

CHAPTER 5: LANDSCAPE AND TERRITORY SCALE SELECTION OF THE EASTERN YELLOW ROBIN (*Eopsaltria australis*) CONSTRAINED BY FINER-SCALE ATTRIBUTES.

5.1 ABSTRACT

In fragmented agricultural landscapes, habitat selection in birds is influenced by a multitude of factors, including the reduction in total amount of available habitat and a reduction in size and quality of remaining remnants. However, only a small proportion of remaining habitat may be suitable to a species, as a result of the reduced size and increased proportion of edge in remaining remnants and the degradation of the habitat. The present study examined landscape and territory scale habitat selection of the Eastern Yellow Robin (*Eopsaltria australis*); a species known to be sensitive to habitat fragmentation. The perimeter to area ratio of the remnant was the principal factor governing landscape scale selection, with occupied remnants harbouring a smaller ratio (i.e., proportionally less edge) than unoccupied remnants. Robins selected territories in sites with a greater density of sapling trees, subcanopy trees and shrubs compared to non-territories. Aspects important in territory scale selection are typically compromised in edge habitat (e.g., reduced plant recruitment due to drier microclimate and grazing). Thus, selection at the landscape scale for remnants with less edge habitat is potentially constrained by the attributes important in territory scale selection. Furthermore, given the importance of sapling and subcanopy trees in territory scale and foraging microhabitat scale selection, territory scale selection may be constrained by selection at the foraging microhabitat scale, with selection at the landscape scale in turn constrained by selection at the territory scale. Results of the present study

indicate that habitat selection by Eastern Yellow Robins may be best represented by a 'bottom-up' model, with finer spatial scale attributes constraining selection at progressively coarser spatial scales.

5.2 INTRODUCTION

Habitat fragmentation is an inevitable consequence of extensive clearing for agriculture, and is best defined by a number of inter-related factors, including a reduction in the total amount of habitat in a landscape and a reduction in size and increased isolation of remaining remnants (Bennett 1999; Villard *et al.* 1999; Brand and George 2001). The implications of these effects on birds extend beyond the immediate impacts of reduced habitat, as only a small proportion of a fragmented landscape may contain suitable habitat for a given species of bird. This is partly due to the sensitivity of species to the size of remaining remnants and increased proportion of remnant edge habitat, especially as landscapes become more severely fragmented (Temple and Cary 1988). A number of researchers suggest that area sensitivity and edge avoidance are interchangeable (see Brand and George 2001) because smaller remnants tend to have a higher proportion of edge habitat than larger remnants (Villard 1998), although the proportion of edge habitat in larger remnants varies considerably according to remnant shape. Separating area from edge effects requires not only an assessment of remnant area and a measure of remnant perimeter to area ratio, but also the inclusion of a wide range of remnants.

Edge habitat and small remnants have different physical and ecological characteristics from interior habitat and large remnants, such as altered microclimates (e.g., elevated wind velocities and temperatures and reduced

humidity)(Hobbs 1993; Murcia 1995), an alteration to vegetation structure such as a reduction in tree and shrub recruitment brought on by grazing and an invasion by weeds (Saunders *et al.* 1991; Yates *et al.* 2000a; Ford *et al.* 2001), and an alteration to the bird community structure, often exemplified by an increase in numbers of large aggressive and/or predatory species and elevated levels of nest predation (Wilcove 1985; Yahner 1988; Catterall *et al.* 1991; Paton 1994; Huhta *et al.* 1999; Luck *et al.* 1999b, 1999a; Saracco and Collazo 1999; Ford *et al.* 2001; Chalfoun *et al.* 2002).

While a number of species show a preference for such habitats, [e.g., Noisy Miner (*Manorina melanocephala*), Pied Currawong (*Strepera graculina*) and Red Wattlebird (*Anthochaera carunculata*)(Catterall *et al.* 1991; Paton 1994; Luck *et al.* 1999a; Ford *et al.* 2001)], other species avoid such habitat. Apart from the direct impact associated with many of these factors (e.g., altered vegetation structure and nest predation), many of these factors (e.g., weed invasion, altered microclimate) have a number of indirect effects on the ecology of many species of birds. Increased weed densities at remnant edges bring about a change in habitat structure (Ford *et al.* 2001), resulting in a reduction in detectability of epigeic invertebrates by ground-foraging insectivorous birds such as robins (Petroicidae) and a reduced detectability of predators by foraging birds in such habitats (Whittingham and Evans 2004). Furthermore, a decrease in leaf litter cover and volume of logs, and the desiccation of remaining leaf litter as a result of microclimatic changes, ultimately reduces food or foraging opportunities and thus foraging efficiency for ground-foraging insectivorous birds (Abensperg-Traun *et al.* 1996; Bromham *et al.* 1999; Abensperg-Traun *et al.* 2000; Ford *et al.* 2001; Van Wilgenburg *et al.* 2001). As

a result, remnants with a high remnant perimeter to area ratio may possess less suitable foraging microhabitat and insufficient food for such birds.

Habitat selection in birds is generally assumed to be hierarchical in nature (George and Zack 2001; Jones 2001). Specifically, the majority of literature suggests that hierarchical habitat selection primarily operates in a 'top-down' manner, with coarser spatial scales constraining selection at finer spatial scales (Wiens 1989; Kristan 2006). However, as the abundance, diversity and detectability of epigeic invertebrates have been shown to be reduced in small remnants (e.g., Burke and Nol 1998; Zhanette *et al.* 2000) and edges (e.g., Van Wilgenburg *et al.* 2001), and many species of Australian woodland birds are ground-foraging (Antos and Bennett 2005), it is possible that habitat selection in many birds is governed by a 'bottom-up' approach, with factors governing habitat selection at finer spatial scales constraining that at coarser spatial scales. There are far-reaching implications if such a 'bottom-up' model of habitat selection can be demonstrated. At present, many species' management plans operate based on a 'top-down' approach and are thus traditionally based on management units at 'manageable scales' such as the regional or landscape scale.

