occupied habitat that had vegetation with low foliage density, but juvenile survival was higher if the group was large (Chapter 8). Lower foliage density was partly due to the changes resulting from the disturbances caused by the grazing of domestic stock (Chapter 5). Such changes in the disturbance regime are influenced by fragmentation. These disturbances have been found to produce strong edge effects; such as lower cover and densities of vegetation, and changes in plant species composition; in remnant vegetation patches which are adjacent to agricultural vegetation (Scougall *et al.* 1993). Consequently, habitat patches in smaller remnants may be subject to greater disturbance levels, because of the greater edge-to-size ratios of the remnants.

The pattern of male dispersal in White-browed Babblers was important to the reproductive success of groups by altering their group size (Fig. 11.2). Male babblers tended to disperse from large to small groups (Chapter 9), because this increased their chances of obtaining a breeding position (Chapter 7). This pattern of male dispersal may have maintained larger groups, and so increased reproductive success, in habitat of lower reproductive quality. However, the process of male dispersal operated at the scale of the social neighbourhood and was adversely affected by habitat fragmentation. Although the proportion of males dispersing from their natal patch was higher in smaller habitat patches, these inter-patch dispersals were restricted to habitat patches which were close together (Chapter 10). Therefore, social neighbourhoods consisted of individual patches, or closely associated clusters of small patches. This means that as fragmentation decreases the size and increases the isolation of habitat patches rates of male dispersal should decline.

The influence of male dispersal on reproductive success, through its effects on group size, means that the reproductive quality of habitat patches is context dependent. Habitat patches which have similar physical characteristics may differ in reproductive quality, because the frequency of male dispersal differs depending on the landscape configuration of the social neighbourhood. The dependence on context of habitat patch quality has important consequences for the proportion of habitat which represents a *sink*, because habitat of moderate quality (HQ2 & 3) changes from *source* to *sink* habitat as the size of the babbler group declines (Chapter 8). Since male dispersal increases the size of small groups, it might be expected that landscape fragmentation would increase the ratio of *sink*-to-*source* habitat by reducing the level of this male dispersal.

Figure 11.2: The effects of landscape fragmentation on the social dynamics and population structure of the White-browed Babbler in the Kellerberrin Landscape. Parameters within the circle represent the social dynamics of babbler groups. Effects occur in the direction of the arrows.



The fragmentation of the landscape in the Kellerberrin area also affects the configuration of local populations of the White-browed Babbler. Dispersal is the major defining process of local population configuration (size and shape). Fragmentation affects dispersal directly through its effect on landscape connectivity and indirectly through its effect on group dynamics (Fig. 11.2). The persistence of local populations of the White-browed Babbler was not assessed directly in this study. However, the size and shape of a local population are likely to be important to its persistence, because populations with more reproductive individuals are less likely to suffer from stochastic extinction (Caughley & Gunn 1996). Local population size also affects the per capita emigration and immigration rates between local populations, which influences the likelihood of population extinction (see Chapter 10).

Group movements add another level of complexity to the relationship between fragmentation and the persistence of local populations. Group movements occurred at a larger spatial scale than the dispersal of individuals (Chapter 10). This may increase the size of local populations, because group dispersals are effectively the mass dispersal of all individuals in the group. However, the loss of groups due to group dispersal is likely to be more pronounced in small local populations which are spatially isolated (Fig. 10.10). This may increase the likelihood of extinction of these local populations.

The dispersal simulation model presented by Brooker *et al.* (1999) showed that the permeability of the boundaries between patches of remnant vegetation and agricultural vegetation (as measured by gap tolerance) alters landscape connectivity in a complex manner (Appendix I). An increasing willingness to cross agricultural vegetation may allow individuals to reach habitat patches which would otherwise have been isolated; but it also alters the spatial pattern of dispersal, which can result in a reduced probability of an individual finding other habitat patches. As gap tolerance increases, remnant vegetation which connects habitat patches becomes less effective in directing dispersal between these patches. These changes in the spatial pattern of dispersal can result in an asymmetry in landscape connectivity between patches (see Chapter 10). Therefore, it is essential that issues of landscape connectivity are considered in a spatially explicit context.

Fahrig (1998) argued, based on the results from a spatially explicit simulation model, that fragmentation of breeding habitat affects population survival only under a very narrow

set of conditions. From these findings she argued that spatially explicit modelling was only necessary when these conditions were met. However, this modelling was done using two underlying assumptions that are not appropriate for many situations of landscape fragmentation. The first of these assumptions is that all of the landscape could be occupied by individuals, but they could only breed in breeding habitat. This assumption, even with different levels of mortality between the matrix and breeding habitat, is inappropriate in many landscapes fragmented by agricultural development. Many species in these landscapes never occupy (except possibly during the short period of dispersal) that portion of the matrix containing agricultural vegetation types (*e.g.* P5 species *sensu* Kitchener *et al.* 1982; and remnant-dependent species *sensu* Saunders 1989; Saunders & de Rebeira 1991). Secondly, Fahrig (1998) limited her modelling to a landscape with a homogeneous matrix, which is unlikely to be common in real landscapes (Wiens 1994, 1997). Species living in landscapes which fail to meet these two assumptions are likely to be affected by spatially explicit fragmentation effects, such as those described for White-browed Babblers.

