

# Chapter 9

## The spatial dynamics of the White-browed Babbler

*"In considering demographic processes, movements of individuals into and out of populations are potentially as critical as births and deaths. And, the impact is not merely on numbers (although this in itself can be substantial), but also on the sex ratios, age structure, social dynamics, and genetics of populations."*

[Stenseth & Lidicker 1992]

### Introduction

An understanding of the spatial dynamics of individuals is fundamental to understanding the population dynamics of a species. For cooperative breeding species two questions have dominated the investigation of spatial dynamics. Firstly, why is there generally a sex-bias, which differs between taxa, in those individuals that disperse (Greenwood 1980; Greenwood & Harvey 1982)? Secondly, what mechanism results in the lack of dispersal from the natal territory (natal philopatry *sensu* Zack 1990), which often occurs in cooperative breeding species (Brown 1974; Woolfenden & Fitzpatrick 1978; Stacey & Ligon 1987, 1991)? The first of these lines of investigation has been driven by research into the dispersal process, while the second originates from work dealing with the evolution of cooperative breeding. The consequence of this is that there has been little interaction between the two approaches and there appears to have been little attempt to merge the ideas generated from these approaches into a single body of theory for dispersal.

A number of processes have been invoked as the causal factor for sex-biased dispersal patterns in birds and mammals. Most common among these are competition for mates or resources (Murray 1967; Dobson 1982; Moore & Ali 1984) and inbreeding avoidance (Dobson & Jones 1985; Pusey & Wolf 1996; Koenig *et al.* 1998). More recently

the view that female choice of breeding partners has played an important role in the evolution of mating systems and consequently will influence dispersal patterns has gained some acceptance (Burley & Parker 1997; Johnson & Burley 1997). Dobson and Jones (1985) argued that these processes are not mutually exclusive and that it was reasonable to expect that they may operate in combination to influence dispersal, though their relative importance may differ for different species.

Greenwood (1980) detailed a model (Mating System model) to explain the dispersal patterns in birds and mammals and especially the observed differences in the sex-bias of dispersal between these taxa. He argued that these patterns were driven by the mating systems of species. The mating system in birds is generally dominated by resource defence and female-biased dispersal occurs, while mammal mating systems predominantly involve the defence of mates and male-biased dispersal occurs.

Seeking the mechanism which results in natal philopatry in cooperative breeding species has dominated research on these species. The Habitat-Saturation model was an early attempt at this (Brown 1974; Woolfenden & Fitzpatrick 1978). This model proposed that natal philopatry was imposed on individuals by a lack of suitable habitat in which to breed. Emlen (1982) expanded on the Habitat-Saturation model in his Ecological Constraints model. As the model's name implies, this theory proposes that natal philopatry is the result of dispersal being constrained by the costs of dispersing and breeding independently. This is the common thread between it and the Habitat-Saturation model, but the Ecological Constraints model does not limit the costs of dispersal to those associated with habitat saturation.

The ecological parameters that have been proposed as possible constraints on dispersal are numerous. The most frequently proposed are a shortage of suitable habitat (Habitat Saturation model), or of mates (Emlen 1982). Emlen (1982) also proposed that extreme environmental harshness in unpredictable environments may constrain individuals from dispersing, because the costs of rearing young are prohibitive. However, this is functionally equivalent to a shortage of suitable habitat. The Critical Resource model proposed by Walters *et al.* (1992) argued that certain resources were critical and their presence greatly increased the quality of the habitat. Their absence would result in habitat being unoccupied despite individuals being available in adjacent areas. This model also

appears to be a specific case of the Habitat Saturation model. The Skills hypothesis proposes that young individuals require time to gain the necessary skills to breed and this can lead to delayed maturity and hence cooperative breeding (Lack 1954; Heinsohn 1991).

Stacey and Ligon (1987, 1991) have argued that two issues are not addressed by the Habitat Saturation and Ecological Constraints models. Firstly, dispersers of many species face ecological constraints which result in their failure to breed, but they do not display natal philopatry. Secondly, in some cooperative breeding species individuals fail to disperse despite suitable habitat being available. This led Stacey and Ligon (1987, 1991) to propose the Benefits of Philopatry model. They argued that natal philopatry is not the result of constrained dispersal, but a choice not to disperse resulting from benefits in remaining in the natal territory.

This chapter describes the spatial pattern of White-browed Babbler groups and the observed dispersal behaviour of both groups and individual birds. Using these data and the model of the social structure of babblers proposed in Chapter 7, I propose a dispersal model for this species. This model is then discussed in relation to dispersal theory.

## Methods

### *Monitoring of Groups*

I visited most habitat patches in Sites A and B regularly (approximately 1-4 times per month) throughout the breeding seasons (July-October) of 1994 to 1996. In addition, some patches were visited during the 1997 breeding season. Visits during the non-breeding season were less frequent, but most habitat patches were visited at least four times during this period of each year.

In addition to the regular searches of Sites A and B, the habitat patches in a third site (Site C) were visited from the beginning of the 1994 breeding season to the end of the 1995 breeding season. After this, these patches were visited once or twice a year. I also searched (approximately once each year) remnant vegetation around the edges of Sites A and B in an attempt to find birds and groups which had left these study sites. These searches were generally conducted during the non-breeding period.

During each visit to a habitat patch I attempted to locate all groups of babblers occupying that patch. If a group was not located I made an intensive search for that group

on my next visit to its habitat patch. These searches included all remnant vegetation near the group's usual location.

For each visit to a group I recorded all banded individuals seen in each group and estimated the number of unbanded birds present. On most occasions when I found a group a high proportion of the banded birds were seen; however, I considered a group had been found when I had seen a minimum of two banded birds from that group. Sometimes members of several groups were observed together. In these cases I considered both groups to be present if I recorded at least two banded birds from each group, the number of birds was consistent with the number in both groups, and I could find no sign of these groups elsewhere.

Occasionally the birds in a group could be spread out over a large area, so I considered each group's location to be the centre of the area where the majority of its members were. During the breeding season the breeding female and the dominant male were frequently near the nest, while the rest of the group could be some distance away. On these occasions I considered the group's location to be where the non-breeding members of the group were. This prevented the group's location from being restricted to the nest area during the breeding season. I recorded all group locations as distances and directions from points easily identified on aerial photographs. These locations were later mapped for analysis of home range size and shape.

Group membership for a given year was defined as those individuals that remained in the group throughout most of the breeding season. If an individual was absent from the group for some part of the breeding season but then returned to the group it was considered a group member for that year. I considered a bird to have been temporarily absent from the group if it was not recorded in the group for a period of at least two months, during which time I must have checked the group at least four times.

Group size was the number of birds considered to be a member of a group and was determined for each year (see Chapter 7). The average density of birds in each habitat patch was determined from the sum of the average group size (over three years) of the groups in a habitat patch, divided by the area of the habitat patch.

### *Home Ranges*

A home range was any area in a habitat patch which was occupied by a babbler group for at least one breeding season. One home range was included despite being unoccupied for the duration of this study, because it was known to have supported a group of babblers in 1991 (*pers. obs.*). A home range was considered to be vacant in a year if it was not occupied by a babbler group during that breeding season.

The home range of a group was measured using the smallest polygon which encompassed all locations of that group. The boundaries of this home range were restricted to native vegetation, because babblers were never found foraging on agricultural land. All locations recorded for a group throughout the three years of the study were combined to estimate its home range size and shape. In a few cases the home range of a group shifted markedly from one year to the next (*i.e.* there was no overlap in the home range between years). In these cases I used the home range for which the largest number of observations were available. Estimates of home range size were calculated for groups which were followed through at least one full year. Those groups which disappeared from the study area for a prolonged period (two or more months) during every non-breeding period were not included in the analysis of home range size, because the extent of their non-breeding home range was not known. The non-breeding home range of those groups which disappeared for only one or two non-breeding periods was calculated from their home range in the years they remained in the study area and so were possibly underestimated.

I defined the breeding territory as that part of a group's total home range that was occupied during the breeding season of each year. As with the estimates of the total home range I combined the observations for all of the breeding seasons the group was present. If a group shifted its breeding territory between nesting attempts I used the breeding territory for which the largest number of observations were made.

A home range was classified as: 1) *linear*, where the home range was restricted to linear strips of vegetation (less than 100m wide); 2) *patch*, where the home range encompassed an area within a patch of vegetation in a remnant; or 3) *linear/patch*, where the home range incorporated habitat from a patch of vegetation in a remnant and associated linear strips of vegetation. The breeding territories of some groups were restricted to a patch of remnant vegetation, but during the non-breeding period these groups extended

their range into associated linear strips of vegetation. These groups were classified as having a linear/patch home range.

Two measures, linear dimension and area, were used to describe the size of home ranges and breeding territories. The linear dimension was defined as the straight line distance between the farthest two points on the boundary polygon of the home range or breeding territory. The area of a home range or breeding territory was measured to the nearest 0.1 hectare, while the linear dimension was measured to the nearest 10 metres. Both measures were calculated using the GIS system GRASS.

The quality of food resources in the habitat of each home range was not measured in this study, but a crude measure of this was obtained from the abundance of invertebrates (major prey items) in each habitat patch. This was based on the invertebrate sampling described in Chapter 6. It included invertebrates caught in the litter, ground debris and from the shrub canopy. The total number of invertebrates caught in the standard sampling regime was used as a measure of habitat quality for each habitat patch. This index measured the abundance of invertebrates in a standard unit of area and so was independent of the size of the habitat patch.

The breeding quality of each home range was defined primarily by the foliage density of the vegetation and secondarily by the habitat configuration where the group nested (see Chapter 8). The best quality home ranges (HQ 4) had high foliage density and nesting areas located in patches of vegetation. Medium quality home ranges either had high foliage density and nesting areas located in linear strips of vegetation (HQ 3), or low foliage density and nesting areas located in patches (HQ 2). Home ranges with low foliage density and nesting areas located in linear strips of vegetation were considered to be the poorest quality (HQ 1).

### *Movements by Individuals*

Movements made by individual White-browed Babblers were classified as either *visits*, which were temporary movements to new groups; or *dispersals*, which were permanent movements of individuals to new groups.

I measured dispersal distances in a straight line from the edge of the home range of the original group to the edge of the home range of the new group. This meant that

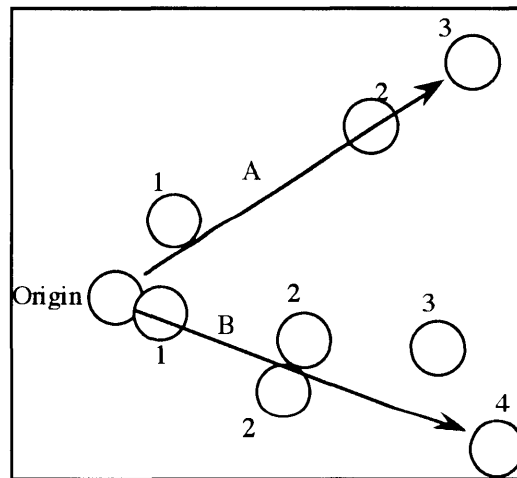
dispersals between groups which had abutting or overlapping home ranges had a dispersal distance of zero metres. Four birds which were banded and moved prior to the start of this study were included in this analysis, because the home ranges of the groups they dispersed to and from were known. Dispersal distances were measured to the nearest 10 m using the GIS system GRASS.

Dispersal distances were classed at 1000 m intervals. The resulting distribution was biased by the finite size of the study sites and the uneven censusing effort of home ranges within these study sites (Barrowclough 1978; Porter & Dooley 1993; Baker *et al.* 1995). Therefore, I adjusted the observed distribution using a method adapted from Matthysen *et al.* (1995). For each home range I counted the number of neighbouring home ranges within five concentric circles with radii which increased by 1000 m. I then calculated the proportion of the home ranges within each concentric circle that were censused for the whole study period. Each home range was weighted relative to the effort made (*e.g.* a home range which was censused for the whole study period was weighted at 1.0, while a home range which was censused for only one of the three years of this study was weighted at 0.3). The average proportion of home ranges censused in each distance class was then used to weight the observed number of dispersals in that distance class.

Dispersals were also represented in terms of the number of home range equivalents that were crossed (Woolfenden & Fitzpatrick 1984; Russell & Rowley 1993b). The usual method of estimating the number of home ranges crossed is to divide the dispersal distance by the average width of a home range. Since much of the landscape in this study contained no home ranges, because it was unsuitable habitat, such a measure would be meaningless. Instead the number of home ranges crossed was estimated as shown in Figure 9.1.

The analysis of the social status of birds which dispersed was based on the members of nine of the 14 groups for which nest observations were made (Chapter 7). The other five groups were not included in this analysis, because their nests were observed at the end of the study, so it was not known what happened to their members after their nests had been watched.

**Figure 9.1:** Method of determining the number of home range equivalents traversed by a dispersing bird. The circles represent the home ranges of babbler groups, and lines represent dispersals. The numbers represent the number of home range equivalents moved. In dispersal A the bird moved 3 home range equivalents, while in dispersal B it moved 4 home range equivalents.



### *Statistical Analysis*

I used the nonparametric Kruskal-Wallis test (H) to analyse differences in home range area and linear dimension, and group size between home ranges with different configurations. A nonparametric multiple comparison test (Q) was then used on all significant results to determine which pairs of configurations differed significantly (Zar 1996). No comparison was made between the area and linear dimensions of a group's non-breeding home range and breeding territory, because breeding territories were defined as a subset of the non-breeding home range, so they were not independent.

Correlation coefficients ( $r$ ) were calculated between the number of individuals in a group and the area of their breeding territories and non-breeding home ranges. I tested if these correlations were significantly different from zero with a Student's  $t$ -test (Zar 1996).

Linear regression was used to assess the relationship between the abundance of invertebrates and the average density of birds in a habitat patch. This was assessed for Spring and Summer estimates of invertebrate abundance.

The Kolmogorov-Smirnov Goodness of Fit test (D) for grouped data was used to compare the likelihood of individuals dispersing to or from groups occupying breeding habitats of differing quality. This is a more powerful test than the Chi-square test when the



categorical variable is ordered, as in this case (Zar 1996). The expected values for these analyses are based on the number of individuals in groups occupying breeding habitat of each quality. The test statistics were compared to the critical values presented by Zar (1996), which require that the number of data is an even multiple of the number of categories, which was generally not the case with the current analyses. Therefore, I used the most conservative critical value for each significance level, as recommended by Zar (1996).

The distribution of dispersal distances was compared to an expected distribution using the Kolmogorov-Smirnov Goodness of Fit test (D) for grouped data (as above). I used an expected distribution that assumed individuals had an equal probability of moving to any home range within a 5000 m radius of their original home range. This distribution was estimated using the average proportion of censused home ranges in each distance class. This was calculated from the average number of censused home ranges within each distance class for all home ranges in the study sites. Since the expected distribution was based on censused home ranges only, the raw dispersal data were used in this analysis.

## Results

### *Territoriality*

#### *Interactions between groups*

I observed 38 interactions between groups of White-browed Babblers. All except two of these interactions were between groups in the same habitat patch. The two exceptions involved groups from adjacent habitat patches, which were connected by remnant vegetation and were only a few hundred metres apart. Most interactions were between two groups (35 interactions), but two interactions involved three groups and one involved four groups.

Interactions between groups were observed at all times of the year, but they were more frequent during the breeding season. The behaviour of group members during these interactions also differed significantly between the breeding season, and the pre- and post-breeding periods (Table 9.1). The most common type of interaction was for members of two or more groups to forage as a single group (*Foraging Interaction*). These interactions could last for several hours. The end of a foraging interaction was never obvious, because

individuals slowly coalesced back into their respective groups. Most foraging interactions occurred during the non-breeding period. Three of the eight foraging interactions I observed during the breeding season occurred between groups that had finished nesting and had young juveniles. Therefore, these cases could be considered as post-breeding interactions.

**Table 9.1:** Types of group interactions and their frequency of occurrence at different times of the year. See text for descriptions of interaction types.  $H_0$ : There is no difference in the frequency of each interaction type between the three time periods.

Time of Year	Interaction Type			Number of Interactions
	Foraging	Calling displays	Chases	
Breeding (July-Oct.)	8	10	3	21
Post-breeding (Nov.-Feb.)	8	1	0	9
Pre-breeding (Mar.-June)	8	0	0	8
$\chi^2_{(4)} = 13.01 \quad p = 0.011$				

Almost all of the other two types of interactions occurred during the breeding season (13 of 14 observations) and all involved calling between members of different groups (*Calling displays*). Calling displays generally involved more than one bird from each group, but not all members of groups were involved on all occasions. Calling displays sometimes led to the third type of interaction (*Chases*), where two birds, one from each group, chased each other (Table 9.1). I was never able to determine which individuals were involved in chases, because the combatants moved too quickly during the chase and after the chase tended to hide in dense vegetation. During calling displays and chases it was common for some members of the groups involved to forage together. However, in contrast to foraging interactions, these interactions were short (less than 20 minutes) and always led to both groups moving some distance away from each other.

### *Breeding territory*

The average area of breeding territories varied significantly between the different habitat configurations ( $H_{(2)} = 13.25$   $p = 0.001$ ) (Table 9.2). Linear breeding territories were smaller than patch and linear/patch breeding territories ( $Q_{(3)} = 3.62$   $p < 0.001$ ,  $Q_{(3)} = 2.44$   $p < 0.05$ , respectively), but there was no significant difference between the average area of linear/patch and patch breeding territories ( $Q_{(3)} = 1.28$   $p > 0.5$ ). As with area, there was a significant variation in the average linear dimensions of different shaped breeding territories ( $H_{(2)} = 8.31$   $p = 0.016$ ). Linear breeding territories were significantly longer than patch territories ( $Q_{(3)} = 2.74$   $p < 0.02$ ). They were also longer than linear/patch territories, but this difference was only weakly significant ( $Q_{(3)} = 2.32$   $p < 0.1$ ). There was no significant difference in the average linear dimensions of patch and linear/patch territories ( $Q_{(3)} = 0.45$   $p > 0.5$ ).

**Table 9.2:** The area (ha) and longest linear dimension (m) of home ranges and breeding territories of different shape. Values are mean  $\pm$  SE.,  $n$  = the number of groups observed with a home range of the given shape.

	Home Range Shape			All Groups ( $n = 30$ )
	Linear ( $n = 8$ )	Linear/Patch ( $n = 11$ )	Patch ( $n = 11$ )	
<b>Area</b>				
Breeding Territory	$2.2 \pm 0.3$	$4.1 \pm 0.5$	$5.3 \pm 0.6$	$4.0 \pm 0.4$
Home Range	$2.9 \pm 0.5$	$7.7 \pm 1.0$	$8.2 \pm 0.8$	$6.6 \pm 0.6$
<b>Linear Dimension</b>				
Breeding Territory	$690 \pm 139$	$397 \pm 51$	$361 \pm 31$	$462 \pm 48$
Home Range	$1028 \pm 164$	$1023 \pm 98$	$555 \pm 24$	$853 \pm 69$

### *Non-breeding home range*

During the non-breeding season groups occupied a home range which encompassed their breeding territory, but covered a substantially larger area. These home ranges

frequently overlapped with those of adjacent groups. The non-breeding home range of a babbler group was on average 65% larger in area and 85% longer than their breeding territory (Table 9.2).

There were significant differences in the average area of different shaped home ranges occupied by babblers in the non-breeding season ( $H_{(2)} = 15.76$   $p = 0.0004$ ) (Table 9.2). The area of patch and linear/patch home ranges did not differ significantly ( $Q_{(3)} = 0.48$   $p > 0.5$ ), but both were larger than linear home ranges ( $Q_{(3)} = 3.72$   $p < 0.001$ ,  $Q_{(3)} = 3.28$   $p < 0.005$ , respectively). The variation in the average linear dimensions of home ranges with different shapes was much greater than that found for breeding territories ( $H_{(2)} = 15.88$   $p = 0.0004$ ). Because of their more circular shape, patch home ranges had significantly shorter linear dimensions than linear and linear/patch home ranges ( $Q_{(3)} = 3.20$   $p < 0.005$ ,  $Q_{(3)} = 3.57$   $p < 0.001$ , respectively). The average linear dimensions of linear and linear/patch home ranges were similar ( $Q_{(3)} = 0.07$   $p > 0.5$ ).