The present study aimed to determine how the ground-foraging Eastern Yellow Robin (*Eopsaltria australis*) selects its habitat at the landscape and territory scale. Apart from the importance of assessing habitat selection at the landscape scale, assessing selection at the territory scale is also pertinent to gaining an overall understanding of habitat selection, as apart from being intimately tied to selection at the landscape scale (i.e., reasons for which remnants are occupied

or not), it may actually constrain selection at the landscape scale. In addition, the quality of habitat at the territory scale will influence breeding success and recruitment. Thus it was also aimed to determine whether habitat selection in this species was governed by a 'bottom-up' or 'top-down' model of habitat selection. Furthermore, this species was chosen for study as there is contradictory evidence on whether it is declining (Barrett *et al.* 2003) with some studies indicating population decline (Reid 1999; Reid 2000; Watson *et al.* 2003), while others note the species as common and widespread (e.g., Radford and Bennett 2005). Determining aspects influencing landscape and territory scale habitat selection of the species may illuminate reasons for this contradictory response.

5.3 METHODS

5.3.1 Study area

Study territories and landscapes were located in remnant woodland and forested tracts on the New England Tablelands (30° 30' S, 151° 30' E) in a 95 km x 65 km area surrounding Armidale, New South Wales, Australia (Figure 5.1). The study area straddles the Great Dividing Range, with sites ranging from 650 m – 1250 m above sea level. Vegetation throughout the study area varies in its species composition, with New England Stringybark (*Eucalyptus caliginosa*) the dominant woodland tree species to the east of the range. Woodlands of White Box (*E. albens*), Grey Box (*E. moluccana*), Yellow Box (*E. melliodora*) and Blakely's Red Gum (*E. blakelyi*), along with localised patches of Mugga Ironbark (*E. sideroxylon*) dominate the vegetation to the west of the range. The midstorey and understorey vegetation is varied throughout the study area and is dominated by *Acacia* spp., *Cassinia* spp. and *Bursaria* spp. As a

result of extensive clearing of much of this native vegetation for sheep and cattle grazing by early last century, only 20% of the original vegetation remains (Barrett *et al.* 1994). The size of remnants in the study area varies from 0.69 ha to 14,212 ha to a continuous belt of vegetation to the south-east of the study area (including Oxley Wild Rivers National Park), which incorporates hundreds of thousands of hectares. The degree of connectivity of vegetation in the study area varies considerably, with remnants to the central west of the study area more connected and variegated than remnants directly surrounding Armidale where the extent of vegetation clearance has been more severe, although it is still effectively variegated. Variegated landscapes are characterised by a mosaic of forest, open woodland and scattered trees (Lord and Norton 1990; McIntyre and Barrett 1992; Bennett 1999). The implications of such findings are of great consequence, in that the permeability of variegated landscapes by dispersing individuals is potentially different from that in fragmented systems (see Chapter 1).

The study area has a cool temperate climate, with the majority of rain falling in summer months. Maximum temperatures average 26.3°C in the warmest month (January), with temperatures rarely exceeding 35°C. Minimum temperatures average 12.5°C in January, and rarely drop below 7°C. Winters are particularly cold, dry and frosty, with occasional snowfalls. Maximum temperatures average 12.3°C in the coldest month (July), although occasionally drop to 5°C, with minimum temperatures averaging -0.3°C and regularly dropping to below -5°C. Annual rainfall averages 788 millimetres in Armidale, although it varies across the study area according to local elevation and topographical changes.