This study has shown that the fragmentation and modification of landscapes resulting from their development for agriculture represent a complex set of processes which affect many aspects of a species' life history at a number of different spatial and temporal scales. Many of these effects and the interactions between them have important consequences for the persistence of a species (*e.g.* the influence of landscape connectivity and habitat patch size on babbler dispersal behaviour). Others may have little consequence for species persistence, such as changes in hatchability caused by the social disruption of babbler groups resulting from landscape fragmentation (Chapter 8). The essence of good generalisation is retaining those aspects which are important to the process in question, while ignoring those which are not. Therefore, it is necessary to understand the complexity of the interactions between a species' life history characteristics and the characteristics of the landscapes they occupy, in order to obtain appropriate generalisations about landscape fragmentation.

Approaches to the Research of Conservation Management

The destruction and fragmentation of habitat by human development (*e.g.* agriculture) is considered to be one of the principal threats to the persistence of species throughout the world (Wilcove *et al.* 1986; Hobbs *et al.* 1993; Wiens 1994; Caughley & Gunn 1996). In dealing with landscape fragmentation problems there has been some debate about the effectiveness of single-species studies compared to ecosystem approaches (Franklin 1993, 1994; Hobbs 1994; Tracy & Brussard 1994; Wilcove 1994; Lambeck 1997). Single-species approaches have been criticised because they cannot be done at a sufficient rate and consume a disproportionate amount of funding for the results achieved (Franklin 1993; Hobbs 1994). Ecosystem approaches attempt to deal with higher levels of organisation, but critics argue that ecosystems are vague entities and this approach tends to be descriptive rather than prescriptive (Tracy & Brussard 1994; Wilcove 1994; Lambeck 1997). The advocates of both of these approaches argue for a combination of single-species and ecosystem methodologies, and so the difference between these approaches is really one of emphasis. Ultimately, landscapes can only be managed by considering landscape processes, but these processes are species specific.

Lambeck (1997) outlined a methodology which deals with the landscape as a whole, but acknowledges the species specific nature of landscape processes. This methodology attempts to identify a set of species (Focal species) whose requirements for persistence define those attributes of the landscape which must be present to meet the requirements of other species that occur there. He argues that focal species achieve this, because collectively they are the most demanding species for all of the processes which are contributing to the decline of species in that landscape. The Focal species approach is effectively a methodology for decision making. Although this decision making process is sound, the approach presented by Lambeck (1997) depends on the assumption that ecological processes which contribute to the decline of species in a landscape are simply additive. This approach fails to acknowledge that such processes interact and that these interactions are complex, species specific and spatial explicit, as shown in the current study.

Metapopulation Theory and Landscape Ecology deal with different aspects of the interaction between landscape processes and their effect on the persistence of species. The

synthesis of these two disciplines may provide both the theoretical framework and the tools needed to address the interaction between spatial complexity and the processes which affect the persistence of species (Hanski & Gilpin 1991; Wiens 1997; With 1997). One of the major difficulties in achieving this synthesis has been dealing with the complexity of the interactions between processes. Modelling approaches; such as the coupling of neutral landscape models, derived from Percolation Theory, and metapopulation models (With 1997; With & King 1999); are a major step toward dealing with this problem. However, the conclusions based on modelling procedures are only as valid as the simplifying assumptions they operate under. With and King (1999) showed that the location of extinction thresholds predicted by some metapopulation models varied dramatically, sometimes disappearing completely, when assumptions about habitat distribution and dispersal behaviour were modified. Modelling procedures can also be sensitive to the parameter settings under which they are run. Ruckelshaus *et al.* (1997) showed that even small errors in dispersal parameters resulted in large errors in the predictive ability of a spatially explicit population model. They also found that these errors were greatest in landscapes with low proportions of suitable habitat. These are the very landscapes which are of most interest to issues of conservation. Modelling procedures will always provide an answer to questions related to landscape fragmentation, but if the assumptions upon which these models operate are inappropriate then the answer will have little value to scientists and managers. Because of this problem some have criticised the use of general principles derived from modelling procedures in Conservation Biology (Doak & Mills 1994; Wennergren *et al.* 1995).

The problem with these modelling approaches is not the models, but the lack of good empirical data. This empirical data needs to address the validity of the assumptions used in models, but equally modelling research must seek to investigate the influence different sets of assumptions have on model outcomes. Without the effort to improve the empirical base upon which modelling is done the generalisations about how landscape fragmentation affects the persistence of species will continue to elude scientists.

The study of the White-browed Babbler presented in this thesis was not designed to produce specific outcomes which could be used to manage the Kellerberrin landscape. Instead it sought to identify how some aspects of a species' life history interact and how

these interactions influence the species response to the process of landscape fragmentation. It is studies such as this which I believe are essential if the synthesis of Metapopulation Theory and Landscape Ecology is to produce generalisations which will enable a shift from single species “crisis” management of fragmented landscapes to management of whole landscapes which prevent such crises.

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