#### *Relationship between group size and home range*

There was a significant, but weak, correlation between the area of a group's home range and the maximum number of individuals in the group ( $r = 0.45$ ,  $t_{(28)} = 2.65$   $p < 0.02$ ). However, there was no significant correlation between the area of a group's breeding territory and maximum group size ( $r = 0.36$ ,  $t_{(28)} = 2.00$   $p < 0.1$ ).

Group size varied significantly between groups occupying home ranges of different shapes ( $H_{(2)} = 14.74$   $p = 0.0006$ ) (Table 9.3). Groups occupying linear home ranges were smaller than those occupying linear/patch or patch home ranges ( $Q_{(3)} = 3.77$   $p < 0.001$ ,  $Q_{(3)} = 2.44$   $p < 0.05$ , respectively). There was no significant difference in group size between groups occupying linear/patch and patch home ranges ( $Q_{(3)} = 1.44$   $p > 0.2$ ).

There was no significant relationship between the abundance of invertebrates in habitat patches during Spring and the average density of birds in those habitat patches (Adj.  $R^2 = 0.11$ ,  $F_{(1,7)} = 1.86$   $p = 0.222$ ). There was also no significant relationship between invertebrate abundance during Summer and the average density of birds in those habitat patches (Adj.  $R^2 = 0$ ,  $F_{(1,7)} = 0.1$   $p = 0.762$ ).

**Table 9.3:** Variation in the size of groups occupying home ranges with different shapes.

Group Size	Home Range Shape		
	Linear	Linear/Patch	Patch
Number of Groups	8	11	11
Mean $\pm$ S.E.	4.0 $\pm$ 0.4	8.8 $\pm$ 0.9	6.6 $\pm$ 0.6
Range	2-6	3-13	4-10

### *Group Budding*

During this study six new groups were formed in a similar way to the *budding* process described by Woolfenden and Fitzpatrick (1978, 1990) for Florida Scrub-jays. Group budding involved individuals splitting from their group and attempting to breed. Generally (5 of 6 cases) these new groups occupied a portion of the original group's home range. In three groups which split the only birds to separate from the original group were the new breeding pair, while in the other three cases one or two other group members joined the new breeding pair. Four of the six groups split at the beginning of the breeding season. The other two groups split during the post-breeding period (November to February).

In four cases of group budding the breeding pair of the new groups comprised a resident male from the original group and a female which had dispersed into the original group sometime during the previous year. The origins of the new breeding pairs in the remaining two group buddings were uncertain. In three cases the status of the new dominant male was known in the previous breeding season (see chapter 7), two were the second ranked males in their original group and the other was a secondary helper in his original group. The latter male appeared to have been absent from his original group for most of the previous breeding season.

In all cases of group budding the original group was large and the number of birds which budded from this original group increased with group size. One group with seven

birds had a pair bud off, two groups with nine birds had three and four birds bud off, one group with 10 birds had four birds bud off, and finally a group of 11 birds had two different pairs bud off in the same year.

The breeding success of new groups formed from group budding was low. Only two groups, both containing four birds, successfully fledged nestlings and only one of these raised a juvenile to recruitment. The persistence of groups formed by budding appeared to be related to group size, four (a pair, the group of three and both groups of four) persisted for more than one year, while two pairs disappeared in their first summer.

### *Group Movements*

Most babbler groups occupied the same area from one year to the next. However, I observed a number of babbler groups moving out of their breeding territory during the non-breeding season of one or more years. This was different from the expansion of the breeding territory observed in most groups. These groups moved to a new area which did not encompass the breeding territory. On most occasions the location of this area was unknown, because it was outside the study sites and those areas searched adjacent to them. In the majority of group movements the group did not return to their original breeding territory and was never seen again. These movements I have called *group dispersals*. Some groups, however, returned to their breeding territory prior to the next breeding season. I have called these movements *group visits*.

Despite failing to find groups when they moved beyond the area around their breeding territories, it is unlikely that these events represented groups breaking up or mass mortality. This is based on three pieces of evidence: 1) some groups returned after movements, 2) I found two groups in road verges 600-800 m from their breeding territories just before they disappeared for the Summer, and 3) new groups dispersed into the study sites.

The number of groups that moved varied from a low of 22% (6 of 27) in 1995/96, to 28% (9 of 32) in 1994/95, and 30% (8 of 27) in 1996/97 (Appendix 9.1). Of these 23 group movements, 14 (61%) were group dispersals and seven (30%) were group visits. Two other groups moved in 1996/97, but it was not known if they returned, because their original home ranges were not searched in the 1997 breeding season. In addition to the

dispersal of groups out of the study sites, there were six groups which dispersed into the study sites during the period 1994 to 1996. The origin of these new groups was unknown, because none contained banded birds.

The abundance of invertebrates in Summer was significantly lower in habitat patches from which at least one group moved compared to habitat patches where no group movement was found ( $U_{(3,6)} = 17$   $p = 0.039$ ) (Table 9.4). There was no significant relationship between the abundance of invertebrates in Spring and group movements ( $U_{(3,6)} = 16$   $p = 0.071$ ). The average area of habitat patches from which groups moved was similar to that of habitat patches from which groups did not move ( $U_{(5,5)} = 15$   $p = 0.602$ ) (Table 9.4).

**Table 9.4:** Differences in the average abundance of invertebrates and the area of habitat patches from which groups moved or did not move. The index of invertebrate abundance is the total number of invertebrates collected from a standard sampling regime from litter, logs and shrub canopies. All values are mean  $\pm$  S.E.

	Index of Invertebrate Abundance		Habitat Patch Area
	Summer	Spring	
Group Movements	146 $\pm$ 24	604 $\pm$ 61	15.2 $\pm$ 4.4
No Group Movements	269 $\pm$ 24	423 $\pm$ 11	12.9 $\pm$ 5.1

The shape of the home range occupied by groups had no significant effect on the likelihood of a group moving during the Summer ( $\chi^2_{(2)} = 0.33$   $p = 0.850$ ). The number of groups which moved was too small to test for the effect of breeding habitat quality on the likelihood of groups moving. However, breeding failure significantly increased the likelihood of groups not returning from a move (*i.e.* group dispersal) ( $\chi^2_{(1)} = 10.72$   $p = 0.001$ ). Eighty six percent of groups that dispersed failed in their attempts to fledge young or their juveniles died prior to dispersing, while all groups which made group visits had successfully fledged young and had juveniles when they moved.

### *Group Turnover*

Most new groups found in the study areas were the result of group dispersals or group budding (Fig. 9.2). The only exception was a group which was formed, in a vacant home range, by individuals dispersing from at least two different groups.

When groups budded the new group generally occupied a part of the original group's home range. There was one exception in which the new group occupied a vacant home range adjacent to their original group's home range. New groups which arose from group dispersals generally occupied vacant home ranges; although, one dispersing group took over most of the home range of an existing group, which continued to occupy the remainder of its original home range.

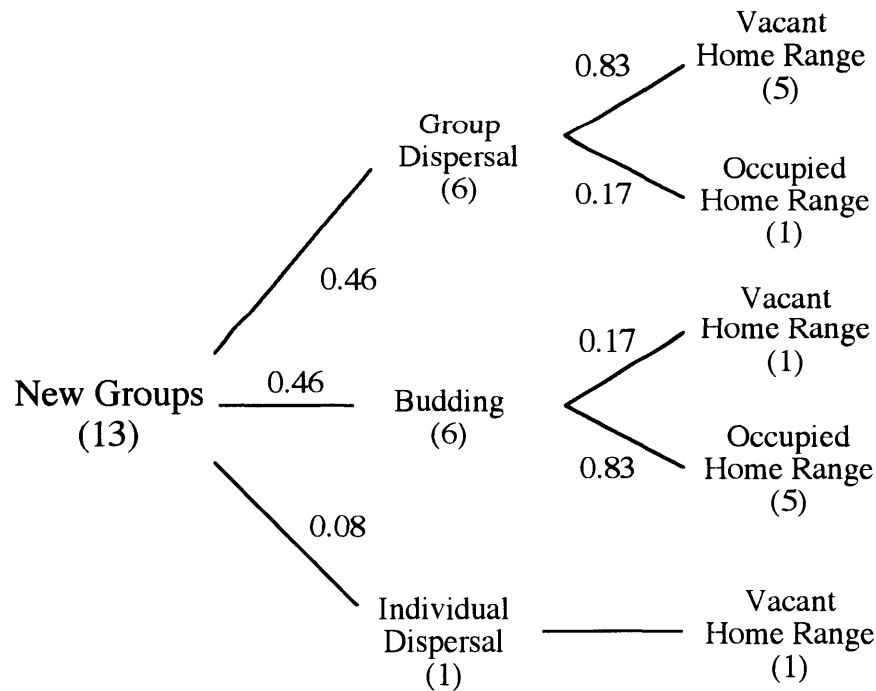
A total of 20 home range vacancies were available during the study period (Fig. 9.3). Five of these existed when the study started in 1994. All but one of the remaining 15 vacancies were the result of group dispersals. The one exception was a group which lost members periodically over a two year period until the home range became vacant.

Twelve (60%) of the vacant home ranges were occupied during the study; five were occupied by groups dispersing into the study area; while the others were occupied, in various ways, by individuals in groups originating from the study area (Fig. 9.3).

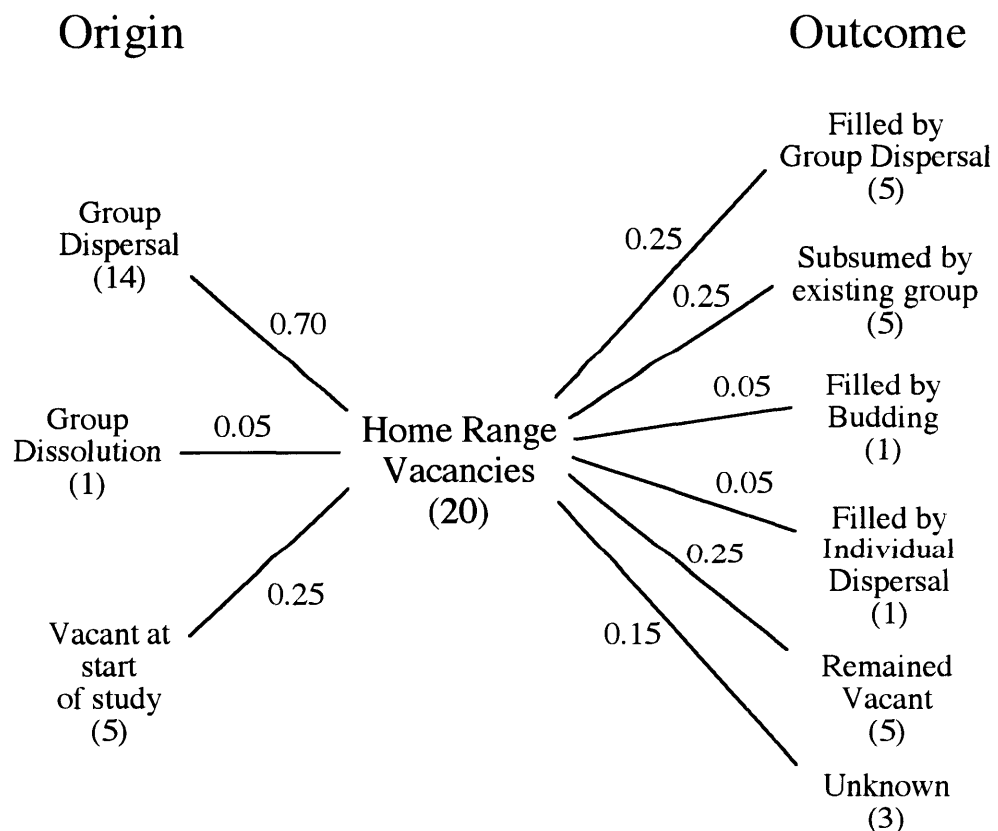
The probability of a home range being occupied in any one year increased with increasing breeding habitat quality (Fig. 9.4), but the differences were not significant ( $F_{(3,26)} = 0.46$   $p = 0.714$ ).



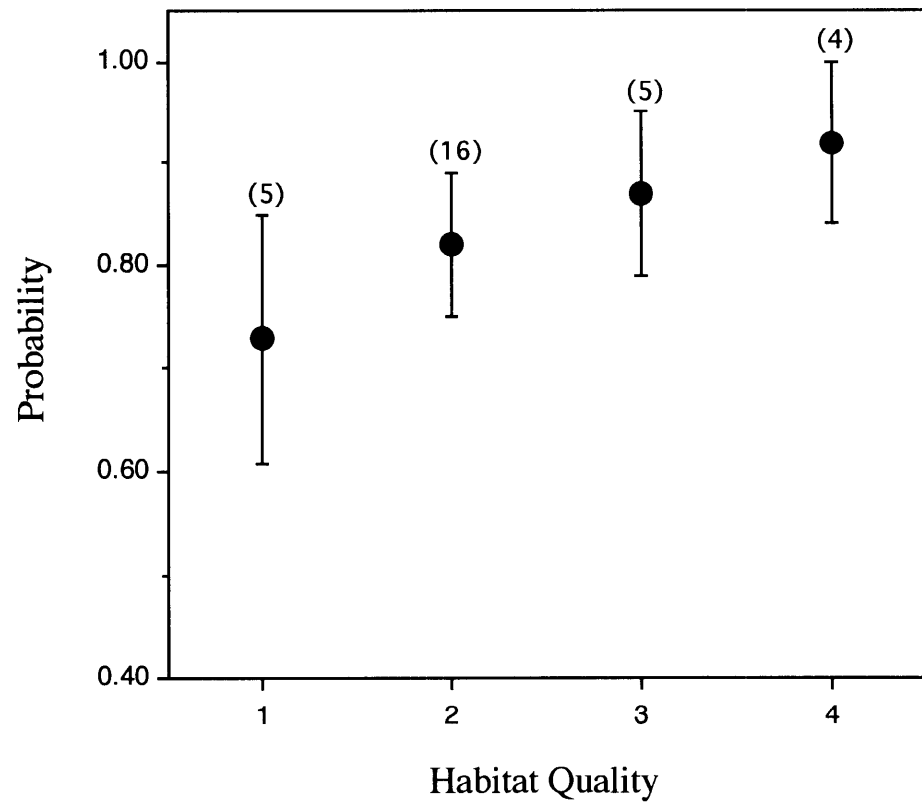
**Figure 9.2:** A probability tree for group formation, based on observations from 1994 to 1997. The values associated with each line represent the probability of a new group forming by following that pathway. The values in parentheses indicate the number of groups.



**Figure 9.3:** A probability tree of the origin and outcome of home range vacancies based on observations from 1994 to 1996. The values associated with each line represent the probability of a vacancies forming or being filled by that method. The values in parentheses indicate the number of vacancies.



**Figure 9.4:** The probability of home ranges of different breeding quality being occupied for a year. Values represent mean  $\pm$  S.E. Sample sizes are shown in parentheses.



## *Movements by Individuals*

### *Visits*

From 1994 to 1997 sixteen individuals were observed visiting 20 groups. In 18 of these visits the bird was seen in a new group on only one occasion, so it was not possible to determine the duration of visits. In the other two cases the visiting birds were seen twice (12 and 13 days apart) in the visited group. These observations suggest that birds visit groups for only short periods, but visiting birds were frequently absent from their own group for periods of several months. Since birds were never seen wandering alone in the study sites, it seems likely that they were visiting more than one group. If this was the case then visits were probably much more frequent than was observed. This is supported by the fact that another 18 individuals were found to have similar absences from their group to those of visiting birds, but were not found in any other group.

Seventeen of the 20 observed visits were to groups in the same habitat patch as the visiting bird's own group and most of these (15 of 17) were visits to adjacent groups. The three visits observed to groups in a different habitat patch were made by one bird, which visited three groups in an adjacent habitat patch (650 m away) during two separate visits.

All birds which were found to have prolonged absences from their group are considered to be visiting other groups in the following analyses. Individuals of both sex were found visiting other groups, but it was found more commonly in males. Seventeen (50%) of the birds that are considered to have been visiting other groups were males, twelve (35%) were females, and five (15%) were of unknown sex. Two females were known to be the breeding female in their group when they made visits.

Males and females left their groups to visit other groups at different times of the year (Table 9.5). Males were rarely absent from their group during the breeding period, while females were absent during both the breeding and non-breeding periods.

Birds that had visited other groups were equally likely to remain in their own group or disperse afterwards. Nine (56%) males remained in their own group after visiting other groups, while six (35%) dispersed, and two (9%) disappeared (*i.e.* dispersed or died). For females, six (55%) remained in their own group, one (9%) dispersed, and four (34%) disappeared.

**Table 9.5:** The timing of prolonged absences from their group by male and female babblers. The values represent the number of periods of prolonged absence observed in 17 males and 12 females.  $H_0$ : There was no difference between males and females in the timing of prolonged absences.

	Non-breeding period (November - June)	Breeding Season (July - October)
Males	21	3
Females	7	8
$\chi^2_{(1)} = 5.72 \quad p = 0.017$		

### *Dispersals*

From 1994 to 1997 forty one individuals were observed dispersing to 42 different groups. Six birds were found moving to groups for a short period of time before they continued their dispersal to another group, where they stayed for the remainder of the study. I considered these multiple-group dispersals to be single dispersals from their original group to the final group, because the birds joined intermediate groups during the non-breeding period, or were not in these groups for long enough during the breeding season to contribute significantly to a breeding attempt.

I found little difference in the frequency of female and male dispersal, with 19 (46%) females, 17 (42%) males and 5 (12%) birds of unknown sex dispersing. However, 62% (25 of 40 birds) of birds known to have joined groups were female (see also Table 7.2). This suggests that there may be a slight female-bias in the frequency of dispersal.

Males generally started dispersing during the breeding season (12 of 14 males) with only one starting during each of the pre- and post-breeding periods ( $\chi^2_{(2)} = 7.99 \quad p=0.018$ ). In contrast, females started dispersing at any time of the year ( $\chi^2_{(2)} = 0.55 \quad p=0.758$ ), with seven starting during each of the breeding and post-breeding periods and four starting in the pre-breeding period. It was not known when the dispersals of four birds (3 males and 1 female) started, because they dispersed before the start of this study (see methods).

The breeding quality of the habitat in a home range had no effect on the groups from which birds dispersed (Table 9.6). Both sexes dispersed from large (7-13 birds) and small

(3-6 birds) groups with probabilities equivalent to those expected based on the number of birds in groups of each size (Males  $\chi^2_{(1)} = 0.18$   $p = 0.669$ ; Females  $\chi^2_{(1)} = 0.004$   $p = 0.950$ ). The previous nesting success of the group also had no significant effect on the groups from which males or females dispersed (Males  $\chi^2_{(1)} = 0.03$   $p = 0.870$ ; Females  $\chi^2_{(1)} = 0.01$   $p = 0.920$ ).

**Table 9.6:** The relative frequency of birds dispersing from groups occupying home ranges of different breeding habitat quality (1 represents the lowest and 4 the highest quality home ranges). The expected frequencies are based on the proportion of individuals occupying home ranges of each habitat quality and assume an equal frequency of dispersal from each.