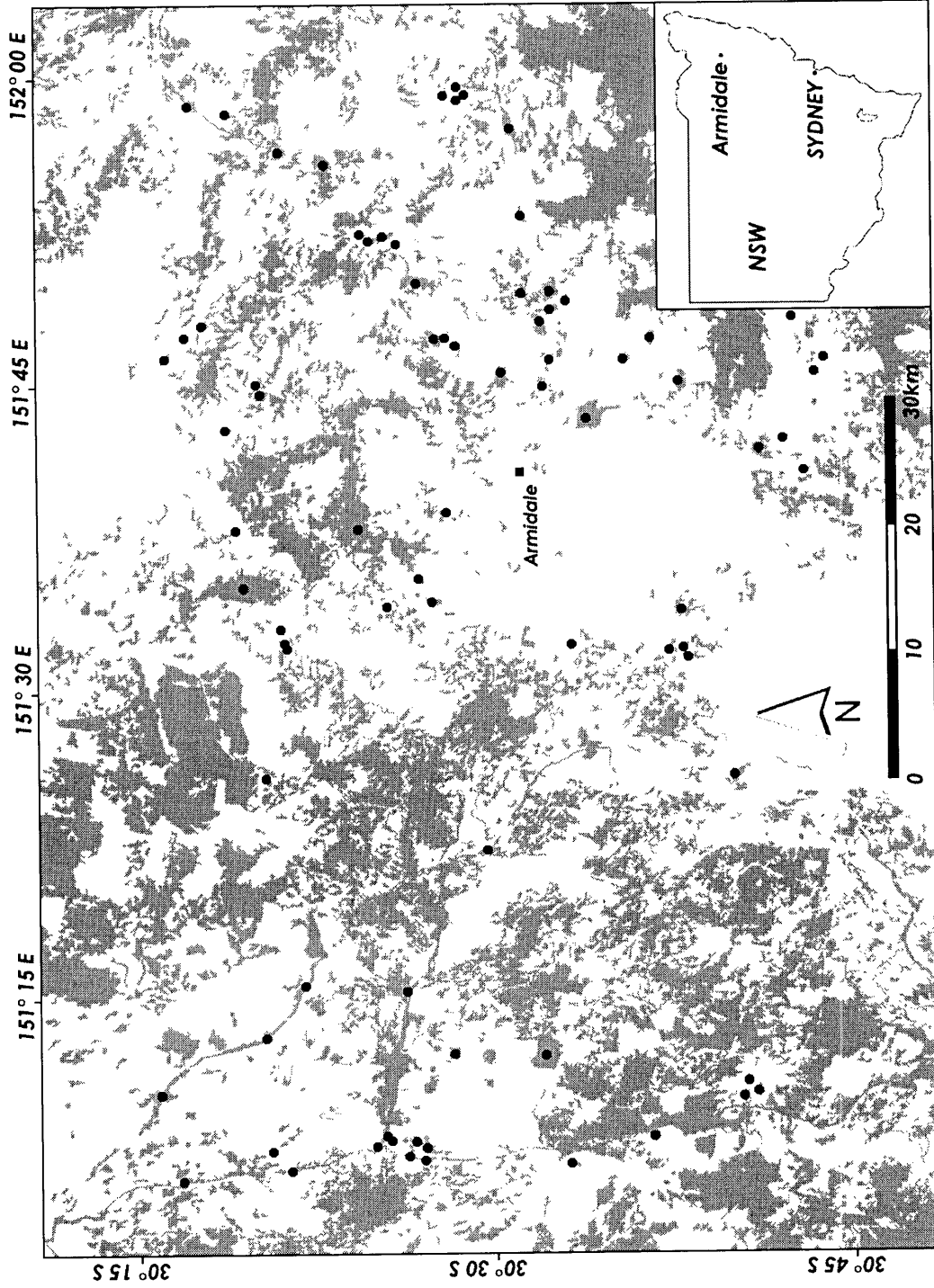


Figure 5.1 Map of the study area showing the location of the 81 sampled remnants (black dots at the approximate centre of the remnant). Grey areas in map denote wooded areas, with white areas denoting cleared areas. Lat and long co-ordinates presented according to the Australian Geodetic Datum 1966 (AGD66).

5.3.2 Study species

The Eastern Yellow Robin (*Eopsaltria australis*) is a medium-sized (20 g) ground-foraging insectivorous Australo-Papuan robin (Petroicidae), which is endemic to east and southeast Australia. Although it is found in a variety of habitats throughout its range from dry eucalypt woodlands to temperate and subtropical rainforest (Higgins and Peter 2002), the Eastern Yellow Robin is sensitive to habitat fragmentation and degradation (Loyn 1985; Barrett *et al.* 1994). As a result, the species has shown a marked decline in distribution and abundance, especially in the woodlands of the wheat-sheep belt of NSW (Barrett *et al.* 1994; Reid 1999). Previous research has suggested that the area-sensitivity of the Eastern Yellow Robin is a response to reduced availability and poor quality of food, as well as reduced breeding success due to high nest predation rates in small remnant patches in fragmented woodland (Doyle 1996; Zanette 2000; Zanette *et al.* 2000; Debus 2006a). Zanette (2000) proposed that population viability of Eastern Yellow Robins declines with decreases in the amount of forest cover in a landscape, although she did not test this. Watson *et al.* (2001) also suggested that Eastern Yellow Robins were sensitive to isolation; not occurring in remnants further than 1.5 km from surrounding remnants. Furthermore, at a smaller spatial scale, Barrett *et al.* (1994) suggested that although Eastern Yellow Robins were relatively common (although declining) on the Armidale plateau, they were dependent on healthy undisturbed woodland, and were usually absent from small or degraded remnants.

5.3.3 Landscape scale sampling

Within the study area, characteristics of landscape elements associated with occupied remnants were compared to unoccupied remnants. I sampled 81 remnants for the presence of robins between July and October 2005. Remnants sampled represented a variety of sizes (average 157.2 ha; 24 remnants <20 ha, 26 remnants 20 – 50 ha, eleven remnants 50 – 100 ha, nine remnants 100 – 200 ha, eight remnants 200 – 1000 ha and three remnants > 1000 ha) and were chosen from the landscape based on a combination of assessment of 1:25,000 maps and ArcView GIS 3.2a™ digitised maps. Remnants had to be small enough to ensure that the whole remnant could be accurately assessed for the presence of robins. I made an effort to select remnants that exhibited varying degrees of isolation from surrounding remnants and forested areas. I sampled the remnants by traversing all remnants and looking and listening for individuals of the species. As the Eastern Yellow Robin is generally considered sedentary and occupies year-round territories (pers. obs., Higgins and Peter 2002), I assumed that if an individual was seen, it was resident in the remnant rather than transient. As I undertook this study during the breeding season, I also used playback of recorded calls in every remnant to determine presence of the species, and if present, was always met by at least one scolding individual. Once an individual or pair of robins was located in a remnant, I ceased searching to reduce the impact on any breeding activities. I deemed a remnant unoccupied only if a systematic assessment for robins with the aid of call playback failed to locate any robins. This assessment involved me traversing the whole remnant by walking transects not separated by more than 50 – 75 m until the whole remnant was surveyed or an individual was located. In combination with playback, I believed this methodology would accurately

determine the presence of robins within the remnant. All landscape scale variables were calculated from GIS digitised maps and data presented in ArcView GIS 3.2a™.

In order to determine aspects characterising remnants occupied by robins and the landscapes surrounding occupied remnants, six variables were recorded. I recorded the size of remnants, as it has been suggested that a minimum area threshold (20 ha) exists for Eastern Yellow Robins in the New England region (Barrett 1995). The perimeter of remnants was also noted in order to calculate a remnant perimeter (m) to remnant area (ha) ratio. This measure is effectively an index of core habitat area, with higher values indicating sites with a higher proportion of edge compared to core habitat. Although the landscape is effectively variegated (Lord and Norton 1990; McIntyre and Barrett 1992) rather than fragmented, the boundaries of surveyed remnants still closely aligned that provided in the ArcView GIS digitised maps. Furthermore, any discrepancy in extent or location of edge was so minimal as to make no difference to the final measure of remnant size or perimeter.

The influence of landscape scale factors on remnant occupation is not mutually exclusive from those factors governing remnant scale selection, with robins more likely to occupy small remnants only if larger forest tracts are nearby (Barrett 1995). As such, I calculated a number of variables within a 10 km x 10 km (10,000 ha) area surrounding occupied and unoccupied remnants. I selected this sized area as it represents the scale at which Eastern Yellow Robins have been documented moving through the study landscape (e.g., with an individual traversing 7 km between Yina Nature Reserve and Imbota Nature

Reserve, Debus 2004). The percentage cover of wooded areas within the 10 km x 10 km area was calculated as a measure of vegetation extent within the immediate vicinity of the remnant. I calculated this measure (independently of spatial configuration), as total habitat cover in a landscape can often have a greater effect on species persistence than spatial configuration (Villard *et al.* 1999).

I assessed the degree of connectivity of the vegetation within the 10 km x 10 km landscape area through the calculation of an average inter-remnant distance measure. This measure was developed during the course of the study and is calculated as the average distance between remnants in eight cardinal compass directions from the centre of the occupied remnant in the 10 km x 10 km landscape area (Figure 5.2). The inclusion of inter-remnant distances between wooded areas of the same remnant was also included (e.g., x_1 and x_7 in Figure 5.2) as while some species opt for a longer route (i.e., going around the forest), some species prefer the shorter option of traversing across cleared areas (Uezu *et al.* 2005). This is especially the case when the ratio of distance around the wooded area to the distance across the cleared area is high. I also included distances between outlying remnants and the boundary of the 10 km x 10 km landscape area (e.g., x_3 and x_6 in Figure 5.2), irrespective of the vegetation outside this area, as the purpose of the study was to determine the average inter-remnant distance for an idealised dispersing individual only within the 10 km x 10 km landscape.

The inter-remnant distance effectively measures the structural connectivity in the landscape. Although not taking into account functional connectivity (see

Uezu *et al.* 2005), I devised the method as it represents a standardised method for calculation of the interception of wooded or forested areas within and to the edge of a 10 km x 10 km area for an idealised dispersing individual along linear vectors radiating from the central occupied remnant. Given the variegated nature of some of the landscape, the permeability of the linear vectors between remnants to a dispersing individual varies according to the characteristics of the inter-remnant matrix (see Chapter 1).

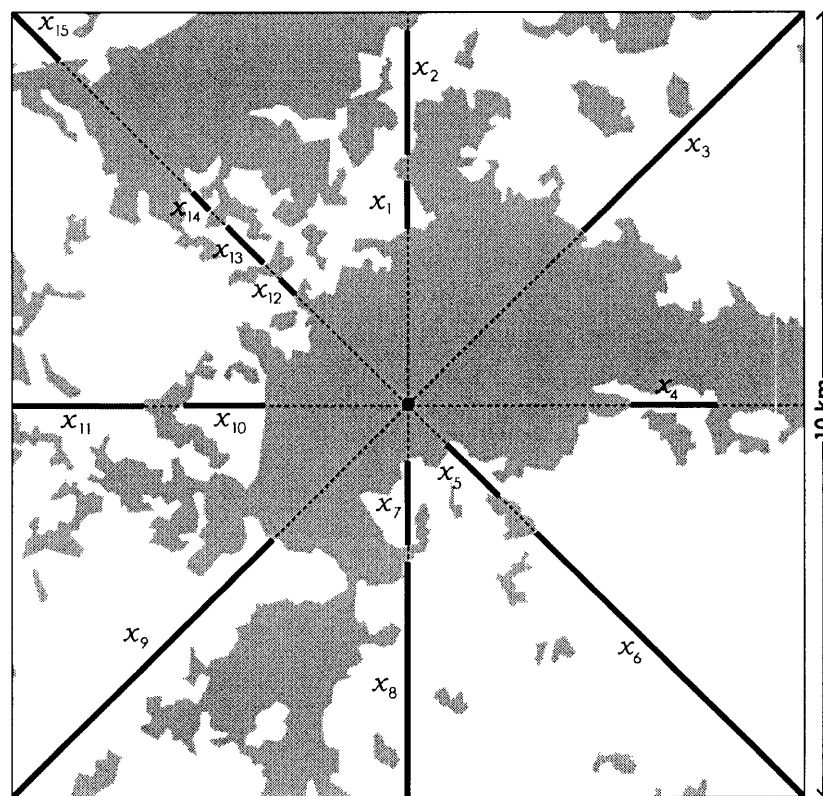


Figure 5.2 Pictorial representation of the 10 km x 10 km landscape used to calculate the average inter-remnant distance. Average length of the dark line segments ($x_1 - x_{15}$) is calculated to determine the average inter-remnant distance within the 10 km x 10 km landscape. The figure shows examples of inter-remnant distances between the same remnant (x_1 , x_4 , x_7 and x_{14}) as well as between isolated remnants (x_2 , x_5 , x_{10} , x_{12} and x_{13}) and to the edge of the 10 km x 10 km area (x_3 , x_6 , x_8 , x_9 , x_{11} and x_{15}). Cover of wooded areas represented by grey shaded areas and is totalled to give percentage cover in the whole 10 km x 10 km landscape.

The isolation of remnants was calculated as a single measure of distance to nearest large remnant. The criteria selected for justifying a ‘large remnant’ was

based loosely on a number of calculations including the area needed to maintain an effective population size (see Barrowclough and Shields 1984; Couvet 2002). Thus, the distance to nearest remnant larger than 2,000 hectares was also included as a subjective estimate of the remnant size of a self-sustaining source population.

5.3.4 Territory scale variables

Habitat selection at the territory scale was assessed by determining those habitat attributes that distinguished occupied territories from unoccupied territories. Twenty territories and their paired non-territories were assessed in seven study sites. Eighteen of the twenty territories (and paired non-territories) were located in the study remnants presented in the landscape scale sampling section (section 5.3.2) with two territories located in continuous forest sites to the north-west of Armidale.

I assessed territory scale selection by examining habitat attributes along a single 100 m x 5 m transect in each territory. Territory boundaries were approximated by noting any territorial behaviour of robins, and reactions to call playback. Transects were located along the central axis of known territories, and where possible, intersected the location of any nests to maximise idealised territory habitat. Sampling in any given territory was never carried out while females were brooding eggs or while there were nestlings, to avoid potential predation by known nest predators such as Pied Currawongs (*Strepera graculina*), Grey Shrike-thrush (*Colluricincla harmonica*) and Grey Butcherbirds (*Cracticus torquatus*) (Debus 2006a, 2006b). In those sites where nests were not located, the approximate boundary of territories was designated according

to areas used by an individual or pair of robins followed for at least 30 minutes. Territory transects were then located within the centre of the territory boundaries. Non-territories were located no less than 300 m from territories, and were only considered non-territories if an individual or pair of robins was not detected within 45 minutes using call playback. The location of non-territories was mapped in relation to the location of territory sites using ArcView GIS 3.2a™, with approximately 300 – 400 m separating territories from non-territories.