	Home Range Quality				Kolmogorov-Smirnov Goodness of Fit Test
	1	2	3	4	
<b>Males</b>					
.... Observed	1	11	3	1	$D_{(4,16)} = 3.1$ $p > 0.20$
.... Expected	4.1	8.3	2.3	1.5	
<b>Females</b>					
.... Observed	2	9	4	1	$D_{(4,16)} = 2.1$ $p > 0.50$
.... Expected	4.1	8.3	2.3	1.5	

Breeding habitat quality had no significant affect on which groups male and female dispersers joined (Table 9.7). However, the size of the groups males and females joined differed. Males joined groups smaller than their original groups more often than expected ( $D_{(3,14)} = 5.7$   $p < 0.05$ ). Nine (64%) males left large groups (7-13 birds) to join small groups (3-6 birds), five (36%) left small groups to join small groups (4 of these joined groups which were smaller than their original group), and no male was observed joining a large group. Females showed no tendency to join larger or smaller groups than their original group ( $D_{(3,19)} = 0.5$   $p > 0.50$ ).

It was not possible to determine the age at which most males and females dispersed, because I observed dispersals by only seven birds born during the study (one male, three females, and three birds of unknown sex). All but one of these birds dispersed as one year

olds. The exception was a bird of unknown sex which dispersed as a two year old. The observations from this study suggest that babblers do not disperse until after they are one year old. In addition, dispersal appeared to occur at an older age in males than in females. Nine of the 17 males (53%) that dispersed were known to be at least two years old, while this was the case for only four of the 19 females (21%).

**Table 9.7:** The relative frequency of birds joining groups occupying a home range of different or equivalent breeding habitat quality to that of the group they dispersed from. The expected frequencies are based on the number of individuals occupying home ranges of each habitat quality and assumes an equal frequency of dispersal to each.

	Breeding Habitat Quality			Kolmogorov-Smirnov Goodness of Fit Test
	Lower	Same	Better	
<b>Males</b>				
..... Observed	9	5	2	$D_{(3,16)} = 3.0 \quad p > 0.20$
..... Expected	6	5.8	4.2	
<b>Females</b>				
..... Observed	4	6	3	$D_{(3,13)} = 0.8 \quad p > 0.50$
..... Expected	4.8	4.7	3.5	

### *Dispersal distance*

The majority (95%) of the White-browed Babblers found to have dispersed moved less than 2000m, while the longest recorded dispersal was 4760 m (Fig. 9.5). The distribution of these dispersal distances was significantly different from that expected if birds dispersed with equal probability to all home ranges within a 5000 m radius of their original home range ( $D_{(6,41)} = 21.4 \quad p < 0.001$ ).

The adjusted distribution of dispersals suggests that 13% of dispersals from the study groups were missed due to the finite area of the study sites (Fig. 9.6). This low frequency of missed dispersals is supported by the data on juveniles born in 1994 and recruited into the population in 1995. There were 18 recruits: six (33%) were still resident in their natal group in 1996; eight (44%) had dispersed into another group, or had split

from their natal group by group budding; and 4 (22%) had disappeared. Since the annual adult survival rate was estimated at 78% (Chapter 8), four of these recruits would have been expected to have died during 1996. Therefore, it is unlikely that more than one or two of the juveniles born in 1994 could have successfully dispersed to groups outside of the study sites.

The dispersal patterns of males and females differed, with females showing a greater range of dispersal distances than males ( $\chi^2_{(3)} = 8.16$   $p = 0.043$ ) (Fig. 9.7). Nineteen percent of adjusted female dispersals were greater than 2000 m and the median dispersal distance was in the 1000-2000 m distance class, while males were never observed dispersing more than 2000 m and their median dispersal distance was in the 1-1000 m distance class.

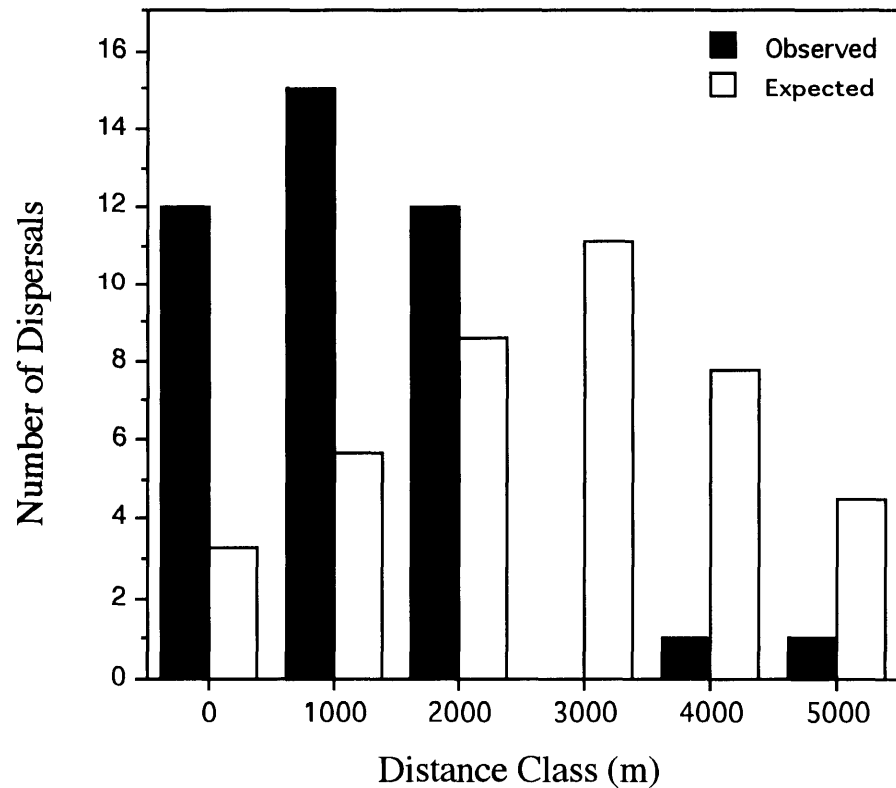
When dispersal distances are expressed in terms of the number of home ranges moved the same differences in dispersal pattern between males and females was evident, but the differences were not significant ( $\chi^2_{(3)} = 5.14$   $p = 0.162$ ) (Fig. 9.8). The majority of males (65%) and females (50%) moved to adjacent home ranges, but the maximum number of home ranges moved by males was three, while for females 15% (3 of 20) moved more than three home ranges from their original group.

### *Social Position of Dispersing Birds*

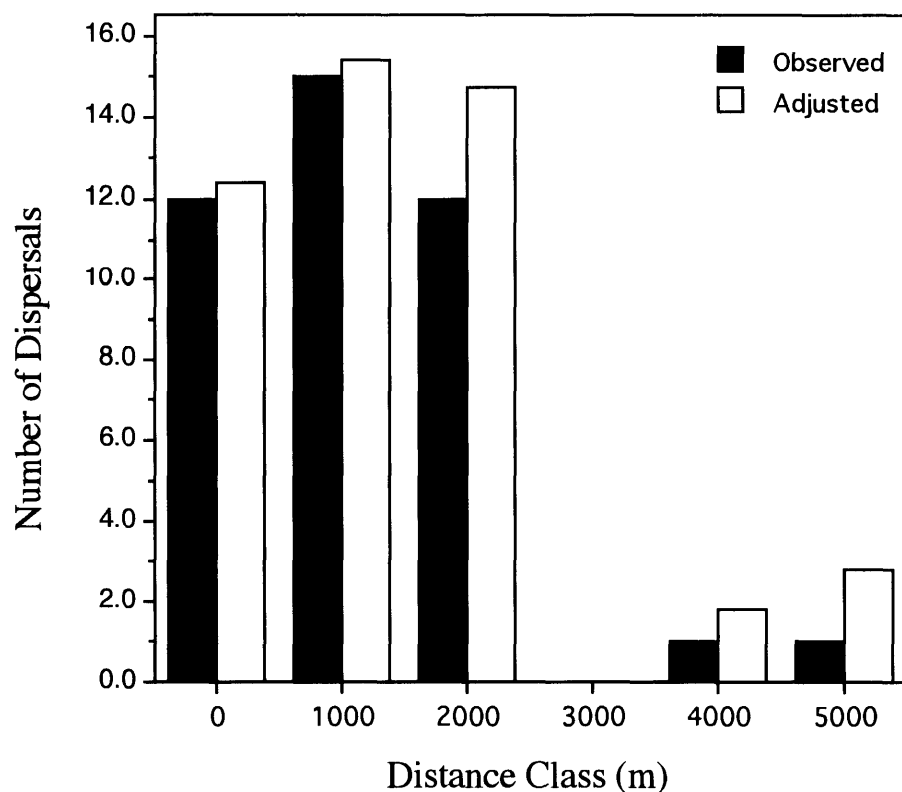
It was not possible to determine the relative frequencies of dispersal by birds of different social status (see chapter 7), because the social status prior to dispersal was not known for most dispersers. However, this information can be estimated, less directly, using the turnover of individuals in groups for which the social hierarchy was determined.

All secondary male helpers disappeared from their groups before the next breeding season and this level of turnover was significantly higher than for primary male helpers and dominant males (Table 9.8). This higher turnover in secondary male helpers corresponded to a higher proportion of these birds visiting other groups (includes visits and prolonged absences from their group).

**Figure 9.5:** A comparison of the observed and expected distribution of dispersal distances. The expected values are calculated based on the number of censused home ranges in each distance class. The maximum value of each distance class is displayed. The 0 distance class represents dispersals between groups with abutting home ranges.

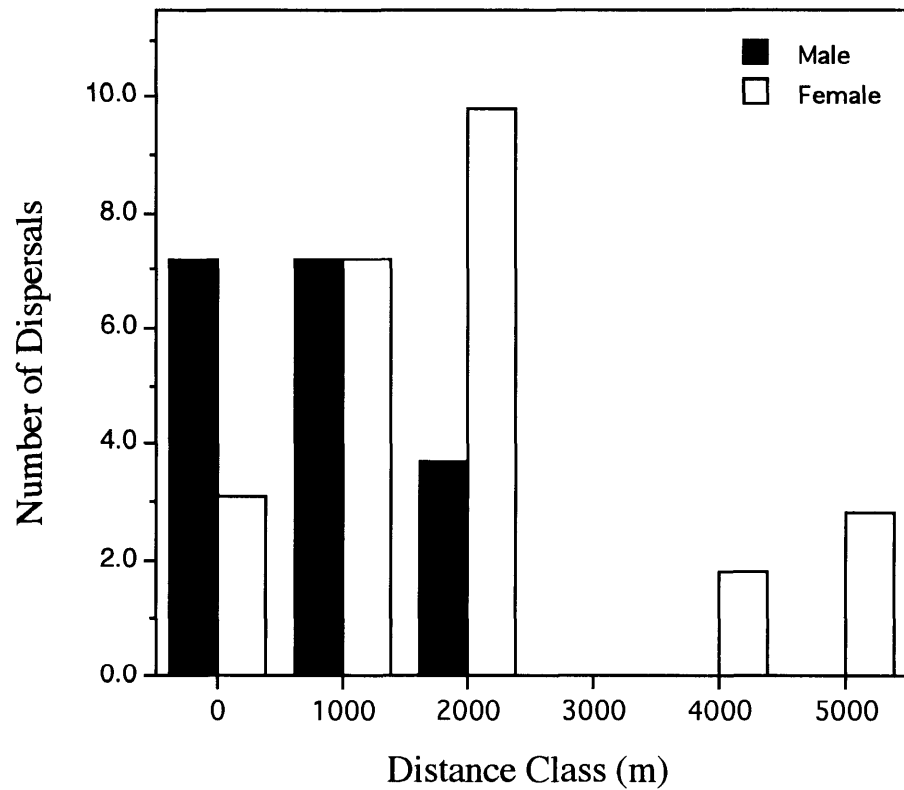


**Figure 9.6:** A comparison of the distribution of the raw dispersal data and the data adjusted for the census effort in each distance class. The maximum value of each distance class is displayed. The 0 distance class represents dispersals between groups with abutting home ranges.

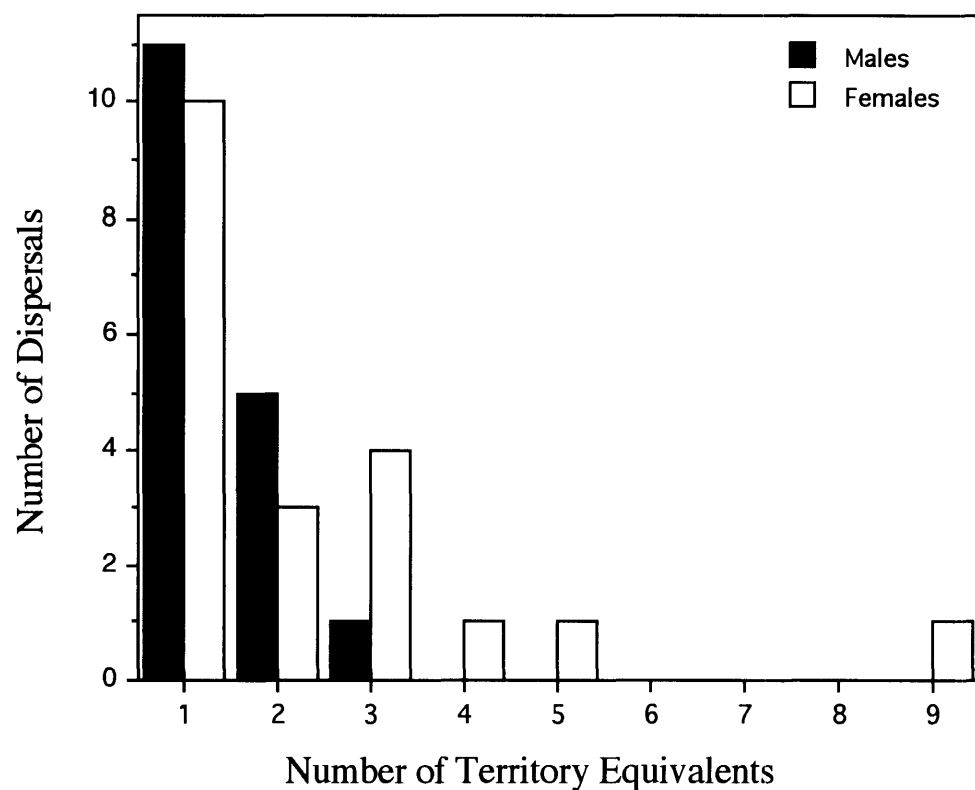




**Figure 9.7:** The adjusted distribution of male and female dispersal distances. The maximum value of each distance class is displayed. The 0 distance class represents dispersals between groups with abutting home ranges.



**Figure 9.8:** The distribution of male and female dispersals measured in the number of home range equivalents.



There was no significant difference in the turnover of secondary female helpers, primary female helpers and breeding females (Table 9.8). There was also no significant difference in the proportion of females of different status which visited other groups, though the proportion for secondary female helpers which did so was higher.

**Table 9.8:** Patterns of turnover in male and female babblers of different social status in nine groups. Social status was determined from observations at the nest. The Chi-square analyses tests the hypothesis that the relative frequencies are the same for birds of each social position.

Social Status	Did not visit other groups	Visited other groups	Remained in group	Disappeared from group
<b>Males</b>				
Dominant Male	9	0	7	2
Primary Helper	14	7	12	9
Secondary Helper	1	3	0	4
	$\chi^2_{(2)} = 7.91$ $p = 0.019$		$\chi^2_{(2)} = 5.58$ $p = 0.033$	
<b>Females</b>				
Breeding Female	9	0	7	2
Primary Helper	9	1	6	3
Secondary Helper	5	3	4	4
	$\chi^2_{(2)} = 5.01$ $p = 0.082$		$\chi^2_{(2)} = 1.45$ $p = 0.483$	

Males and females which dispersed became both breeding birds or helpers in their new groups. Of the 17 male dispersers five became the dominant male in their new group and two became helpers. It was not known what social position the other 10 males attained in their new group. Of the 20 female dispersers, six became the breeding female, four became helpers and the social position attained by the other 10 females was not known.

### *Dispersal Model*

I propose the following model of the pathways White-browed Babblers may take to obtain a breeding position (Fig. 9.9). The pathways for males and females are different. Most male options are associated with remaining in their natal group, while all female options involve natal dispersal.

I propose that males are generally philopatric and queue for inheritance of their natal group (Queuing model, see Chapter 7). Although males queue in their natal group they are not limited to waiting for the inheritance of this group to obtain a breeding position. These males also visited nearby groups monitoring them for breeding vacancies, or they split from their natal groups (group budding) with females which had recently joined the group. Males obtained breeding positions by these two methods at similar frequencies. Of 11 new dominant males five had dispersed from nearby groups, and 6 had split from their original group.

Some males dispersed to become helpers in nearby groups or groups which had split from their natal group. The change in rank which resulted from such dispersals could only be determined for two males. One was the lowest ranked male (fourth) in his original group and became the only male helper in his new group, while the other was ranked fourth of seven males in his original group and joined a group where he was one of only two males in the group. So, the rank of both males increased after dispersal. Males which dispersed to become helpers in their new group had the same pathways to a breeding positions as they had in their natal group.

I propose that all females disperse from their natal group, but the timing of this dispersal varies. Some females didn't leave their natal group until after their first breeding season and these birds served as primary helpers in their natal group (Chapter 7). Other females dispersed and joined a group distant from their natal group during their first breeding season. These females were likely to serve as secondary helpers in their new group and visit nearby groups monitoring them for breeding vacancies. These females then had three pathways to a breeding position. The first possibility was that the breeding position in their new group could become vacant through the death or dispersal of the existing breeding female; two females obtained a breeding position in this way.



The second pathway to a breeding position was to form a new group, with a senior male helper, by group budding. This occurred in at least four group buddings. The final pathway to a breeding position for females was to disperse to a group, they were monitoring, where a breeding vacancy had arisen; one female was observed doing this. This female joined her new group during the non-breeding period, but during the next breeding season obtained a breeding position in an adjacent group.

Those females which delayed dispersal until after their first breeding season dispersed prior to the next breeding season, either to a vacant breeding position (observed on one occasion), or to a group where they are likely to become a secondary helper. The latter females then obtained a breeding position through the same pathways as females which dispersed during their first breeding season.

Three breeding females were also found dispersing to nearby groups; two dispersed to adjacent groups and one to a group two home ranges away. All three breeding females moved from home ranges of low breeding quality (HQ 1 or 2) to home ranges of better or similar quality. Two breeding females were also seen making visits to adjacent groups. This suggests that they also monitor nearby groups for breeding vacancies and sometimes disperse to them.

## Discussion

It has generally been assumed that White-browed Babblers, like Grey-crowned and Hall's Babblers, are territorial (Counsilman & King 1977; Boles 1988); however, little evidence has been presented to support this claim. Boles (1988) assumed they were territorial, because Gould (1865) found them performing a display (huddle display *sensu* King 1980), which King later observed being performed by Grey-crowned Babblers during territorial disputes. However, King also observed this behaviour when the group was alone and sometimes when the female was incubating, so it is not exclusively a territorial display.

I encountered groups of White-browed Babblers interacting and some of these interactions (calling displays and chases) resulted in the groups separating from each other. However, these displays were only evident during the breeding season and on some occasions not all members of the groups were involved. This was different from the territorial disputes described for the Grey-crowned Babbler (Counsilman 1977; King 1980)

and Hall's Babbler (Balda & Brown 1977). In these species most individuals from each group were involved in disputes and for Grey-crowned Babblers disputes occurred throughout the year. In addition, the home ranges of White-browed Babbler groups in the Kellerberrin area overlapped during the non-breeding period and groups sometimes foraged together (foraging interactions). Some groups also made much bigger movements during the non-breeding period, returning to their breeding area the next year (group visits).

I have interpreted these observations as indicating that White-browed Babblers are territorial during the breeding season, but that they relax their territorial behaviour during the non-breeding season. This is similar to the behaviour of some other cooperatively breeding species, such as the White-winged Chough (Rowley 1978) and the Hoatzin *Opisthocomus hoazin* (Strahl & Schmitz 1990), which leave their territories during the non-breeding period and sometimes aggregate in large flocks. However, these observations could be interpreted in another way. The size of home ranges during the breeding season may be restricted by the location of the nest and this could result in groups occupying mutually exclusive areas without invoking territoriality (see below). Given that there appears to be competition for breeding positions in both sexes and males guard females (see Chapter 7), calling displays and chases may be related to mate defence and not territoriality. However, I believe this is unlikely, because some calling disputes involved a large proportion of the birds in both groups and this would not be expected if these interactions were related to mate defence.

Due to the lack of observations on the spacing behaviour of the White-browed Babbler throughout its range, it is not possible to assess whether the behaviour observed in the Kellerberrin landscape is typical of this species, or if it is a consequence of the fragmentation of the landscape. Baldwin (1975) stated that White-browed Babblers in the Inverall district of New South Wales became nomadic after breeding, but she does not give any details of this behaviour. This suggests that at least some White-browed Babbler groups at this location were not territorial during the non-breeding season. However, this area was also modified by agricultural activity, though Baldwin does not detail the extent of this modification.

### *Home Range Shape*

The size of the breeding territories occupied by White-browed Babbler groups depended on the shape of the remnant vegetation. The more dependent a group was on linear strips of vegetation the smaller the area and the longer the linear dimensions of the territory. This was also found by Lynch *et al.* (1995), using radio-telemetry, for four bird species (including the White-browed Babbler) in the same landscape as the current study.

Central Place Theory predicts that for optimal foraging, individuals should restrict themselves to a circular area around their nest (Covich 1976; Andersson 1981; Recher *et al.* 1987) and, as was argued in Chapter 8, this also applies to defending the nest from predators. So, how similar the area of a breeding territory is to that of a circle of the same diameter (linear dimension) is a measure of the efficiency of the territory. Therefore, groups living in linear strips of vegetation had less efficient breeding territories (25% of the area of a circle of equivalent diameter was available) than groups which lived in remnant patches of vegetation (71% of the area of a circle of equivalent diameter was available). Those groups living in linear/patch home ranges had breeding territories of similar efficiency to groups with patch home ranges, because most nested in their remnant patch. That most groups in linear/patch home ranges nested in their patch suggests that whenever possible these birds are seeking to increase the area of suitable vegetation around their nest and so is consistent with the Central Place Theory.

Home ranges during the non-breeding period expanded to different degrees depending on the configuration of the vegetation. This expansion was most notable in groups with linear/patch home ranges. These groups more than doubled the linear dimensions of their home ranges, despite the limited increase in area that resulted. This is possible during the non-breeding period, because the group is released from the *central place* (nest location). This suggests that breeding territories may be limited by the distance birds can move from the nest. The consequences of this are that groups living in linear strips of vegetation are forced to use an area which may be smaller than optimal for obtaining the resources necessary for raising their nestlings. This was not reflected in nestling survival for babblers (no nestlings died of starvation, Chapter 8), but other aspects of nestling development, such as growth rates, were not measured and may have been affected. For instance,

reductions in the growth rates of nestlings resulting from increased foraging distance was found in Carnaby's Cockatoo (Saunders 1980, 1982).

The size of a group was weakly correlated with the area of its total home range, but not with the area of its breeding territory. The biggest differences in group size were related to the shape of the home range, with linear home ranges having significantly smaller groups. This suggests that landscape configuration is a more important influence on group size than area. If group size was limited by the area a group occupied, then groups should increase in size when they expand their home ranges. This was not the case. Only one of the five groups which expanded their home ranges increased in size and three groups actually declined in size after they expanded their home range.

### *Group Movements*

Some White-browed Babbler groups moved during the non-breeding period and the probability that a group would move was related to the Summer abundance of invertebrates in the habitat patch they occupied. This data indicates that some of the habitat patches used by babblers in the study sites suffered food shortages during some Summers. However, not all groups within these habitat patches moved and it appears likely that the configuration of the landscape also influences the likelihood that groups will move during the Summer (see Chapter 10). Other cooperative breeding species which move to other areas during the non-breeding season were found do so because of changes in the availability of some essential resource. White-winged Choughs moved because of localised declines in food (Rowley 1978); while the Hoatzin moved to areas of permanent water, because they need to drink due to their vegetarian diet (Strahl & Schmitz 1990).

Group movements were of two types, visits and dispersals. However, these movements appeared to be the same in all aspects except their outcome. The difference between group visits and dispersals was that dispersing groups failed to return to their original home range. The reason for this is unknown, because these groups left the study sites and were never seen again. However, six groups were also found moving into the study sites. All of these took up permanent home ranges, mainly in vacant habitat, and attempted to breed in the next breeding season. This indicates that groups which dispersed



from the study sites probably failed to return, because they found suitable habitat elsewhere.

Why some groups return from these movements and others do not is not clear. It may simply reflect the frequency with which moving groups find suitable habitat. However, there was a significant difference between the previous breeding success of groups which dispersed (86% failed) and those that made group visits (none failed). This suggests that previous breeding success may influence the likelihood of moving groups establishing a new home range somewhere else. High breeding site fidelity has been found in a number of nomadic and migratory Australian passerines and appears to be maintained regardless of previous breeding success (Bridges 1994; Ley *et al.* 1996; Ford 1998). However, a lack of site fidelity by breeding units in other species has generally been associated with breeding failure (Harvey *et al.* 1979; Greenwood & Harvey 1982; Weatherhead & Boak 1986). Sometimes this is moderated by territory quality, with breeding units in high quality territories being more likely to remain in the same site after a breeding failure (Weatherhead & Boak 1986).

### *New Groups*

The majority of new groups in the study sites were the result of two processes, group budding and the dispersal of a group from outside the study site. Group dispersals are not strictly the formation of new groups. However, at the local scale of the study sites they function in the same manner, by providing new breeding pairs and potential recruits (see Chapter 10 for a discussion of the issue of scales).

Group budding superficially resembles plural breeding (more than one pair of birds breeding in the same group), because there is a close association between the new and original groups in their first breeding season. Plural breeding has been reported in the White-browed Babbler (Chandler 1920). However, I believe the observations in my study are group budding, because in all cases where the group persisted after breeding (4 of 6 cases) it behaved as an independent group, which is not consistent with plural breeding. In the other two cases the individuals from the new group disappeared after failing to breed, instead of rejoining their original group as would be expected if they had been cases of plural breeding.

Group budding in babblers differs from that in the Florida Scrub-jay, where the behaviour was first described (Woolfenden & Fitzpatrick 1978), in that groups which bud did not expand their home range prior to the budding process. Woolfenden and Fitzpatrick (1978) proposed that group budding was a strategy by which non-breeding birds could obtain the space necessary for breeding. Central to this idea was that groups grew, because of increased productivity resulting from helping behaviour. This allowed them to expand their territory boundaries through competition with adjacent groups. The expanded territory had sufficient area for part of the group to bud and take over a portion of the original group's home range. This hypothesis is not consistent with the observations in the White-browed Babbler. Although babbler groups were more productive when they had helpers, group size did not result in an expansion of the home range occupied and there did not appear to be competition for vacant home ranges. Therefore, helping did not increase the chances of obtaining breeding habitat through budding, as the same area was available to these helpers prior to their years of helping. One possible explanation for these inconsistencies is landscape fragmentation. The spatial configuration of suitable habitat in fragmented landscapes is dramatically changed and I have already argued that this affects the area of a group's home range. It is possible that the regular process of group budding, as observed in Florida Scrub-jays, is disrupted by these changes in landscape configuration. A test of this idea would be to compare the budding process of babblers in unfragmented habitat with my observations.

An alternative explanation for budding in babbler groups is that it is the only viable means of creating a new group which is stable. Helpers are not gaining space for breeding by helping, but are possibly gaining the opportunity to recruit acquainted helpers for a new group. Wiley and Rabenold (1984) proposed that cooperative breeding could result from individuals queuing for breeding positions and this is consistent with the evidence in babbler groups (Chapter 7). As part of the Queuing model Wiley and Rabenold argued that queues are stable structures, because there are mutualistic interactions between acquainted individuals. A consequence of this idea is that group cohesion may be dependent on established relationships between group members. If babblers queue for breeding positions then whenever new birds enter a group social disruption is likely to occur until their position in the queue is established. This would be a minor disruption when a single bird

enters an established group. However, a group forming from individuals which had no previous relationship would need to develop this social structure and the resultant competition could lead to major disruptions in breeding attempts. Disruptions in breeding due to competition between group members has been observed in some cooperatively breeding species (Koenig 1982; Zahavi 1990; Komdeur 1994). If this hypothesis is correct then groups formed by unacquainted individuals should be rare and this was found in the current study. Only one group, consisting of three birds, formed from individuals dispersing from different groups and it is possible that two of these birds came from the same group.

### *Group Turnover*

Group dispersals and group budding as methods of group formation have very different consequences for the spatial dynamics of babbler groups. Group dispersals were predominantly involved in filling vacant home ranges and so maintained the density of groups in the available habitat. In contrast, group budding generally created new home ranges by splitting occupied home ranges and so increased the density of groups in habitat already occupied.

The turnover of babbler groups was quite high and was possibly related to the quality of breeding habitat. Fifteen home ranges became vacant and at least 7 of these were later occupied (the outcome for three more was unknown), and five new home ranges were created by group budding. The increased density of groups caused by these group buddings was balanced by five of the home range vacancies being subsumed by existing groups. This resulted in localised changes in group density, which fluctuated from year to year.

A result of this group turnover is that throughout this study there were always some home ranges which were unoccupied. These tended to be in lower quality breeding habitat and sometimes were isolated from existing groups. Therefore, suitable habitat in the study areas was not saturated, but the best quality breeding habitat may have been.

### *Visiting by Individuals*

White-browed Babblers made two kinds of individual movements, permanent dispersals and temporary visits to other groups. It is not clear how frequently birds visited

other groups, but from the observations made it appears likely that the frequency of these visits has been underestimated. Visits are made by both sexes, but non-breeding birds are more likely to visit than breeding birds and male secondary helpers were the most frequent visitors. Since male secondary helpers generally disperse, it is possible that visits are a prelude to dispersal. This is supported by the timing of visits, with males generally visiting during the non-breeding period and then dispersing during the breeding season, while females visit and disperse at any time of the year. However, not all birds which visit other groups disperse.

I believe that visits are a mechanism by which non-breeding birds can monitor other groups for breeding vacancies and to enable them to have some social interaction with members of groups that they may eventually join. This is equivalent to the “assessment spheres” proposed by Zack and Stutchbury (1992) for floaters. White-browed Babblers which visit other groups were similar to floaters found in other cooperative breeding species, such as the White-throated Magpie-Jay *Calocitta formosa* (Langen 1996); except that these babblers were still clearly associated with one particular group and were never found foraging or roosting alone.

Zack and Rabenold (1989) found that proximity of a female Stripe-backed Wren’s group to a breeding vacancy increased the chances of the bird acquiring the vacancy. The competitive advantage associated with proximity is believed to be a result of the greater familiarity these birds have with nearby territories and this familiarity is the result of visiting these territories (Zack & Stutchbury 1992). So, visiting by individuals along with group interactions would be expected to provide a similar advantage to White-browed Babblers and this suggests that access to other groups may have an important influence on dispersal.

### *Dispersal by Individuals*

Greenwood and Harvey (1982) defined two types of dispersal. *Natal dispersal* is the permanent movement of an individual from the group it was born in to the group where it first breeds, or has the potential to breed; while any subsequent permanent movement is a *breeding dispersal*. It was not possible to determine the relative frequencies of natal and breeding dispersals in this study, because the natal group was not known for 33 of the

dispersing birds. It is certain, however, that some birds do disperse from non-natal groups, because one female dispersed to two groups and nested in both of them. Two other females were also found to breed in a group and then disperse to a new group where they also bred. My inability to distinguish between natal and breeding dispersal makes it difficult to assess dispersal patterns, because these two types of dispersal generally differ with respect to the distance travelled and possibly the types of groups that birds join (Greenwood & Harvey 1982).

I have proposed a dispersal model for White-browed Babblers which is based on the Queuing model of social structure (Wiley & Rabenold 1984) and the observed dispersal patterns. Central to this model is inheritance of the natal group by males. I failed to record any males becoming the dominant male in their natal territories; however, this study had a short time frame (3 years) and so the oldest known aged bird was two years old. Given that there was only a limited number of groups in which the dominant male was known in 1996 (when known aged birds were two) the chances of observing inheritance were low.

Though inheritance of the natal group is expected to be the primary pathway to a breeding position for males, some males did disperse to become helpers in nearby groups or groups which had split from their natal group. This is consistent with the Queuing model, because these males dispersed to smaller groups and so increased their chance of gaining a breeding position by joining a shorter queue.

The proposed dispersal model is based on the assumption that there is a female-bias in dispersal. There was a slightly higher frequency of female dispersal and this was consistent with, though not as great as, the female-bias in the number of birds found joining groups. However, the greatest difference between the sexes was in the distance dispersed. Females moved further than males. In part, this explains the absence of a clear female-bias in observed dispersals. An increase in the distance dispersed increases the likelihood of the dispersals being missed, because birds have moved beyond the boundaries of the study. This is supported by the increase in the female-bias of dispersals when adjusted for census effort (Fig. 9.7).

Three major causal factors for a sex-bias in dispersal are frequently proposed, inbreeding avoidance, and competition for either resources or mates (Murray 1967; Dobson 1982; Moore & Ali 1984; Pusey & Wolf 1996; Koenig *et al.* 1998). Recently the idea that

female choice may play an important role in mating systems and so affect processes such as dispersal has gained some acceptance (Burley & Parker 1997; Johnson & Burley 1997). Of these factors, inbreeding avoidance is the most consistent with the observations in White-browed Babblers, but the influence of female choice could not be assessed with the information available from this study. Competition for resources most likely occurs between members in a group, but it seems unlikely that it can explain the observed pattern of dispersal. If competition for resources was a major causal factor in dispersal then birds should only be allowed to join groups if their contribution is essential for the group's success. Therefore, the observation that unrelated females are allowed to join groups as secondary helpers (*i.e.* they contribute little to the group) while related females which act as primary helpers disperse is not consistent with resource competition being a major causal factor in the dispersal of babblers.

Competition by females for the opportunity to breed also occurs in babbler groups. However, there is more intense competition between the breeding female and female helpers which have joined the group, than with female helpers in their natal group. This suggests that females in their natal group are not serious competitors for the breeding position, yet they disperse. This observation is not consistent with reproductive competition being a major causal factor in babbler dispersal (Koenig *et al.* 1998). However, this observation is consistent with inbreeding avoidance. Females do not compete for the breeding position in their natal territory, and so suffer less aggression, because taking their natal breeding position would frequently require them to mate with a close relative.

Additional support for the Inbreeding Avoidance model is provided by the spatial pattern of dispersals by White-browed Babblers. Females have a bimodal distribution of dispersal distances which is not observed in males (Figs 9.7). This pattern results because females make long distance natal dispersals, and subsequent short distance dispersals to obtain a breeding position in groups which they assess. In contrast, males assess groups from their natal home range and so make only short distance natal dispersals. The long distance natal dispersals made by females shift them to an area where their assessment sphere no longer includes groups near their natal home range, and so decreases the chance of them mating with a close relative (Waser 1985; Pusey & Wolf 1996). This dispersal pattern has also been found in the Red-winged Fairy-wren *Malurus elegans*, where 20

females were found to disperse to helping positions and four of these made a subsequent dispersal to become the breeding female in a nearby group (E. Russell & I. Rowley *pers. comm.*).

The social behaviour and dispersal patterns observed in White-browed Babblers suggest that inbreeding avoidance may be the cause of a sex-bias in dispersal, but they do not explain why the bias is in the female's direction. Greenwood's (1980) Mating System model sought to explain this, but the observations for the White-browed Babbler do not fit simply into this model. The Mating System model predicts that species should have female-biased dispersal when their mating system is based on defending resources. However, this model is based on an underlying assumption that males are the only sex which expends effort in resource defence. White-browed Babblers probably defend resources (territorial defence) at least during the breeding season. However, I have no evidence that males expend greater effort on territorial defence than females and in Grey-crowned and Hall's Babblers both sexes appear to contribute equally to this task (King 1980; Balda & Brown 1977). The Mating System model does not address this situation directly, but if both sexes invest in resource defence there would be a cost for both in dispersing, so in this situation the model is neutral on sex-biased dispersal.

The other component of the Mating System model is mate defence. Greenwood's model has often been incorrectly quoted as indicating male-biased dispersal when mate defence is the major component of the mating system (*e.g.* Langen 1996). What Greenwood (1980) argued was that male-biased dispersal resulted when males did not primarily determine the distribution of females by partitioning resources, not because of mate defence *per se*. In the White-browed Babbler dominant males guarded breeding females (Chapter 7) and so some level of mate defence appears to be operating in this species. However, the primary determinant of the distribution of females appears to be nesting habitat, which is probably defended. Therefore, the Mating System model would predict that the defence of this resource would control which sex was more likely to disperse.

With this interpretation of the White-browed Babbler's mating system, Greenwood's model does not predict a bias in the likelihood of dispersal for either sex and this is not consistent with the observed dispersal patterns. It is possible that resource defence is

dominated by male babblers and so the assumption of the Mating System hypothesis is met. This would result in a female-bias in dispersal as was observed. However, another possibility was suggested by Langen (1996). He argued that secondary breeding strategies may influence the likelihood of one sex or the other dispersing. It is not known to what extent male helpers can obtain copulations with breeding females, but the observations of mate guarding suggest that they may try to obtain copulations. With competition between high ranked males for breeding positions (Chapter 7) and the possibility of extra-pair copulations, males may have various secondary opportunities to breed. In contrast, females appear to have few opportunities to breed in a group where they are not the dominant female. Joint nesting was observed in babblers, but in all cases checked one clutch of eggs (presumably those of the secondary female) was infertile. So, joint nesting rarely resulted in successful breeding for secondary females.

I believe that the secondary breeding opportunities available to males and the requirement of a high ranking position to gain these opportunities provide a mechanism for higher costs in male dispersal (*i.e.* the loss of these secondary breeding opportunities). Therefore, males would be philopatric and inbreeding avoidance would result in the observed female-biased dispersal pattern. This hypothesis requires some level of breeding by male helpers and currently it is unknown if this occurs. Genetic analysis of babbler groups would test this assumption and this analysis is currently in progress (D.M. Bryant *pers. comm.*).

A basic assumption of the proposed dispersal pattern is that philopatry in White-browed Babblers is the result of the benefits of remaining in a group and not due to some ecological constraint. Confirming this was impossible in the current study, because there are numerous possible ecological constraints and not all could be considered. One ecological constraint that can be discounted is habitat saturation. The turnover of groups within the Kellerberrin landscape provides many vacant areas which have supported groups, but these vacancies are not always filled despite the availability of birds to fill them. These vacancies may not be filled because they are generally low quality habitat as is predicted by the Benefits of Philopatry model (Stacey & Ligon 1991). However, dispersal of individual babblers was not correlated with breeding habitat quality, which would be expected under the Benefits of Philopatry model.



One possible reason for the lack of correlation between habitat quality and dispersal is that the measures of habitat quality used in this study are not reliable. Breeding habitat quality was measured, in part, by vegetation structure which varies through time and though it reflected differences in breeding success during the study it may not reflect the long term breeding success of an area (Zack & Stutchbury 1992). Another possible cause for the lack of correlation between habitat quality and dispersal is that habitat quality may not vary sufficiently for it to be a major factor in dispersal. Although I found different levels of reproductive success in different quality home ranges the majority of home ranges were of similar quality (Habitat Quality 2) and there were few high quality home ranges. This bias in the quality of the home ranges may limit the ability of birds to choose home ranges on the basis of quality. This problem would be accentuated by the fragmentation of the landscape as it would reduce the number of home ranges birds could monitor (see Chapter 10).