Along the length of the transect, I counted the number of sapling and subcanopy trees (1 m – 10 m), canopy trees (>10 m) and shrubs (> 0.3 m high and 0.3 m wide). I estimated the cover of herbs (herbaceous vegetation < 0.3 m and grass) and leaf litter as one of five measures of abundance between sparse and dense in 10 m sections along the 100 m transect. This was then averaged, to give a final measure for the territory. I also calculated log volume using the line intercept method for downed wood (Harmon and Sexton 1996). I used this method as it is particularly easy to undertake in the field and is not labour intensive, especially as the lengths of logs are not required to be measured. Instead, only the diameter of every log (fallen timber with diameter > 50 mm and length > 800 mm) that intersected the centre line of the 100 m transect was measured. If a log was noticeably tapered however, an average diameter was recorded. The formula used to calculate the volume of logs per unit area ($\text{m}^3 \text{m}^{-2}$) using the line transect intercept method is:

$$V = 9.869 * \sum(d^2 / 8L)$$

Where d is the log diameter (m), and L is the transect length (m).

One of the criticisms of the line transect method is that it excludes dead standing trees, resulting in an underestimate of total woody debris. However, the aim of the present method was to calculate a coarse approximate volume of fallen logs as these are elements of the woody debris in the habitat that are most utilised by robins as perching and foraging substrates (e.g., see Laven and Mac Nally 1998).

5.3.5 Variable reduction

Before analysis, I reduced the number of landscape and territory variables following a combination of correlation analysis and Principal Component Analysis (PCA).

Landscape scale variables

The final variables utilised in further landscape scale analysis included remnant size, remnant perimeter to area ratio, average inter-remnant distance (see section 5.3.3 above), percentage of 10 km x 10 km landscape area wooded and the distance to nearest remnant larger than 2000 ha. The only landscape variable I eliminated from further analysis was the measure of remnant perimeter as it was highly correlated with remnant size ($r = 0.955$, $df = 80$, $p < 0.001$). I retained remnant size as I deemed it more of an ecologically meaningful variable than remnant perimeter.

Territory scale variables

For the territory scale analysis, the index of herb cover and the index of leaf litter abundance were significantly negatively correlated ($r = -0.720$, $df = 38$, $p < 0.001$), so I replaced these variables with a new composite ground substrate variable computed as principal component scores from a PCA. Larger values of the new ground substrate variable indicated a high index of herb cover and an associated low index of leaf litter abundance. The percent total variance explained by the new composite ground substrate variable was 86.0%. The final variables utilised in further territory scale analysis included the number of canopy trees, number of sapling and subcanopy trees, number of shrubs, volume of logs and an index of ground substrate.

5.3.6 Analysis

Landscape scale

The presence or absence of Eastern Yellow Robins from each remnant represented the dependent variable and was scored as 1 or 0 respectively. The independent variables mentioned in the landscape scale variable section (section 5.3.3) were used to investigate the influence of the remnant and landscape factor variables on the binary dependent variable. As such, I undertook a binary (or binomial) logistic regression analysis.

Territory scale

I initially analysed the habitat elements characterising territory scale selection of robins using a hierarchical linear modelling (HLM) procedure using the HLM6 program (Raudenbush *et al.* 2005). Hierarchical linear modelling (HLM) is a form of regression analysis that is designed to analyse nested or hierarchically

structured data (Raudenbush and Bryk 2002). Hierarchical structure is widespread in many ecological systems, with many studies failing to address such structure adequately. One of the fundamental assumptions underlying traditional multiple or logistic regression analysis is that observations are independent (Raudenbush and Bryk 2002). In ecological studies, this assumption is frequently violated. For example, habitat attributes of territories and non-territories sampled within a given remnant will tend to be more homogeneous than territories and non-territories sampled randomly from all study sites across the landscape. As habitat attributes of territories and non-territories from a given remnant share similar site-specific characteristics (e.g., topography, species assemblages, biotic effects), these territories are not fully independent. If this assumption of independence is violated, estimates of regression coefficients and associated standard errors are erroneous and can lead to falsely inferred conclusions. As such, it is imperative to first attempt to analyse data taking into account hierarchical structure. In the present study, the data was structured at two hierarchical levels; territories and non-territories within study remnants. As such, I attempted a 2-level hierarchical linear modelling approach on the data. Specifically, due to the binary response variable (territory or non-territory), I undertook a hierarchical generalised linear modelling (HGLM) procedure using the HLM6 program (Raudenbush *et al.* 2005). See Raudenbush and Bryk (2002) for a detailed explanation of hierarchical linear modelling, its component statistics and its application.

Following preliminary HGLM analysis of the data, it was shown that structuring the data at the second level (remnant scale) was ineffective, as determined by the results of a variance component test in HLM6. As a result, I undertook all

analyses using binary logistic regression analysis, as in the landscape scale analysis mentioned previously.

I examined log-likelihood values calculated by the logistic regression procedure for each model, and calculated a modified second-order Akaike's Information Criterion, AIC_c . The AIC_c values are used instead of the first-order AIC when the number of parameters is relatively large compared to sample size (i.e., $n/K < 40$, Burnham and Anderson 2002) and is calculated as:

$$AIC_c = -2\log(L) + 2K + 2K(K+1)/(n-K-1)$$

Where $\log(L)$ = log likelihood of model

K = total number of parameters in the model

n = sample size

From these AIC_c values, models were ranked by rescaling the AIC_c values such that the model with the minimum information criteria had a value of 0:

$$\Delta_i = AIC_i - \min AIC$$

I then calculated normalised Akaike weights (w_i) as they are useful as the 'weight of evidence' in favour of model i being the best model in the set of models.

$$w_i = \exp(-\Delta_i / 2) / \sum \exp(-\Delta_i / 2)$$

The Akaike weights sum to one, with the model showing the strongest support having the largest weight. For each response variable, I chose the model with the greatest Akaike weight for further analysis. In addition, Burnham and Anderson (2001) suggest that models with Δ_i values less than two still have substantial support, so I also included these models. I assessed adequacy of the final selected models by examining the regression coefficients and their 95% confidence intervals. If the regression coefficient confidence intervals included zero, then it indicated that the relationship between the response variable and the predictor variable(s) was too variable to be certain of a definite positive or negative association.