## Summary

White-browed Babblers are territorial during the breeding season, but groups move over larger overlapping home ranges during the non-breeding season. These non-breeding home ranges provide a degree of local mixing of individuals as groups frequently forage together for short periods. Some groups moved great distances during the non-breeding period and sometimes established themselves in new home ranges. The likelihood of such movements appeared to be related to the quality of the group's original home range. These movements provided opportunities for mixing of individuals from different groups over a much larger scale than resulted from the extension of the home range during the non-breeding period.

The data from this study indicates that the habitat quality of White-browed Babbler home ranges varies in the Kellerberrin landscape. This variation in quality is the result of a complex interaction between the availability of food resources, vegetation structure, and the shape of the remnant vegetation. Habitat quality not only had an effect on the reproductive success of babbler groups, but also influenced the spatial dynamics of the species.

Suitable habitat for babbler groups was not saturated in the study areas. The turnover of groups was found to be common and this provided numerous home range vacancies, though these vacancies tended to be of poorer quality habitat. Individual dispersers rarely filled vacancies, with most being filled in one of two ways; group dispersal or group budding. Both of these processes produce groups of individuals which already had established social structures, and this may be important for the successful establishment of new groups.

I proposed a dispersal model for White-browed Babblers that is based on a social structure where males queue for inheritance of their natal group. This results in male philopatry and female natal dispersal, primarily to avoid inbreeding. Birds of both sex visit nearby groups to monitor them for breeding vacancies and to gain familiarity with group members and their home ranges. This probably improves their chances of gaining vacancies when they arise. Because females frequently make long distance dispersals prior to assessing groups for breeding vacancies, the distribution of their dispersal distances is bimodal, while that of the philopatric males is skewed toward short distance dispersal. Landscape fragmentation has the potential to disrupt this dispersal pattern, because the spatial configuration of groups is less clustered. This is discussed in the next chapter.

**Appendix 9.1a:** History of the groups monitored in study site A from 1994 to 1997. \*\*\*\*\* represents a group in its home range, and ? represent periods when a group was not monitored. **Visited** indicates a group which left its home range and later returned, **Dispersed** indicates a group that left its home range and was never seen again, **New Group** indicates a group that dispersed from outside the study area and established in a vacant or new home range, and **Budded** indicates the development of a new group or pair by group budding. <sup>1</sup> This new group occupied part of the original home range of group A7. <sup>2</sup> This group disappeared over a long period of time through the progressive loss of members.

	1994/95		1995/96		1996/97	
	breeding	summer	breeding	summer	breeding	summer
A1	*****	Visited	*****	*****	*****	Visited
A2	*****	*****	*****	*****	*****	*****
A3	*****	*****	*****	*****	*****	*****
A4	*****	*****	*****	*****	*****	*****
A4a				Budded	*****	*****
A5	*****	*****	*****	*****	*****	*****
A5a			Budded	*****	*****	*****
A6	*****	*****	*****	*****	*****	*****
A6a					Budded	*****
A7	*****	*****	*****	*****	*****	*****
A7a		New group <sup>1</sup>	*****	*****	*****	*****
A8	*****	*****	*****	*****	*****	*****
A9	*****	Dispersed				
A10	*****	*****	*****	Visited	*****	*****
A12	*****	*****	*****	*****	*****	*****
A13	?	*****	*****	*****	*****	*****
A14	*****	*****	*****	*****	*****	*****
A16	*****	*****	*****	*****	Died <sup>2</sup>	
A17	*****	*****	*****	Visited	*****	Dispersed
A17a					Budded	Dispersed
A17b					Budded	Dispersed
A18	*****	Visited	*****	?	*****	?
A19	*****	Visited	*****	?	*****	?
A21		New group	*****	*****	*****	*****

**Appendix 9.1b:** History of the groups monitored in study sites B & C from 1994 to 1997. \*\*\*\*\* represents a group in its home range, and ? represent periods when a group was not monitored. **Visited** indicates a group which left its home range and later returned, **Dispersed** indicates a group that left its home range and was never seen again, **New Group** indicates a group that dispersed from outside the study area and established in a vacant or new home range, and **Budded** indicates the development of a new group or pair by group budding.<sup>1</sup> This group was formed from dispersing members of a number of other groups in the study area.<sup>2</sup> One bird occupied this home range for a short period during the breeding season. **NB:** not all groups were reliably monitored in the 1997 breeding season and so the outcome of some movements is not known. These are shown as "Visited ?".

	1994/95		1995/96		1996/97	
	breeding	summer	breeding	summer	breeding	summer
B1	*****	*****	*****	*****	*****	Dispersed
B2	*****	Dispersed				
B3	*****	*****	*****	Dispersed		
B4	*****	*****	*****	Dispersed		
B5	*****	*****	*****	*****	*****	*****
B6	*****	Dispersed				
B7	*****	*****	*****	Visited	*****	Visited ?
B8		Budded	*****	*****	*****	Visited ?
B9	*****	*****	*****	*****	*****	*****
B10	*****	Dispersed	New Group	Dispersed	New Group	*****
B11	*****	*****	*****	*****	*****	*****
B12	*****	*****	*****	*****	*****	Dispersed
B12a					Formed <sup>1</sup>	*****
B15		New Group	*****	*****	*****	*****
C1	*****	Dispersed	One bird <sup>2</sup>			
C2	*****	Dispersed	New Group	?	?	?
C3	*****	*****	*****	?	?	?
C4	*****	*****	*****	?	?	?
C5	*****	*****	*****	?	?	?

# Chapter 10

## The effect of the landscape mosaic on the spatial structure of White-browed Babbler populations

*“The essence of spatial ecology is that the spatial structure of ecological interactions affects populations as much as do average birth and death rates, competition and predation. The rapid destruction of natural habitats has highlighted the importance of spatially explicit ecological models.”*

[Hanski 1998]

### Introduction

In landscapes modified by humans for extensive agriculture, native species often face the loss and fragmentation of their habitat. These changes include a decline in the size of habitat patches and an increase in their spatial isolation (Saunders *et al.* 1991). It has generally been assumed that these changes lead to a reduction in the exchange of individuals between patches (Simberloff 1988; Opdam 1990; Saunders *et al.* 1991); although, some have stressed that the response will be species specific (Saunders *et al.* 1991). This view of the effect of fragmentation on population dynamics developed from an extrapolation of Island Biogeography Theory to terrestrial landscapes, and has been criticised as being too simplistic (Wiens 1994). A new view of landscapes is now developing which acknowledges their complexity. This view considers that population processes are affected not only by the shape and spatial distribution of a species' habitat, but also by the structure of the landscape mosaic in which these patches occur (Dunning *et al.* 1992; Taylor *et al.* 1993; Ims 1995; Wiens 1995, 1997).

Ims *et al.* (1993) suggested that a species' dispersal pattern might have one of two responses to fragmentation; a *fusion* response where increased fragmentation results in reduced dispersal, or a *fission* response where the frequency and/or the distance of inter-patch dispersals increases with increasing fragmentation. The Root Vole *Microtus*

*oeconomus* was found to display both of these responses to fragmentation (Bjornstad *et al.* 1998). The different responses were made by individuals from two geographical strains of this species and were attributed to differences in their social behaviour (Bjornstad *et al.* 1998). Differences in the dispersal responses of three small mammals to fragmentation were found by Diffendorfer *et al.* (1995), but all increased the distances dispersed while reducing the frequency of inter-patch dispersals.

Studies of the dispersal behaviour of the Nuthatch *Sitta europaea* (Matthysen *et al.* 1995) and the Columbian Ground Squirrel *Spermophilus columbianus* (Wiggett & Boag 1989) found that the scale of dispersals can be altered by changes in the configuration of patches in the landscape. In these species, absolute distances dispersed by juveniles increased with fragmentation. However, dispersal patterns between units (*i.e.* territories or colonies) did not change, because of the dilution of these units in the landscape (*i.e.* fragmentation resulted in greater distances between territories/colonies). Changes at the scale of the individual home range can also affect population processes. For example, the social structure of Capercaillie Grouse *Tetrao urogallus* changed from a lekking system to one of solitary displaying males when fragmentation increased within their home ranges (Ims *et al.* 1993). These studies indicated that understanding the dynamics of a species at both the patch and landscape scale is essential for determining how population processes will be affected by changes in the landscape mosaic.

Using a spatially explicit dispersal model, Brooker *et al.* (1999) showed that dispersal by two bird species (Blue-breasted Fairy-wren *Malurus pulcherrimus* and White-browed Babbler) in the Kellerberrin area was probably dependent on the distribution of remnant vegetation through which individuals dispersed (Appendix I). Although dispersals were likely to be made through remnant vegetation, both of these species were capable of crossing gaps in this vegetation (*gap tolerance*). Therefore, the connectivity of the landscape for these species was not dependent simply on corridors of remnant vegetation between habitat patches. These species could traverse patches of agricultural vegetation if the distances between associated remnant vegetation patches was smaller than the species' gap tolerance. Therefore, such landscape mosaics were still connected from the perspective of these species. This view of landscape connectivity is similar to that proposed by Taylor *et al.* (1993). Fairy-wrens appeared to be able to cross only small gaps in remnant

vegetation patches (<60 m), while babblers were able to cross much larger areas of agricultural land (at least 270 m). This means that the level of connectivity between patches in the same landscape mosaic might differ for these two species.

This model of White-browed Babbler dispersal behaviour suggests that the structure of the landscape mosaic associated with each habitat patch is likely to be an important determinant of the level of association between groups occupying different habitat patches. In Chapter 4 I showed that the White-browed Babbler occupied patches of suitable habitat which varied in size and shape and which had an aggregated distribution across the region. Based on this spatial pattern I proposed a simple conceptual model of the scales at which the level of interaction between groups might change, and thereby define local population boundaries (see Fig. 4.3). The aim of this chapter is to investigate the effect of patch and landscape characteristics, at these three scales, on interactions between babbler groups, in order to determine the spatial structure of their populations.

## Methods

### *Habitat Patch Scale*

The average number of groups occupying each habitat patch was calculated from the number in each year from 1994 to 1996. A number of different types of interactions occurred between babbler groups, which resulted in social contact between members of these groups (see Chapter 9). An index (Interaction Rate) was calculated to describe differences in the frequency of these interactions in habitat patches which contained different numbers of groups. The Interaction Rate (IR) was calculated using the formula:

$$IR = (\sum I_a) / (N * V_{10} * T)$$

where  $\sum I_a$  is the sum of the interactions for each group within a habitat patch, N is the number of groups within the habitat patch,  $V_{10}$  is the number of visits I made to the habitat patch to monitor groups (V was measured in groups of ten visits to prevent very small values of IR), and T is the number of years over which these interactions occurred. This index standardises the number of interactions between groups with respect to the number of groups present and the frequency with which those groups were monitored.

Each habitat patch was placed into one of four group size classes: those containing only one group, those containing two or three groups, those containing four or five groups and those containing six or seven groups. The number of dispersals originating in a habitat patch of a certain size class was averaged for the number of years that habitat patch was monitored. In some cases the number of groups within a habitat patch varied from one year to the next. If these changes shifted a habitat patch from one size class to another it was treated as a different patch for each year.

The number of dispersals originating in a habitat patch of a given size was calculated per patch (the total number of dispersals from patches of that size divided by the number of patches of that size), or per group (the number of dispersals from patches of that size divided by the total number of groups in patches of that size). The latter measure standardises the dispersal rate for the increased number of groups in large patches.

The distance between habitat patches was measured from the closest edge of one habitat patch to the closest edge of the other. These distances were measured to the nearest 100 m using the GIS system GRASS.

### *Local Population Neighbourhoods*

In Chapter 4 I argued that it was necessary to identify a biologically meaningful spatial scale at which to define patch clusters. This was attempted using a spatially explicit dispersal model (Brooker *et al.* 1999: see Appendix I). The model was used to measure the relative likelihood of dispersal from one White-browed Babbler group to another. The rate of dispersal between groups defines local population boundaries; therefore, I have called the patch clusters determined from the results of this simulation model *Local Population Neighbourhoods* (Addicott *et al.* 1987).

The simulation model was run using all groups in the two study sites and those in the regional survey area (see Fig. 4.1). The regional survey area was too large to be run as a single simulation, so four smaller areas with large boundary overlaps were used. In the dispersal simulation the animal moves randomly through remnant vegetation from a designated origin group until it reaches the designated target group, or the time limit of 10 000 steps (one step equals 30 m) has expired. This model has one user-defined parameter, gap tolerance, which sets the rules for the movement of the simulated animals



across agricultural landscape elements (see Appendix I). Brooker *et al.* (1999) used my observed dispersals of White-browed Babblers in Site A to determine the value of this parameter which best represented the pattern of real dispersals in this landscape. The same value for gap tolerance was used in the current simulations (*i.e.* 270 m).

Each run of the simulation model consisted of 100 iterations of the dispersal of a simulated animal. One of the outputs from this model was the number of times the simulated animal found the designated target group (*e.g.* 50 hits from 100 iterations). These results were used as a measure of the relative association between pairs of babbler groups. Local population neighbourhoods were defined as those groups which were associated at a pre-defined level (*e.g.*  $\geq 50$  hits from 100 iterations or 50%). *Neighbourhood models* were the local population neighbourhoods generated at one of three pre-defined levels of association, 25%, 50%, or 75%. Unidirectional associations between local population neighbourhoods occurred when the association between groups in one direction met the criterion for inclusion in the same local population neighbourhood, but did not meet this criterion in the opposite direction.

The simulation model allowed free movement of the disperser through all remnant vegetation, though if a choice was available the disperser used habitat patches in preference to other remnant vegetation (see Appendix I). Movement through agricultural vegetation patches was limited to crossing areas where remnant vegetation was no further away than the distance defined by gap tolerance. This meant that large agricultural vegetation patches could be crossed when there were sufficient remnant vegetation patches to act as stepping stones. Other agricultural vegetation patches were barriers to dispersal, because they covered distances greater than the gap tolerance of the disperser. *Dispersal barriers* for White-browed Babblers were defined as any breaks in the continuity of remnant vegetation patches which were greater than 270 m; and were extensive enough to prevent movement from one part of the landscape to another, or restricted movement to a single route (bottleneck). Breaks in the continuity of the remnant vegetation greater than 270m were common throughout the study area; but most had little effect on movement, because there were other routes close by which could be taken to reach the same location. Therefore, such cases were not considered to be *Dispersal barriers*. I identified dispersal barriers by observing the patterns of dispersal from the simulation model.

Real White-browed Babbler populations could occur at a number of spatial scales; within habitat patches, within the local population neighbourhoods defined by different neighbourhood models, or at a scale larger than the study sites. To determine which of these scales best fit the observed dispersal pattern I compared the frequency of dispersals at three scales:  $D_w$  dispersals among groups within the same habitat patch,  $D_b$  dispersals among groups occupying different habitat patches within the same local population neighbourhood, and  $D_{LPN}$  dispersals among groups occupying habitat patches in different local population neighbourhoods (see Fig. 4.3). I did this for the three study sites using the local population neighbourhoods defined by the three neighbourhood models.

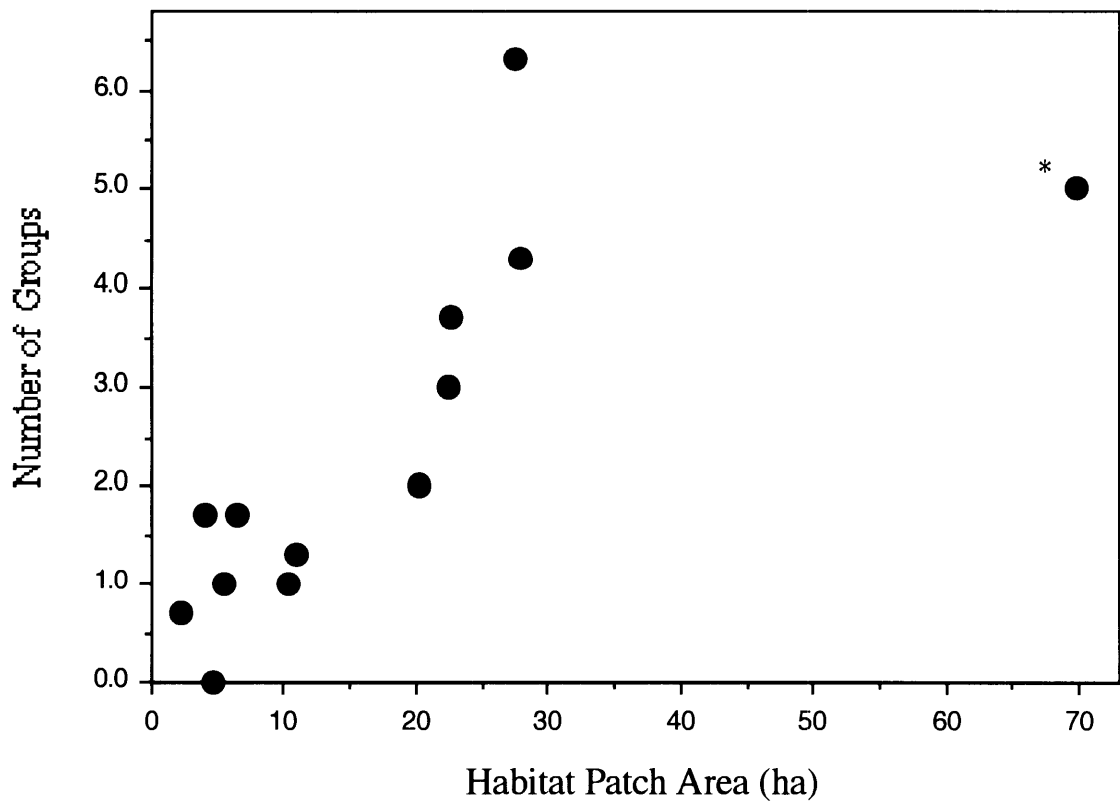
I estimated the edge-to-size ratio (ESR, Stamps *et al.* 1987) of each local population neighbourhood defined by the 50% neighbourhood model. To do this I drew the smallest polygon which encompassed all habitat patches within a local population neighbourhood. The edge-to-size ratio was then calculated as the proportion of groups which had home ranges on the edge of a local population neighbourhood (*i.e.*  $ESR = 1.0$  when all groups are situated on the edge of the local population neighbourhood). A group was considered to have a home range on the edge of its local population neighbourhood if it was adjacent to the polygon boundary.

## Results

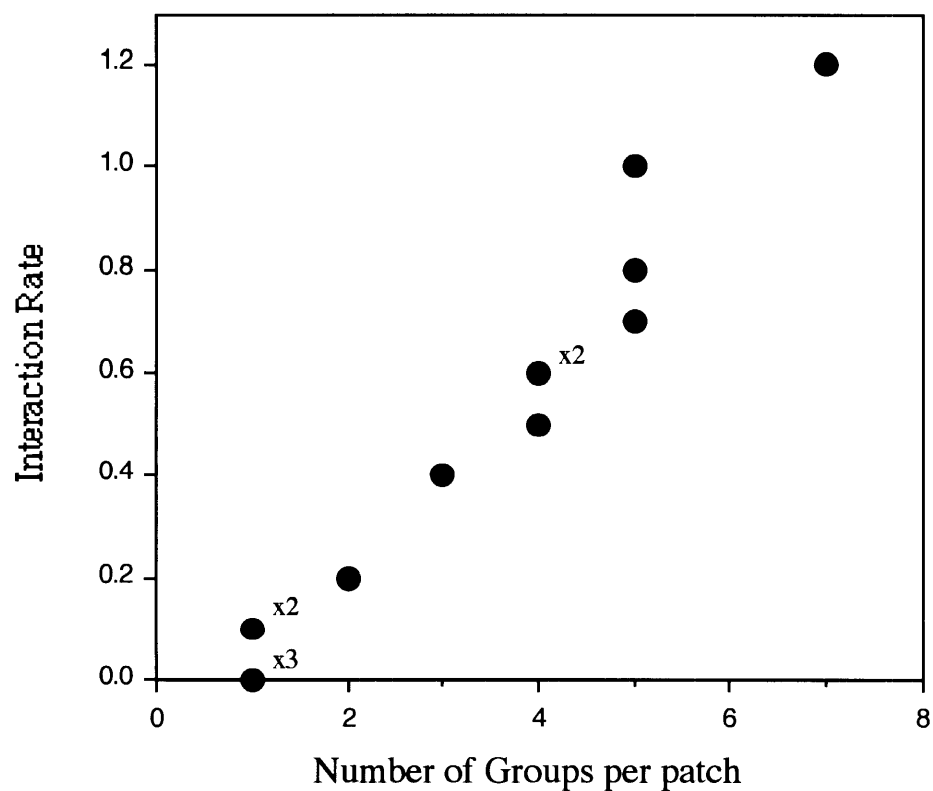
### *Habitat Patch Scale*

There was a significant positive relationship between the area of a habitat patch and the average number of groups that occupied that habitat patch between 1994 and 1996 (Adj.  $R^2 = 0.74$ ,  $F_{(1,10)} = 32.40$   $p = 0.0002$ ) (Fig. 10.1). One patch, in site B, was excluded from this model, because it was an outlier. This patch had been burnt in 1991 and had fewer groups in it than would be expected given its area. It was likely that some of the habitat in this patch was not suitable for babbler groups at the time of the study. The regression model was  $Number\ of\ Groups = 0.005 + 0.16(Habitat\ Patch\ Area)$ . This model predicts that the number of groups in a habitat patch will increase by one with an increase of 6.2 ha in the area of the habitat patch. There was a significant positive relationship between the Interaction Rate and the number of groups within a habitat patch (Adj.  $R^2 = 0.96$ ,  $F_{(1,11)} = 288.23$   $p = 0.0001$ ) (Fig. 10.2).

**Figure 10.1:** The relationship between the area of habitat patches and the average number of groups occupying that habitat patch from 1994 to 1996. \* This value was excluded from the regression model as an outlier (see text).



**Figure 10.2:** The relationship between the number of groups in a habitat patch and the frequency of interactions between those groups. Interaction Rate equals the number of interaction/group/10 observations/year. x2 and x3 indicate points which represent two or three patches respectively.



### *Dispersal*

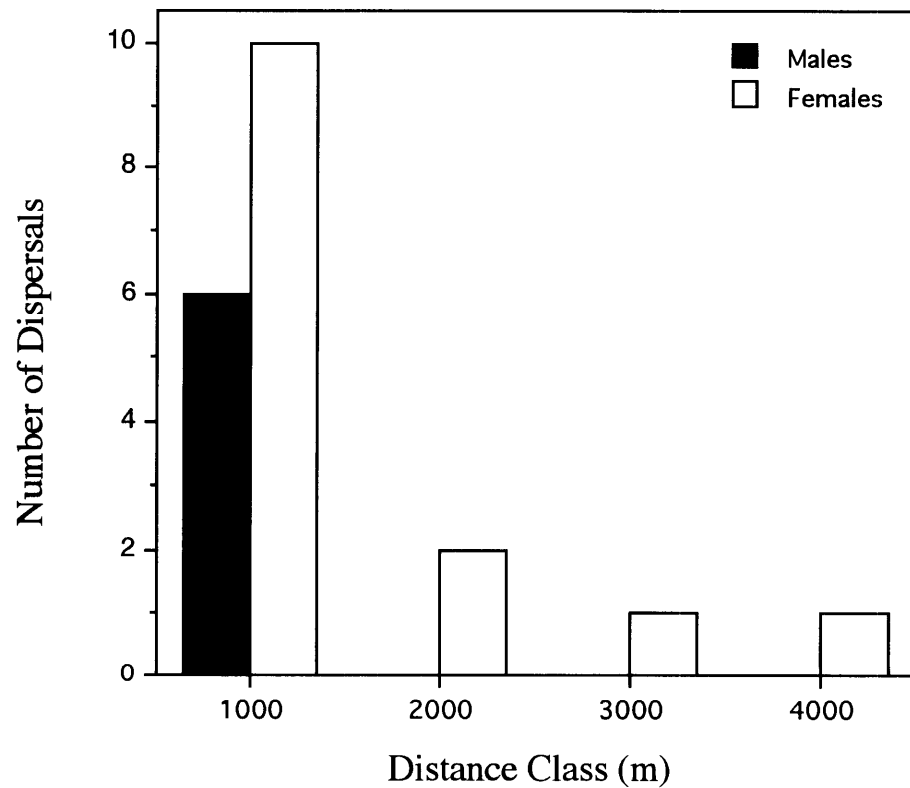
Twenty two (52%) of the 42 dispersals found in this study were between groups in different habitat patches. A significantly higher proportion of dispersing females (excluding breeding females) (82%) moved between habitat patches than did dispersing males (35%) ( $\chi^2_{(1)} = 5.95$   $p = 0.015$ ) (Table 10.1). Females moved to distant habitat patches more frequently than males did, when they left their original habitat patch (Fig. 10.3).

**Table 10.1:** The frequency of dispersals within and between habitat patches for male and female White-browed Babblers. Five dispersing birds were excluded, because their sex was unknown. Breeding females are those females which dispersed after nesting in a group.

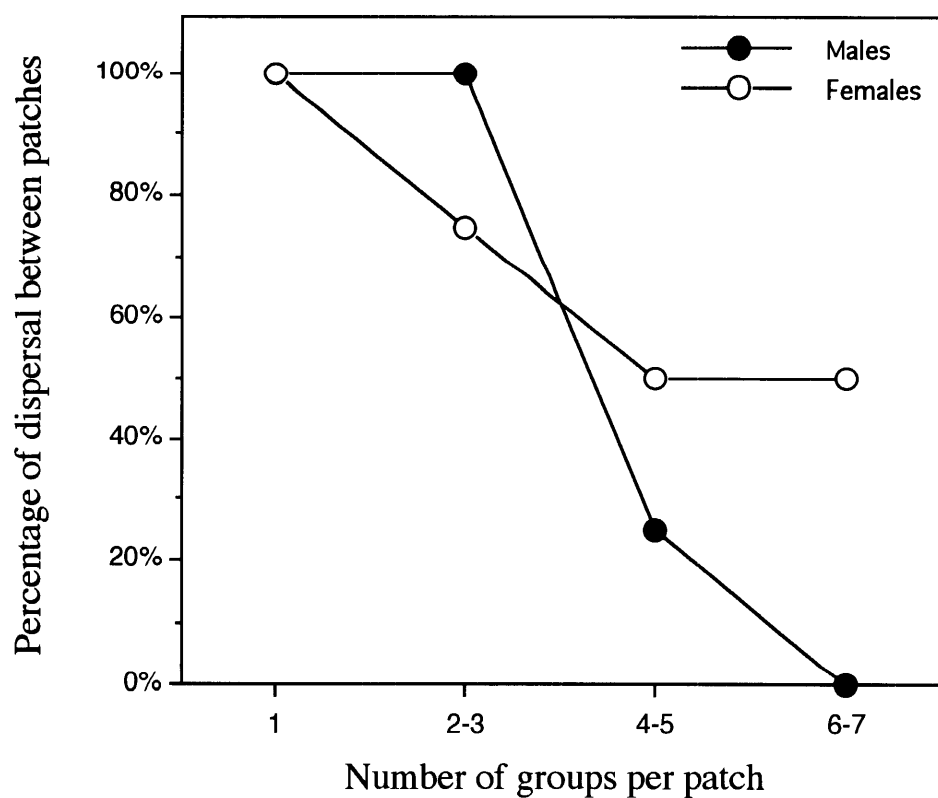
	Number of Dispersals	
	Within Patches	Between Patches
Males	11	6
Females	3	14
Breeding Females	3	0
Total	17	20

There was a significant increase in the number of dispersals per patch as the number of groups in patches increased ( $F_{(3,16)} = 3.88$   $p = 0.029$ ) (Table 10.2). However, when standardised for the number of groups per patch the dispersal rate was not significantly different ( $F_{(3,16)} = 0.17$   $p = 0.910$ ). The percentage of dispersals which resulted in emigration from the habitat patch declined as the number of groups in the habitat patch increased (Table 10.2). However, the proportion of dispersals resulting in patch emigration differed between the sexes (Fig. 10.4). Females showed a smaller decline in the level of patch emigration than males, and the proportion of female dispersals resulting in patch emigration never dropped below 50%.

**Figure 10.3:** Sexual differences in the distribution of dispersal distance between habitat patches. Dispersal distances were measured between the edges of habitat patches.



**Figure 10.4:** Sexual differences in the relationship between the percentage of dispersals between habitat patches and the number of groups in habitat patches.



**Table 10.2:** The variation in the rate of dispersal and the frequency of patch emigration from habitat patches occupied by different numbers of groups. The % of dispersals between patches represents that proportion of all dispersals which resulted in movement between habitat patches (patch emigration). Values for the number of dispersals are means  $\pm$  S.E.

	Number of groups per Habitat Patch			
	1	2-3	4-5	6-7
Number of Dispersals/patch/year	0.7 $\pm$ 0.2	1.4 $\pm$ 0.4	2.1 $\pm$ 1.1	5.0 $\pm$ 3.0
Number of Dispersals/group/year	0.7 $\pm$ 0.2	0.6 $\pm$ 0.2	0.5 $\pm$ 0.3	0.7 $\pm$ 0.4
% of Dispersals between patches	100	75	42	10

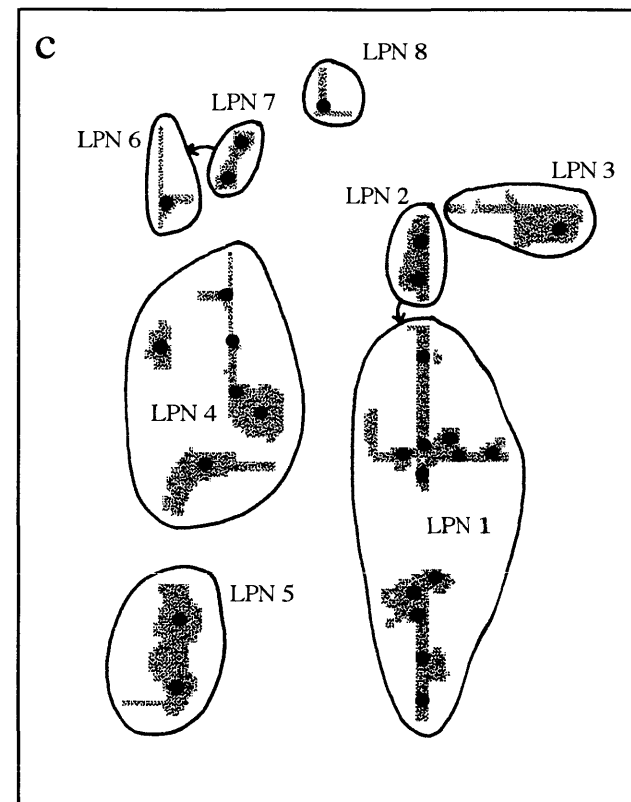
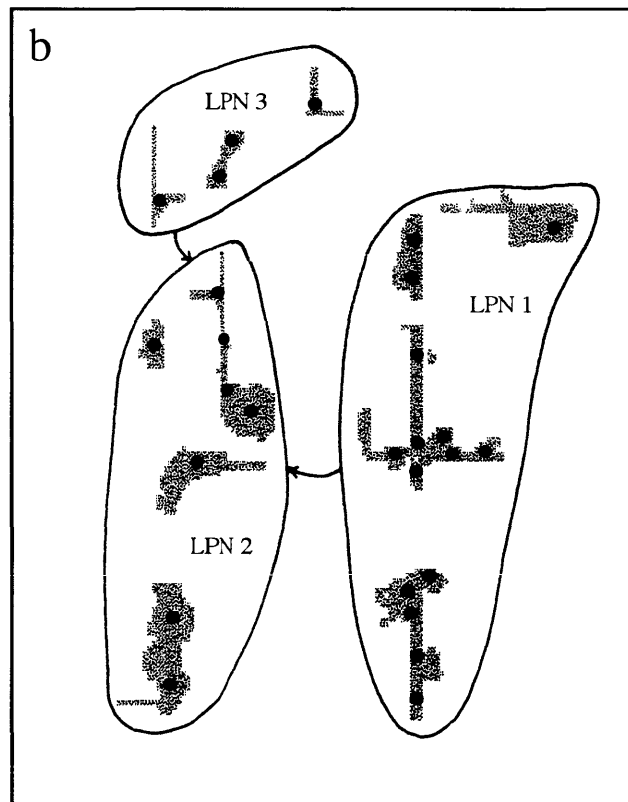
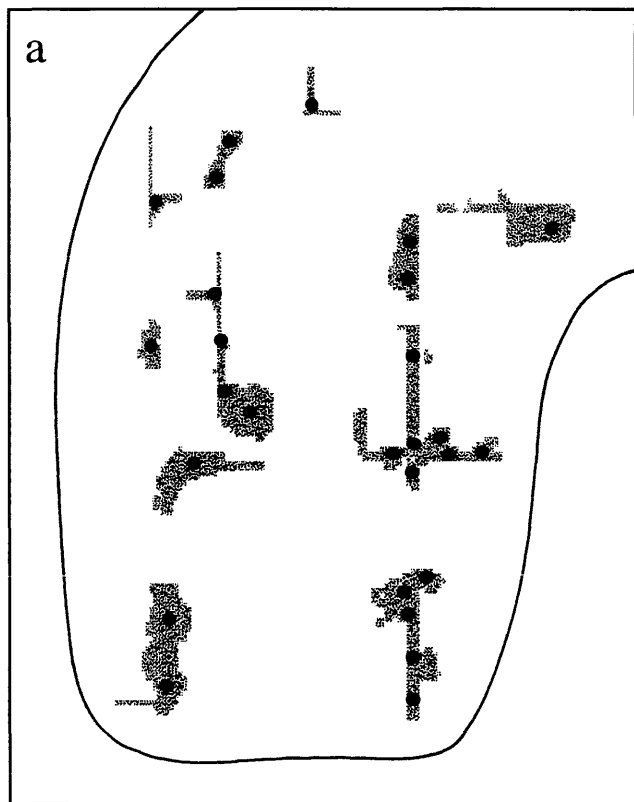
### *Local Population Neighbourhoods*

#### *Neighbourhood models*

The level of association between groups within the same habitat patch was generally  $\geq 75$  hits in 100 iterations ( $\geq 75\%$ ) and never fell below 65%. Those group pairs with levels of association below 75% were always in habitat patches containing more than two groups and always had high levels of association in common with other groups in the patch.

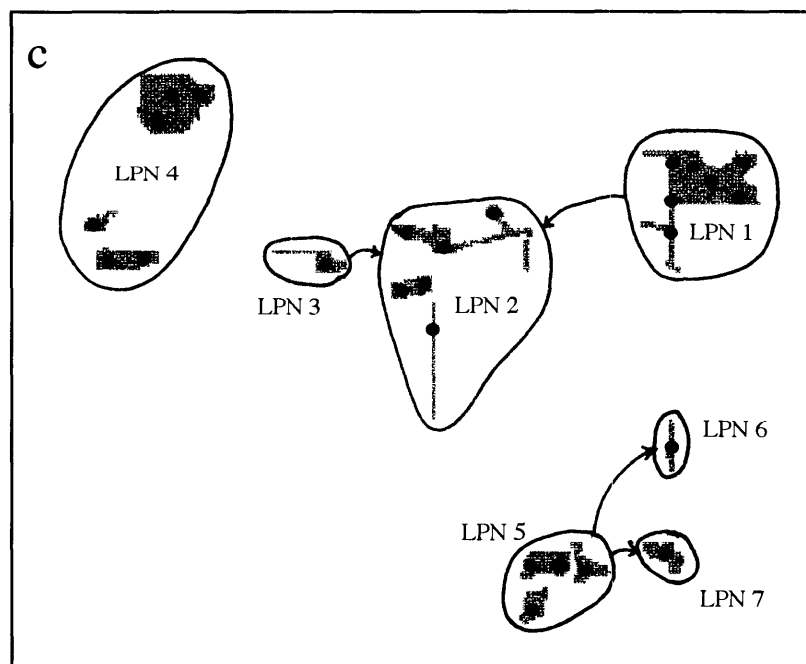
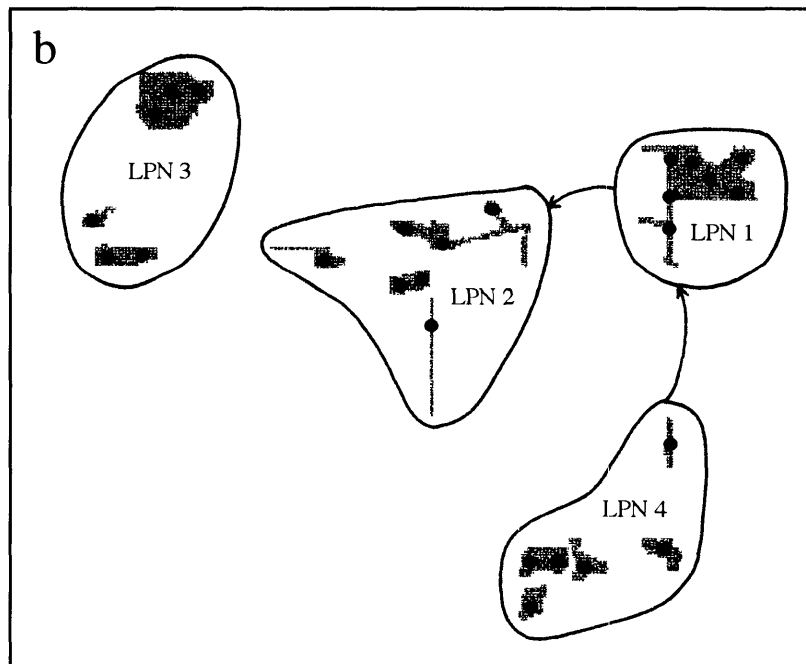
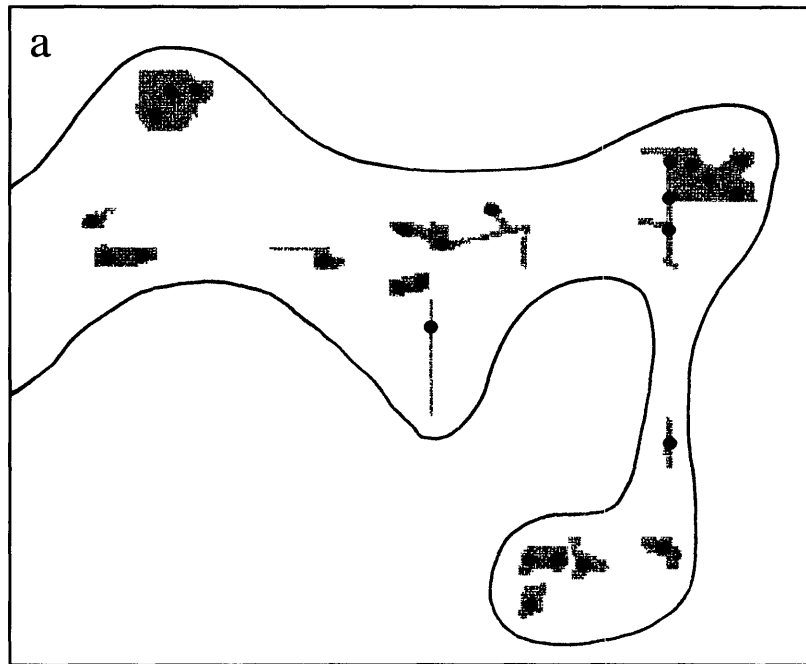
In Site A the 25% neighbourhood model had only one local population neighbourhood (Fig. 10.5a). This was divided into three local population neighbourhoods in the 50% neighbourhood model (Fig. 10.5b). However, there were unidirectional associations between LPN1 and LPN2 (Maximum association in opposite direction 45%), and LPN3 and LPN2 (Maximum association in opposite direction 46%), which almost met this model's criterion for inclusion in the same local population neighbourhood (Fig. 10.5b). Eight local population neighbourhoods occurred in the 75% neighbourhood model, but there was a unidirectional association between LPN2 and LPN1 (Maximum association in opposite direction 72%) in this model which was just below the model's criterion (Fig. 10.5c). There was another unidirectional association in this model between LPN7 and LPN6 (Maximum association in opposite direction 59%).