Rather than focusing on a 'best model' approach, I assessed the importance of predictor variables across all models (Burnham and Anderson 2002). I undertook this in the present study by the multi-model inference procedure. This procedure was achieved by summing the Akaike weights for all models containing a given predictor variable. The final sum represents a weight of evidence for that variable across all models. This process is particularly important in those circumstances when there is a number of almost equally well supported models (Burnham and Andersen 2001).

5.4 RESULTS

5.4.1 Landscape scale selection

The 81 surveyed remnants varied in size from 3.2 ha to 2,404.0 ha, with an average size of 140.6 ha. Eastern Yellow Robins occupied 29 (35.8%) of the 81 surveyed remnants, with the average size of these occupied remnants

approximately 308.4 ± 110.7 ha; mean \pm standard error (Figure 5.3a) and unoccupied remnants of 72.8 ± 28.9 ha.

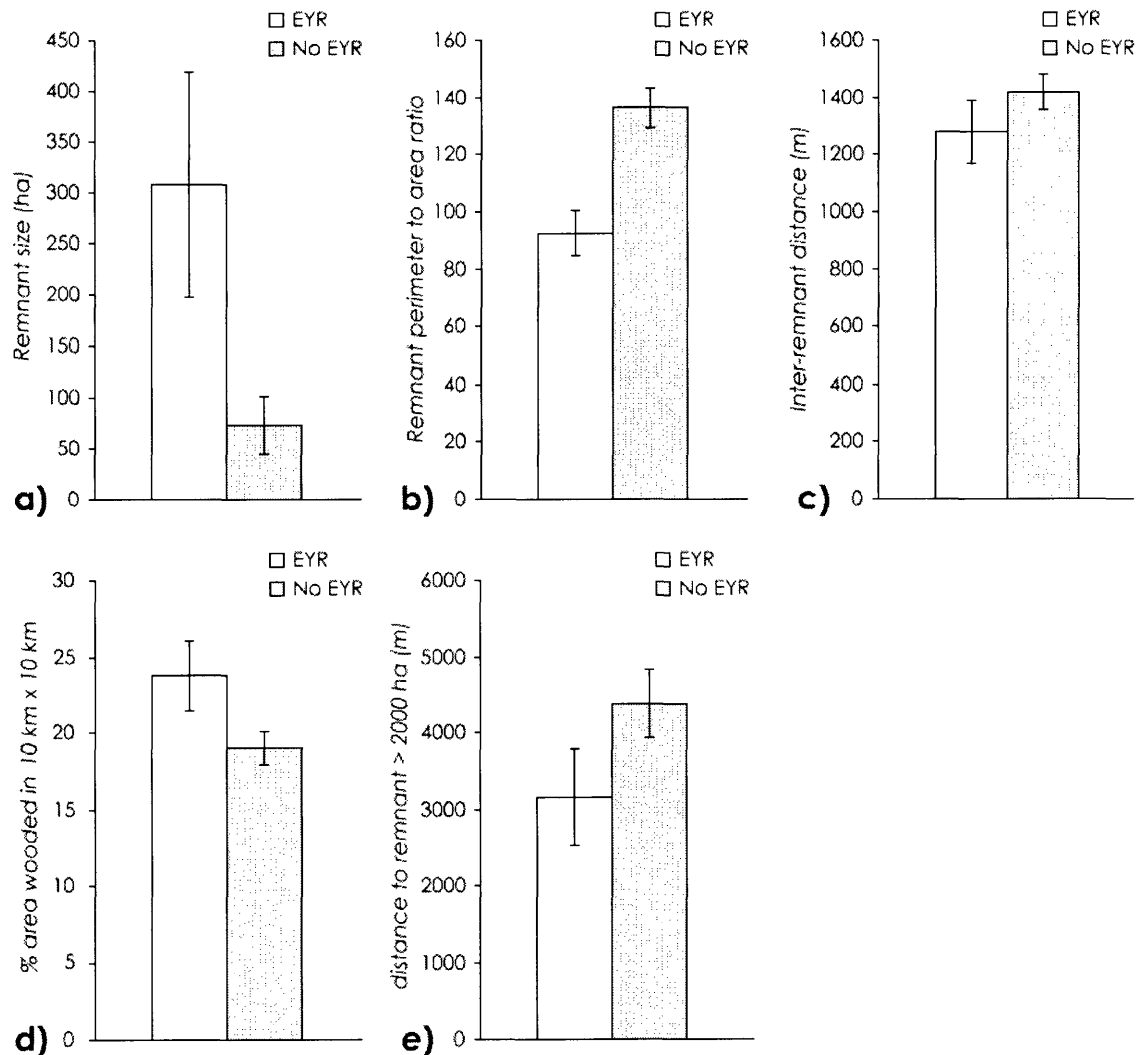


Figure 5.3 a) the average size of remnants occupied by Eastern Yellow Robins (EYR: $n = 29$) and unoccupied by Eastern Yellow Robins (No EYR: $n = 52$), b) the remnant perimeter to area ratio of occupied and unoccupied remnants, c) the average inter-remnant distance in 10 km x 10 km area surrounding occupied and unoccupied remnants, d) the % area of 10 km x 10 km area wooded surrounding occupied and unoccupied remnants and e) the distance to nearest remnant larger than 2000 ha from occupied and unoccupied remnants. All graphs show the average \pm standard error.

The smallest occupied remnant was only 6.9 ha in size, although 27 of the 29 occupied remnants (93.1%) were larger than 20 ha. The largest unoccupied remnant was 1,486 ha. The degree of variability in remaining habitat throughout

the 10 km x 10 km study landscapes is exemplified by the differences in percentage area wooded; varying from 5.2% to 51.7%. The average percentage area wooded in 10 km x 10 km landscapes surrounding occupied remnants was higher ($23.8 \pm 2.3\%$) than that surrounding unoccupied remnants ($19.0 \pm 1.1\%$, Figure 5.3d). The average remnant perimeter (m) to area (ha) ratio was smaller in occupied remnants (92.4 ± 7.8) than unoccupied remnants (136.3 ± 7.0 , Figure 5.3b). The average inter-remnant distance was similar in landscapes surrounding occupied remnants ($1,278.3 \pm 111.0$ m) and unoccupied remnants ($1,417.0 \pm 63.3$ m, Figure 5.3c). The distance to nearest remnant larger than 2,000 ha was smaller for occupied remnants ($3,150.4 \pm 624.6$ m) than for unoccupied remnants ($4,376.1 \pm 453.1$ m, Figure 5.3e).