**Figure 10.5:** The local population neighbourhoods for Site A defined by three neighbourhood models; a) 25%, b) 50%, and c) 75%. The black circles represent babbler groups, stippled areas represent habitat patches and the solid lines represent the boundaries of local populations. The arrows represent unidirectional associations at the prescribed level.





**Figure 10.6:** The local population neighbourhoods for Sites B/C defined by three neighbourhood models; a) 25%, b) 50%, and c) 75%. The black circles represent babbler groups, stippled areas represent habitat patches and the solid lines represent the boundaries of local populations. The arrows represent unidirectional associations at the prescribed level.



The neighbourhood models generated for Sites B/C indicate that from the perspective of White-browed Babblers Site C is part of the same landscape as Site B. As in Site A, the 25% neighbourhood model for Sites B/C had only one local population neighbourhood (Fig. 10.6a). The 50% neighbourhood model had four local population neighbourhoods. One of these LPN4 contained all of the habitat patches in Site C. There was a unidirectional association between LPN1 and LPN2 in this neighbourhood model. The level of association in the opposite direction between these two local population neighbourhoods was low (26%) (Fig. 10.6b). The 75% neighbourhood model had seven local population neighbourhoods, but unidirectional associations between LPN2 and LPN3, and LPN5 and LPNs 6 and 7 all had levels of associations in the opposite directions (70%) which were just below this model's criterion (Fig. 10.6c).

### *Observed dispersals*

A total of 42 dispersals by individuals were observed during the three years of this study. This represents an average of 14 dispersals per year from an average of 30 groups, or one dispersal per group every two years. I calculated the number of dispersals that occurred within and between habitat patches and the local population neighbourhoods defined by each neighbourhood model shown in Figures 10.5 and 10.6. Since the 25% neighbourhood models for Site A and Sites B/C had only one local population neighbourhood all dispersals were within local population neighbourhoods.

For Site A, half of the observed dispersals occurred between groups in different habitat patches (Table 10.3). Approximately one in every four dispersing birds moved between local population neighbourhoods defined by the 75% neighbourhood model, which was more than twice as high as for those local population neighbourhoods defined by the 50% neighbourhood model.

In Sites B/C the total number of dispersals observed was low (12 dispersals in three years). More than half of these observed dispersals were between groups in different habitat patches (Table 10.3). One in three dispersing birds moved between the local population neighbourhoods defined by the 75% neighbourhood model. No dispersals were observed between groups occupying the different local population neighbourhoods defined by the 50% neighbourhood model.

**Table 10.3:** The number of actual dispersals which occurred within and between the local population neighbourhoods defined by the three neighbourhood models and using habitat patches as local population neighbourhoods (Habitat patch model). NA indicates situations where all dispersals were within LPNs, because only one LPN was defined.

Model	Dispersals		
	within LPN	between LPNs	% between LPNs
<b>Site A</b>			
25% neighbourhood model	30	NA	NA
50% neighbourhood model	26	4	13
75% neighbourhood model	22	8	27
Habitat Patch model	15	15	50
<b>Sites B and C</b>			
25% neighbourhood model	12	NA	NA
50% neighbourhood model	12	0	0
75% neighbourhood model	8	4	33
Habitat Patch model	5	7	58

Using the 50% neighbourhood model,  $D_w$  (dispersals between groups occupying the same habitat patch) and  $D_b$  (dispersals between groups occupying different habitat patches in the same local population neighbourhood) were approximately the same for both landscapes and both were higher than  $D_{LPN}$  (dispersals between groups occupying habitat patches in different local population neighbourhoods) (Table 10.4). The values for each local population neighbourhood varied greatly. Those local population neighbourhoods where few dispersals were observed generally had low values of  $D_{LPN}$ .

**Table 10.4:** The number of actual dispersals within and between the local population neighbourhoods (LPN) defined by the 50% neighbourhood model. % $D_b$  is the percentage of dispersals within a local population neighbourhood that occurred between different habitat patches, while % $D_{LPN}$  is the percentage of all dispersals that resulted in emigration from the local population neighbourhood. LPN3 from Site B was excluded because only two groups in one habitat patch had banded birds. There was one dispersal observed within this habitat patch. NA: There was only one habitat patch in LPN1 from Sites B/C, so  $D_b$  was not applicable.

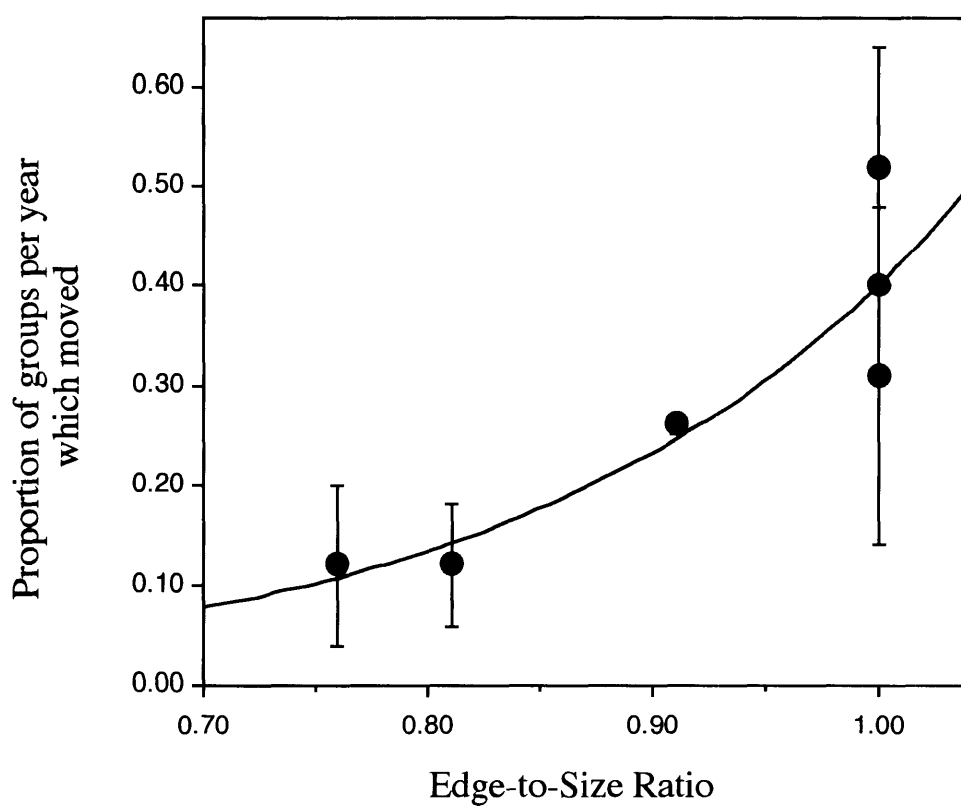
	Dispersals within LPNs			Emigration from LPNs	
	$D_w$	$D_b$	% $D_b$	$D_{LPN}$	% $D_{LPN}$
Site A					
LPN 1	12	5	29	3	15
LPN 2	3	5	62	0	0
LPN 3	0	1	100	1	50
Total	15	11	42	4	13
Sites B & C					
LPN 1	2	NA	NA	0	0
LPN 2	2	5	71	0	0
LPN 4	0	2	100	0	0
Total	4	7	64	0	0

### *Group movements*

A higher proportion of monitored groups on the edge (18 of 36 groups, 50%) compared to the interior (1 of 8 groups, 12%) of local population neighbourhoods made group movements. Due to the small number of interior groups this difference was only weakly significant (Fisher Exact-test  $p = 0.058$ ).

The proportion of groups in a local population neighbourhood (defined by 50% neighbourhood model) that made group movements increased with the edge-to-size ratio (ESR) of that local population neighbourhood. This relationship was best described by an exponential curve ( $R^2 = 0.91$ ,  $F_{(1,4)} = 16.39$   $p = 0.016$ ) (Fig. 10.7). This means that as the edge-to-size ratio of local population neighbourhoods approach one (*i.e.* all groups on the edge of the local population) the proportion of groups which are likely to move increases dramatically.

**Figure 10.7:** The relationship between the edge-to-size ratio of local populations (based on the 50% neighbourhood model) and the proportion of groups from the local population that made group movements. The values are the mean  $\pm$  S.E. of three years data. An exponential curve of best fit is shown.



### *Regional neighbourhood models*

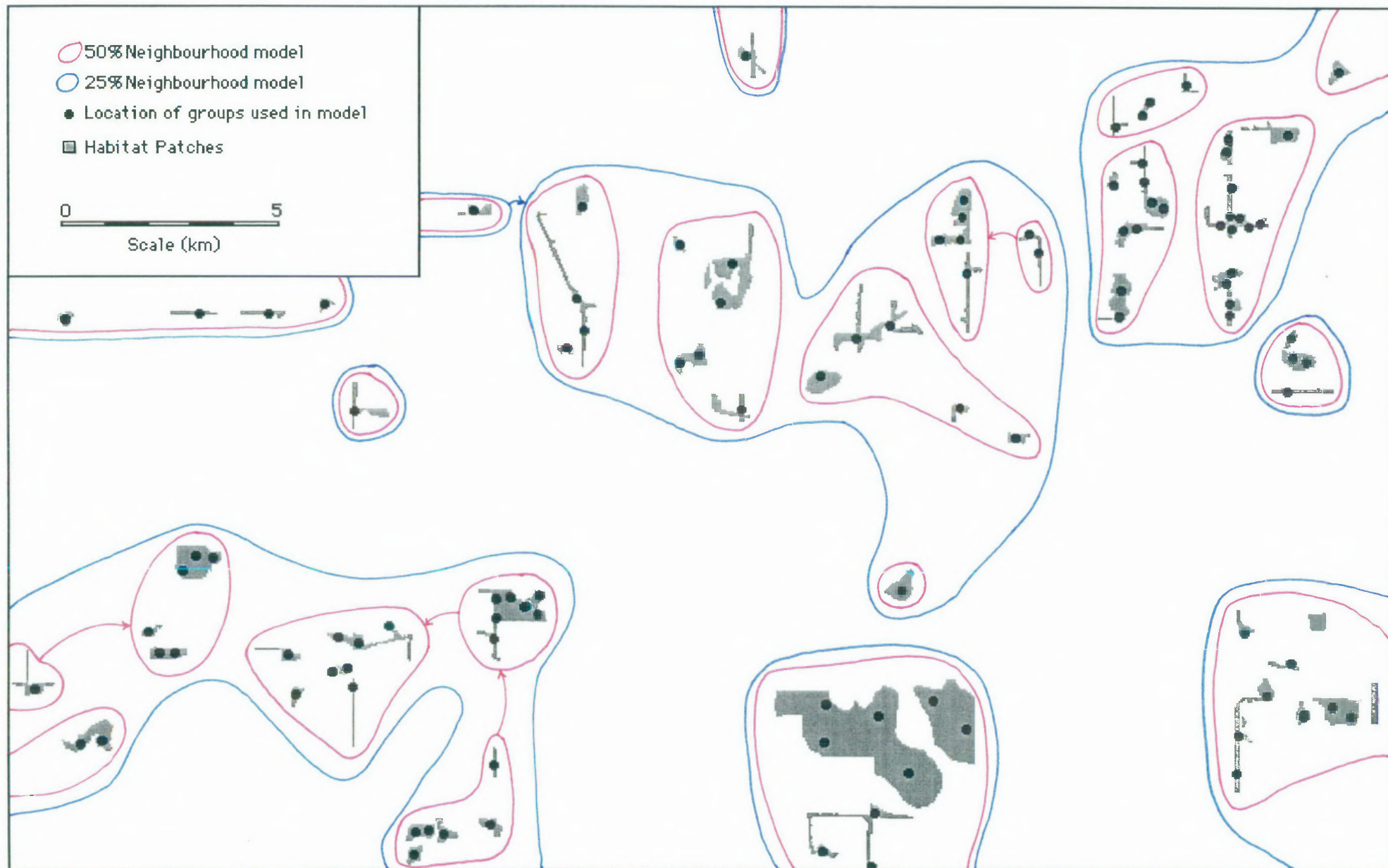
The 50% neighbourhood model for the regional survey area had 23 local population neighbourhoods (Fig. 10.8). There were five unidirectional associations between local population neighbourhoods defined by this model (red arrows in figure 10.8). The local population neighbourhoods defined by this model varied in size from single habitat patches containing a single White-browed Babbler group to multiple habitat patches containing as many as 14 groups.

Only ten local population neighbourhoods occurred in the 25% neighbourhood model and consequently most contained many more White-browed Babbler groups than those found in the 50% neighbourhood model (Fig. 10.8). The largest contained at least 30 White-browed Babbler groups in at least 16 habitat patches (Sites B/C). There was only one unidirectional association between local population neighbourhoods defined by this model. The boundaries of several of the local population neighbourhoods in this model were convoluted due to low levels of predicted dispersal between some groups. This was caused by breaks in the connectivity of the landscape (*i.e.* dispersal barriers).

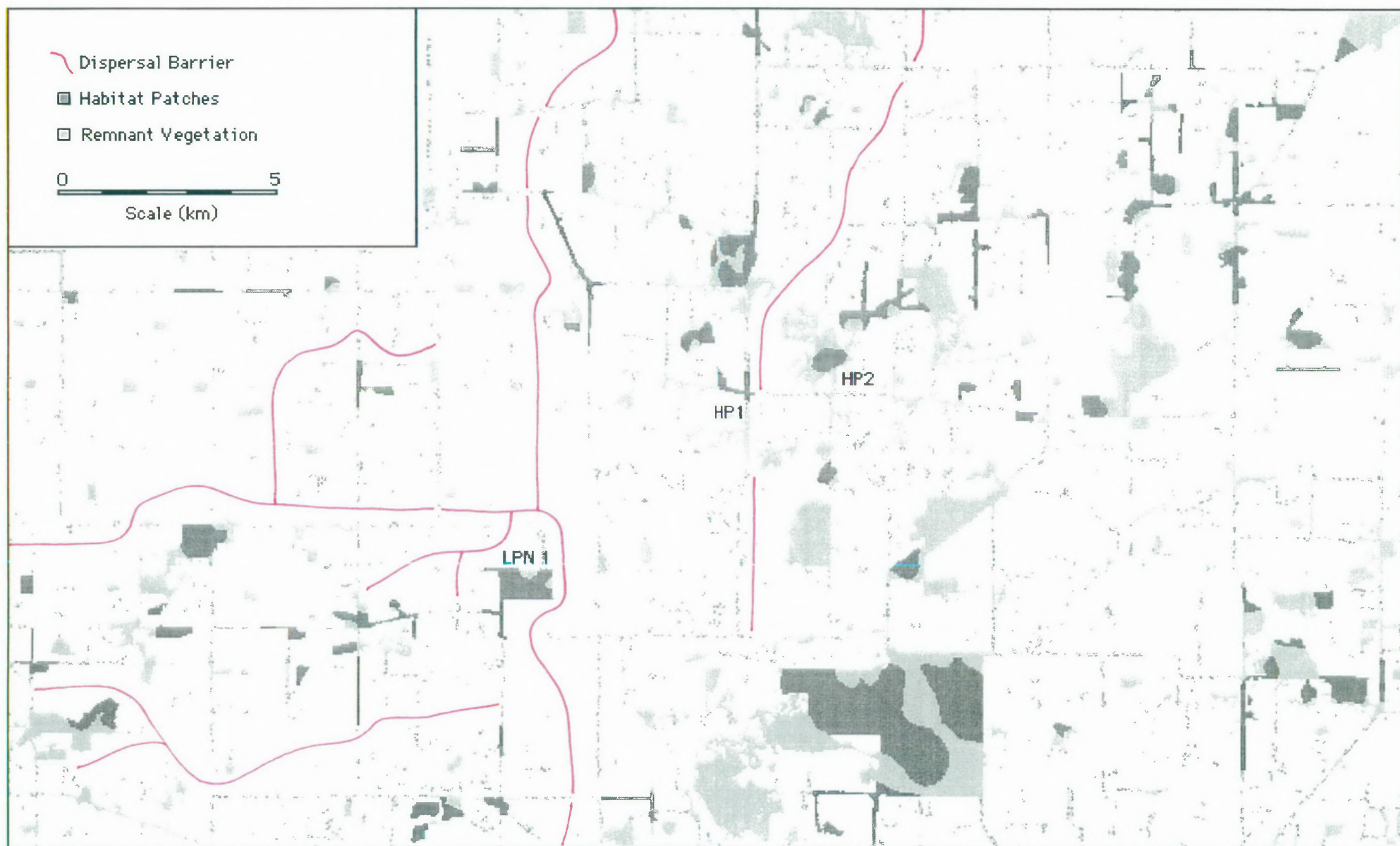
Dispersal barriers were found in a number of locations, especially in association with Sites B and C (Fig. 10.9). These dispersal barriers isolated Sites B and C from the rest of the survey area, with only three known routes along which dispersals could be made into or out of Site B. The central local population neighbourhood defined by the 25% neighbourhood model was almost divided in half by a dispersal barrier, but two habitat patches (HP1 and HP2 in figure 10.9) linked the two halves of this local population neighbourhood.

**Figure 10.8:** The local population neighbourhoods defined by the 25% and 50% neighbourhood models for the Kellerberrin survey area.





**Figure 10.9:** Dispersal barriers for White-browed Babblers in the Kellerberrin area, based on the dispersal rules of the simulation model and a gap tolerance of 270 m. Dispersal routes represent breaks in dispersal barriers which allow movement from one side to the other. LPN1: this remnant is one of the local population neighbourhoods in Sites B/C defined by neighbourhood models. HP1 and HP2 are habitat patches which link two halves of the 25% local population neighbourhood encompassing these patches (See text for discussion of these particular cases).



## Discussion

For a species which is dependent on remnant vegetation, such as the White-browed Babbler, one of the major consequences of habitat loss is a reduction in the size of habitat patches. This results in fewer groups occupying each habitat patch. Since the relative frequency of social interactions between groups declined as the number of groups in a patch declined, declining patch size corresponds to a depression in social interaction. A consequence of this reduction in social interaction is that in small habitat patches the individuals from different groups would have less social contact. This social contact between individuals from different groups is important to the dispersal process in cooperatively breeding birds, such as the White-browed Babbler (see Chapter 9). Therefore, changes in patch size are not only likely to have a negative effect on the social interactions between groups, they may also change the dispersal behaviour of individuals.

Group interactions are not the only form of social contact between individuals from different groups. Some individuals visited other groups temporarily. It is possible that the visiting behaviour of birds may compensate for the decline in group social interactions. This could not be assessed in the current study, because the frequency and spatial distribution of such visits is poorly known for the White-browed Babbler (Chapter 9). However, the observed increase in patch emigration as the number of groups occupying the patch decreases, suggests that visits between groups in different habitat patches may increase as patch size decreases.