The results of the logistic regression modelling indicated that three models were selected where landscape elements best distinguished occupied remnants from unoccupied remnants (Table 5.1). The best of these models was the bivariate model (Akaike weight of 0.2249) incorporating remnant perimeter to area ratio and the percentage cover of wooded areas in 10 km x 10 km landscapes. Occupied remnants were characterised by smaller remnant perimeter to area ratios than unoccupied remnants (i.e., less edge), while the percentage cover of wooded areas in 10 km x 10 km landscapes around occupied remnants was higher than that around unoccupied remnants. This bivariate model had good explanatory power as a result of the regression coefficient confidence intervals for both remnant perimeter to area ratio and percentage cover of wooded areas in 10km x 10km landscape variables not including zero.

A trivariate model incorporating remnant size, remnant perimeter to area ratio and percentage cover of wooded areas in 10km x 10km landscapes was also selected as best approximating the data, although the Akaike weight was considerably lower (0.0930, Table 5.1). In this trivariate model, remnant area was added to the two variables in the bivariate model. Occupied remnants were larger than unoccupied remnants. Only the perimeter to area ratio variable had any explanatory power in this model, as the regression coefficient confidence interval of this variable did not include zero.

A univariate model incorporating the perimeter to area ratio (Akaike weight of 0.0865) was also selected, with the same response and confidence intervals as in the bivariate model (see Table 5.1).

Table 5.1 Results of logistic regression modelling for landscape attributes associated with remnant occupancy by Eastern Yellow Robins.

Final models for each response variable were chosen based on those candidate models with ΔAIC_c values less than 2.0. Akaike weights are calculated from the relative likelihood values as determined by ΔAIC_c values. EA ratio = remnant perimeter to area ratio, Per area = percentage cover of wooded areas in 10 km x 10 km landscape, Rem size = remnant size. † = Coefficients for which the 95% confidence interval does not include zero.

<i>Predictor variable(s)</i>	ΔAIC_c	Akaike weight	Model variable(s)	Coefficient	Std err	Confidence interval
EA ratio + Per area	0	0.2249	EA ratio	-0.021	0.006	-0.0328, -0.0092 [†]
			Per area	0.053	0.027	0.0001, 0.1059 [†]
Rem size + EA ratio + Per area	1.7666	0.0930	Rem size	0.001	0.001	-0.0010, 0.0030
			EA ratio	-0.019	0.007	-0.0327, -0.0053 [†]
			Per area	0.050	0.027	-0.0029, 0.1029
EA ratio	1.9102	0.0865	EA ratio	-0.021	0.006	-0.0328, -0.0092 [†]

Examination of the multi-model inference procedure for the five predictor variables indicates the dominant role of the remnant perimeter to area ratio in distinguishing landscape elements associated with occupied sites from those of unoccupied sites, with a weight of evidence of 0.9916. This was followed by the percentage cover of wooded areas in 10 km x 10 km landscapes with a smaller weighting of 0.5771, with all other variables having a similar smaller weighting of < 0.3300 (Table 5.2).

Table 5.2 Multi-model inference weight of evidence (WoE) for predictor variables contributing to landscape scale selection response variable models.

Rem size = remnant size, EA ratio = remnant perimeter to area ratio, Inter-rem = inter-remnant distance, Per area = percentage cover of wooded areas in 10 km x 10 km landscape, Dist 2000 = distance to nearest remnant > 2000 ha.

<i>Predictor</i>	<i>WoE</i>
Rem size	0.3021
EA ratio	0.9916
Inter-rem	0.3234
Per area	0.5771
Dist 2000	0.3226

5.4.2 Territory scale selection

Habitat attributes from all territories and non-territories varied considerably, indicating the broad vegetation structures associated with the forests and woodlands within the study area. The number of canopy trees in all 100 m x 5 m transects varied from two to 41 (a projected density of canopy trees between 40/ha and 820/ha), with the number of sapling and subcanopy trees ranging from five to 53 (a projected density of sapling and subcanopy trees between 100/ha and 1,060/ha). More notably, there was a very large range of densities in numbers of shrubs per transect; between one and 227 (a projected density of shrubs between 20/ha and 4,540/ha). Eastern Yellow Robin territories were

characterised by a higher ground substrate index (although there was high variability within territories and within non territories, Figure 5.4e), a higher density of sapling and subcanopy trees (Figure 5.4b), a higher density of shrubs (Figure 5.4c), and a higher volume of logs (Figure 5.4d) compared to non territories, while the density of canopy trees (Figure 5.4a) varied little between territories and non-territories.