The relationship between the number of groups in a habitat patch and the proportion of dispersals resulting in patch emigration differed for males and females. This difference can be explained by sexual differences in dispersal behaviour resulting from the social structure of White-browed Babblers. Male babblers monitor groups near their natal territory, seeking breeding vacancies or groups where they have a higher probability of obtaining a breeding position (*i.e.* an assessment sphere, see Chapter 9). In habitat patches with many groups, the male's assessment sphere is encompassed by the patch, so the majority of his dispersal opportunities occur within the same patch. However, when habitat patches contain only one or two groups, a male's assessment sphere must extend beyond the boundaries of the patch or he must accept fewer opportunities to disperse. Therefore, patch emigration should increase if habitat patch size decreases due to

fragmentation. Matthysen *et al.* (1995) found a similar dispersal pattern in Nuthatches and described the phenomenon as a dilution effect of fragmentation. This dilution effect not only increased the frequency of patch emigrations by Nuthatches it also increased the distances dispersed by individuals, because inter-patch distances were large (Matthysen *et al.* 1995). In the White-browed Babbler dispersal distances associated with patch emigration did not increase greatly (Fig. 10.3), because most inter-patch dispersals were between patches which were close together. This suggests that the frequency of dispersal by male White-browed Babblers occupying habitat patches which are isolated (*i.e.* greater than 1000 m from another habitat patch) may decline due to this isolation.

The dispersal behaviour of female White-browed Babblers differed from that of males. Natal dispersal in females appears to be more common and these dispersals are generally over greater distances (Chapter 9). These dispersal distances are substantially larger than the spatial scale of the habitat patches found in the Kellerberrin landscape. Therefore, patch emigration by females making natal dispersals should be common regardless of habitat patch size. This is reflected in the high percentage of patch emigrations by females even in the largest habitat patches (50%). If females made only natal dispersals then there should be no relationship between habitat patch size and the proportion of patch emigrations, which was not the case. This can be explained by the fact that some females also dispersed after their initial natal dispersal. These post-natal dispersals (*i.e.* breeding dispersals plus dispersals to groups as helper) appeared to be confined to the same spatial scale as male dispersals, because, like males, these females assess neighbouring groups for dispersal opportunities (Chapter 9). Therefore, some level of decline in the proportion of patch emigration is expected. A reduction in the spatial scale of breeding dispersals compared to natal dispersals was also found in the Nuthatch (Matthysen *et al.* 1995) and the Blue-breasted Fairy-wren *Malurus pulcherrimus* (Brooker & Brooker 1997). In the latter case breeding dispersals were restricted to groups within the same habitat patch.

Male dispersal and female post-natal dispersal are restricted to groups with a high level of social contact. These dispersals did not define population boundaries, because female natal dispersal occurred at a much larger spatial scale and so connected a greater number of habitat patches. Therefore, the smaller scale dispersals made by males and

breeding females created structure within populations. This is similar to the behaviourally structured population model of Sugg *et al.* (1996), in which populations are made up of groups which prevent complete random mating across the whole population. These social structures within populations play an important role in population demographics (Vucetich *et al.* 1997), and in maintaining genetic variation within populations (Sugg *et al.* 1996). I call this level of association within a population a *social neighbourhood*.

Habitat patch edges appear to be relatively impermeable boundaries to the social dynamics of babbler groups. However, the degree of permeability of these boundaries is dependent on patch size and the context of the patch. When patches and inter-patch distances are small, patch edges appear to be more permeable to social interactions. Therefore, social neighbourhoods are affected by fragmentation of the landscape. Although, these social neighbourhoods are affected by fragmentation it is unlikely that they are a result of it. Work currently in progress on the Rufous Treecreeper, in fragmented and unfragmented woodlands, has found that social neighbourhoods operate in both systems (G. Luck *pers. comm.*).

### *Local Populations*

The response of White-browed Babblers to the dilution effect of fragmentation is complex. Both sexes increase the frequency of dispersals between habitat patches as patch size decreases, but most of this dispersal is related to social neighbourhoods not populations. This is the *fission* response proposed by Ims *et al.* (1993). However, female natal dispersal occurs at a spatial scale larger than that of habitat patches and does not appear to be affected by changing patch size. The consequence of this complex dispersal response is that White-browed Babbler groups within habitat patches cannot be considered to constitute local populations (more than half of the observed dispersals occurred between such patches), but when patches are large they do represent social neighbourhoods. Therefore, the population structure in the Kellerberrin landscapes is patchy (Harrison 1991; Harrison & Taylor 1997).

The importance of female natal dispersal in defining population boundaries is similar to that found for the Blue-breasted Fairy-wren in the Kellerberrin landscape. In that species, 10% of females dispersed between habitat patches compared to only 1.5% of



males (Brooker & Brooker 1997). However, patch emigration in Blue-breasted Fairy-wrens was much lower than in the White-browed Babbler, suggesting that habitat patches may often represent local populations for this species. Blue-breasted Fairy-wrens appear to be more reliant on remnant vegetation for dispersal than the White-browed Babbler, because they can cross only narrow gaps of agricultural vegetation (Brooker *et al.* 1999). Therefore, these differences in the scale of population dynamics may be due to differences in the connectivity of the landscape for these two species.

The high level of patch emigration in White-browed Babblers does not mean that the metapopulation concept is inappropriate for this species. Habitat patches are not evenly distributed within the landscape and the landscape mosaic associated with these patches varies. This results in differences in landscape connectivity (Taylor *et al.* 1993). This spatial aggregation of habitat patches and differences in landscape connectivity mean that the level of association between different habitat patches with respect to dispersal may differ.

Neighbourhood models provide a description of these associations. The local population neighbourhoods defined in these models are not a direct estimate of the probability of dispersal between groups, because they are based on the relative probability of a bird finding different target groups independently of other target groups (Brooker *et al.* 1999). The real probability of dispersal between groups is also dependent on a number of other factors; such as the distribution of vacancies available to the disperser, the level of competition for a given vacancy, and social interactions between the disperser and the members of the new group. Despite these limitations, the neighbourhood models when compared with the observed dispersals, can provide an approximation of the structure of real local populations.

In Chapter 4 I proposed that the population structure of babblers could be considered a metapopulation if there was a discrete difference in the level of dispersal among groups within and between local population neighbourhoods. All three neighbourhood models met this criterion, but the proportion of dispersals that occurred between local population neighbourhoods differed (Table 10.3). There were no observed dispersals out of the local population neighbourhoods defined by the 25% neighbourhood model, because only single neighbourhoods occurred in each Site. However, the dispersal

data suggests that it was likely that a small number of dispersing individuals dispersed beyond the study sites (Chapter 9). These individuals would represent dispersals between neighbourhoods in this model.

Rates of dispersal will always decline with distance, but if the configuration of the landscape produces a discrete set of local population boundaries there should be a step function in the relationship between the percentage of dispersals between local populations and the spatial scale at which local population boundaries are defined (*i.e.* habitat patches, 75%, 50% and 25% neighbourhood models). This was not found (Table 10.3). Therefore, there is no discrete local population structure defined by the configuration of the landscape.

Although all of the neighbourhood models represent metapopulations at different spatial scales, the 50% neighbourhood model is the only one which reflects a spatial structure that is likely to have an important influence on population dynamics. The level of dispersal between groups in different local population neighbourhoods defined by this model is sufficient to influence the persistence of these local populations (Stacey *et al.* 1997). However, this level of dispersal is unlikely to be high enough to prevent the dynamics of these local populations from being independent, which is a requirement of a metapopulation (Hanski & Simberloff 1997). There were no dispersals observed between the local population neighbourhoods in Sites B/C defined by this model, but this is likely an artifact of the small number of dispersals observed in this landscape. If the proportion of dispersals between local population neighbourhoods in Sites B/C was 13%, as in Site A, only 1.6 dispersals between local populations would be expected from the 12 dispersals observed.

The level of dispersals between local population neighbourhoods defined by the 25% neighbourhood model was probably low. Whether this level of dispersal is sufficient to make this population structure comparable to a metapopulation is not known. For the 75% neighbourhood model, dispersals between local population neighbourhoods were so frequent that some of the local populations would probably not have independent population dynamics and so would not represent a metapopulation (Hanski & Simberloff 1997). This data demonstrates that the White-browed Babbler population structure is not



discrete, but lies along a continuum from a single patchy population to one of various metapopulation structures.

Most of the local populations generated by the 50% neighbourhood model consisted of a number of habitat patches (*i.e.* patchy populations *sensu* Harrison & Taylor 1997). Only LPN1 in Sites B/C contained a single habitat patch (Fig. 10.6b). This is similar to the mixed metapopulation structure described by Harrison and Taylor (1997) (see Fig. 1.1). A similar mixed metapopulation structure was also found in the Silver-spotted Skipper butterfly *Hesperia comma* (Hill *et al.* 1996).

The distribution of dispersals within and between these local population neighbourhoods showed considerable variation (Table 10.5). In part, this was the result of habitat patches of different size, but the spatial isolation of patches and the overall size of the local population also appeared to have an effect. Hill *et al.* (1996) found that the per capita emigration rate of the Silver-spotted Skipper was higher in small local populations than larger ones. Though the sample size of dispersals for the White-browed Babbler local populations is extremely small it does show similarities to this relationship. The smallest local population (LPN3 in Site A) produced 25% of the observed emigrations despite producing only 7% of all dispersals in this landscape (Table 10.4).

Another characteristic of the relative levels of association between groups revealed by the neighbourhood models was their asymmetry. Some group pairs had high levels of association in one direction, but not in the other. This characteristic was also found for the European Badger *Meles meles*, using a very different type of dispersal simulation (Schippers *et al.* 1996). The reason for these unidirectional associations is that dispersal between groups is related to landscape connectivity, which is dependent on the configuration of the landscape mosaic surrounding each habitat patch (Taylor *et al.* 1993; Wiens 1995, 1997; Gustafson & Gardner 1996). Two characteristics of the landscape mosaic are likely to influence the connectivity of the landscape for White-browed Babblers: 1) corridors of vegetation connected to the patch, and 2) the distance across agricultural land to the nearest remnant vegetation (Brooker *et al.* 1999). These characteristics affect the number of dispersal options out of a given habitat patch. Unidirectional patterns of dispersal between patches mean that some local populations may face a high rate of emigration to other local populations, which is not compensated by a corresponding high

rate of immigration. This can exacerbate the problems faced by small local populations (Hill *et al.* 1996).

Dispersal barriers represent areas of the landscape mosaic which probably inhibit dispersal of White-browed Babblers from one area to another. These barriers were not common in the Kellerberrin area, but those that existed had substantial influence on the geometry of the local populations generated by the neighbourhood models. In a number of situations dispersal was restricted to a single route (bottleneck), so the groups at either end of these routes were important in determining the level of association between areas (Fig. 10.9). Therefore, small changes in the landscape that resulted in the loss of these routes, or the disappearance of groups which connected either end, could result in the fragmentation of local populations. Conversely fragmented local populations may be reconnected by strategic changes in the landscape which replace lost connectivity (Brooker *et al.* 1999).

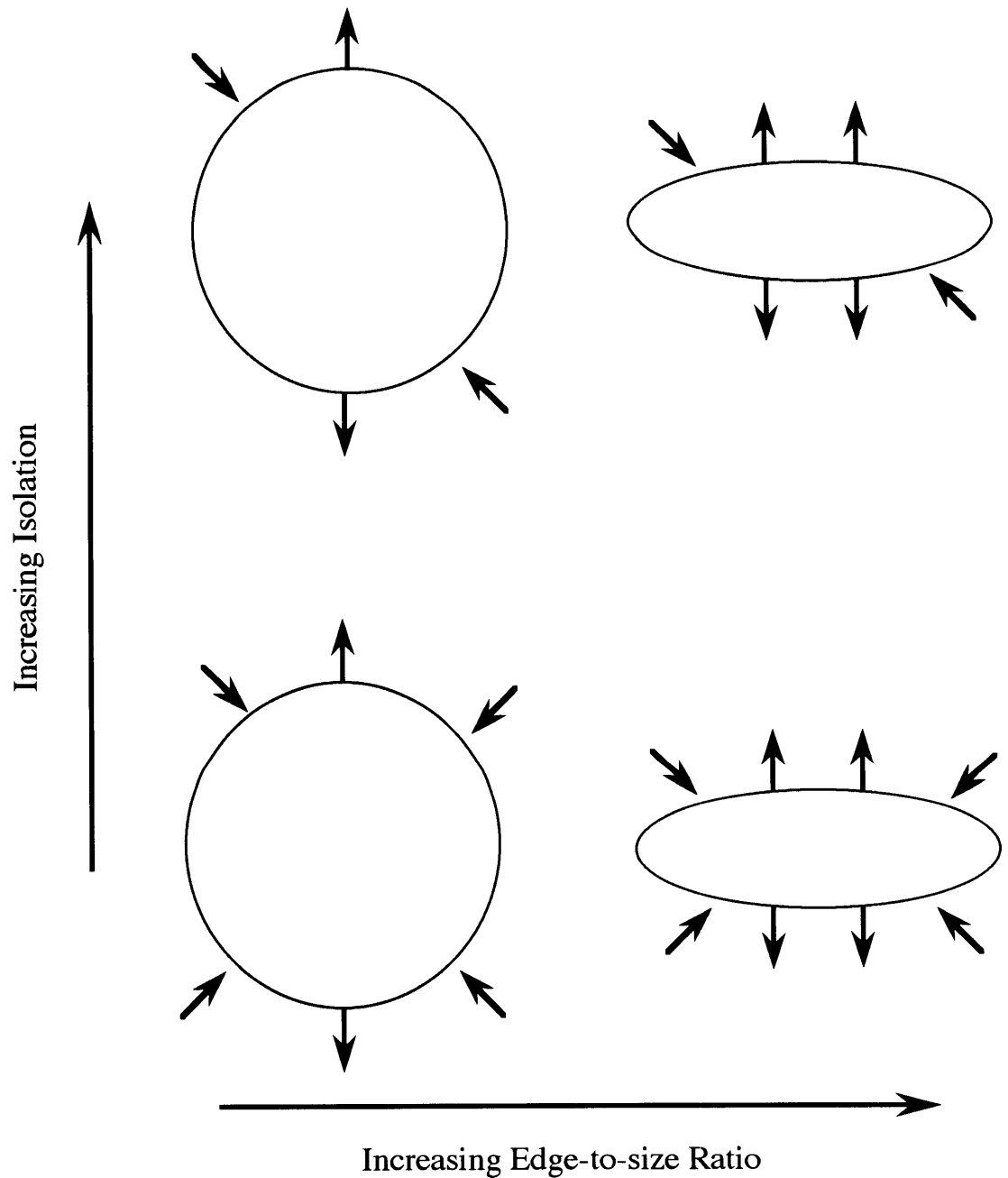
The most extensive dispersal barriers were found around Site B, which was almost completely isolated from the rest of the survey area. If these barriers are real then immigration into populations, such as LPN1 in Sites B/C (Fig. 10.9), should be restricted. No dispersals were observed into this remnant during the current study. In addition, an extensive banding program, which ran for 10 years, failed to record a single dispersal by White-browed Babblers into this remnant (Saunders & de Rebeira 1991). However, other species (Singing Honeyeater *Lichenostomus virescens* and White-eared Honeyeater *L. leucotis*) were found to move into it (Saunders & de Rebeira 1991). In contrast to the White-browed Babbler, these species are likely to be more tolerant to crossing farmland (*pers. obs.*) and so the spatial scale at which they perceive the connectivity of this landscape may be higher.

The determination of local population neighbourhoods has been based on dispersals by individuals and did not take into account movements by groups. Some of these group movements were permanent, and so represented mass dispersals, which could have substantial effects on local populations. These group movements are poorly understood, because no group which made a group dispersal was ever seen again and the origins of those groups which entered the study sites were unknown. This indicates that group dispersals were occurring on a much larger scale than individual dispersals (*i.e.* greater than 5 km which was the extent of the areas searched around each study site). In Chapter 9 I

demonstrated that groups were more likely to move during the Summer if their habitat patch supported low food resources during this period. However, not all groups in these patches moved. The geometry of the local populations also appeared to influence the likelihood of group movement, with the majority of groups which moved having home ranges on the edge of their local population. Stamps *et al.* (1987) showed that patch geometry could be an important factor influencing the level of emigration from patches. Their models indicated that patches with high edge-to-size ratios had much higher rates of emigration. Although their models dealt with dispersals by individuals, the pattern of group movements found in White-browed Babblers appear to be similar. This suggests that the high frequency of group movements found in some areas of the Kellerberrin landscape might be the result of an interaction between differences in the quality of habitat patches, and changes in the landscape mosaic which have increased the edge-to-size ratio of local populations.

Group dispersals result in the loss of groups from local populations, but this is often compensated for by groups immigrating into the local population. As populations decrease in size their edge-to-size ratio increases, and so the likelihood of group movements will also increase. If these small local populations are also isolated, then the higher levels of group emigration resulting from their small size will not be compensated by immigrating groups from neighbouring local populations. Therefore, group dispersal would be most detrimental in small, isolated local populations (Fig 10.10). The effects of this model would be modified by the quality of the habitat patches within local populations. Habitat patches with lower quality breeding habitat had higher rates of group dispersal, but breeding quality did not appear to affect the occupancy of habitat patches by new groups coming into the area (Chapter 9). Therefore, habitat patches of low breeding quality in a local population would exacerbate the effects of increased group emigration due to a high edge-to-size ratio, while habitat patches of high breeding quality would moderate it. This is demonstrated by the group dispersals observed in LPN1 from Sites B/C (Fig. 10.9). This local population is isolated due to dispersal barriers. It also suffered a fire in 1991, which probably reduced the breeding quality of the habitat by reducing vegetation cover. Five of the seven groups in this remnant dispersed during this study and no group immigrations were observed to replace the groups lost.

**Figure 10.10:** The theoretical relationship between local population geometry and isolation with respect to group emigration and immigration. The number of arrows represent the expected proportional rate of emigration (outward) and immigration (inward) in the four hypothetical local populations. As the edge-to-size ratio increases emigration increases, and as isolation increases immigration decreases.



### *Population Structure*

The findings of this study indicate that the population of White-browed Babblers in the Kellerberrin landscape has a hierarchical structure (Fig 10.11). The basic unit of this system is the group, which in the Kellerberrin area represents a single breeding unit. Babbler groups interact socially (*i.e.* group interactions and visits by individuals) with nearby groups. This interaction is generally restricted to groups within the same habitat patch, but when habitat patches are small and have short inter-patch distances the groups which occupy them may also interact. Most male dispersal and probably post-natal dispersal by females is within the same Social Neighbourhood, and this has important consequences for the demography of this species (see Chapter 11). Social Neighbourhoods occur within the same Local Population when the level of dispersal between them is high. This is equivalent to the patchy population concept of Harrison (1991). Local Populations form a Metapopulation, because there is a low level of dispersal between them which influences their dynamics, but is likely to be too infrequent to prevent the dynamics of local populations from changing independently of each other.

The patchiness of the landscape also reflects the structured nature of babbler populations. This structure fits the proposed hierarchical model of heterogeneity proposed by Kotliar and Wiens (1990). The home ranges of White-browed Babbler groups are generally confined to a single habitat patch; although, these contain smaller scales of patchiness with respect to food and breeding habitat quality (Chapter 6). Large habitat patches or clusters of small closely associated habitat patches represent the scale of patchiness associated with social neighbourhoods. Finally, larger clusters of habitat patches represent the patchiness associated with local populations. Therefore, it is essential to consider which organisational level a process is operating at, before assessing how the patchiness of the landscape relevant to that process is structured.

**Figure 10.11:** A Hierarchically Structured Population Model. There are four levels in the hierarchy. Breeding units (solid black circles) are the basic unit and in White-browed Babblers are represented by groups. Social Neighbourhoods are defined by high levels of social interaction between breeding units. Local Populations are clusters of Social Neighbourhoods associated by high levels of dispersal. The Metalopulation is a cluster of Local Populations which have independent dynamics, but are connected by a low level of dispersal.