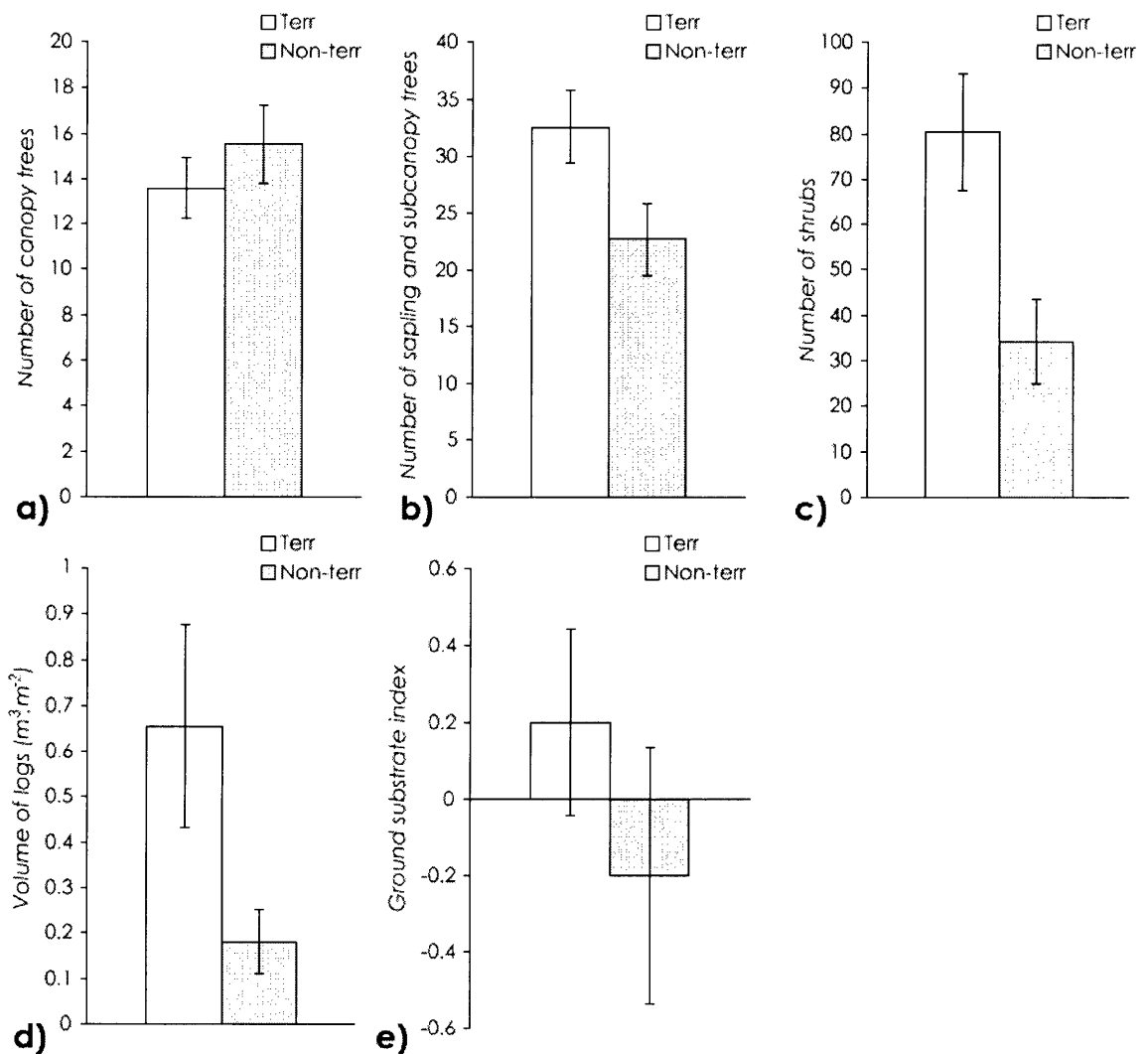


Figure 5.4 a) the number of canopy trees in 100m x 5m transects in robin territories (Terr: n = 20) and non-territories (Non-terr: n = 20), b) the number of saplings and subcanopy trees in territory and non-territory transects, c) the number of shrubs in territory and non-territory transects, d) the volume of logs in territory and non-territory transects and d) the index of ground substrate cover in territory and non-territory transects. All graphs show the average \pm standard error.

The results of logistic regression modelling selected two models that best distinguished habitat attributes characterising robin territories from non-territories (Table 5.3). The better of these models was a trivariate model (Akaike weight of 0.3849) showing that territories were characterised by a higher density of sapling and subcanopy trees, shrubs, and a higher volume of logs than non-territories. This trivariate model had good explanatory power with the regression coefficient confidence intervals for the number of sapling and subcanopy trees and the number of shrubs not including zero. However, the regression coefficient confidence interval for the volume of logs did (albeit just) include zero (Table 5.3). A quadrivariate model was also selected (Akaike weight of 0.1443), with robin territories characterised by a lower density of canopy trees, a higher density of sapling and subcanopy trees, a higher density of shrubs and a lower volume of logs. Although all four variables were included in the model, only the number of sapling and subcanopy trees and number of shrubs had good explanatory power, with the regression coefficient confidence intervals for the number of canopy trees and the volume of logs including zero (Table 5.3).

Table 5.3 Results of logistic regression modelling for habitat attributes associated with territories of Eastern Yellow Robins.

Final models for each response variable were chosen based on those candidate models with ΔAIC_c values less than 2.0. Akaike weights are calculated from the relative likelihood values as determined by ΔAIC_c values. Sap sub = number of sapling and subcanopy trees, Shrub = number of shrubs, Log = volume of logs, Can

trees = number of canopy trees. † = Coefficients for which the 95% confidence interval does not include zero.

<i>Predictor variable(s)</i>	ΔAIC_c	Akaike weight	Model variable(s)	Coefficient	Std err	Confidence interval
Sap sub + Shrub + Log	0	0.3849	Sap sub	0.114	0.043	0.0297, 0.1983 [†]
			Shrub	0.035	0.013	0.0095, 0.0605 [†]
			Log	243.642	136.162	-23.2355, 510.5195
Can trees + Sap sub + Shrub + Log	1.9618	0.1443	Can trees	-0.048	0.059	-0.1636, 0.0676
			Sap sub	0.12	0.046	0.0298, 0.2102 [†]
			Shrub	0.035	0.013	0.0095, 0.0605 [†]
Log	237.132	139.494	-36.2762, 510.5402			

The multi-model inference procedure for the five predictor variables indicates the equally high importance of the number of sapling and subcanopy trees and the number of shrubs in distinguishing territory habitat characteristics from non-territory habitat; with both variables having a weight of evidence over 0.98 (Table 5.4). The volume of logs was the next most important variable, with a weighting of 0.7232, followed by the relatively low weighting for the number of canopy trees and the ground substrate index.

Table 5.4 Multi-model inference weight of evidence (WoE) for predictor variables contributing to territory scale selection response variable models.

Can trees = number of canopy trees, Sap sub = number of sapling and subcanopy trees, Shrub = number of shrubs, Log = volume of logs, Ground = ground substrate index.

<i>Predictor</i>	<i>WoE</i>
Can trees	0.3222
Sap sub	0.9827
Shrub	0.9915
Log	0.7232
Ground	0.2489

5.5 DISCUSSION

5.5.1 Influence of remnant architecture on Eastern Yellow Robins

The remnant perimeter to area ratio was the principal variable governing landscape scale occupancy by Eastern Yellow Robins in the study area, with robins occupying remnants in the landscape with smaller remnant perimeter to area ratios. The percentage area of wooded vegetation in the 10 km x 10 km landscape was also selected in one of the models, emphasising the importance of high amount of vegetation in the surrounding landscape in assisting the occupancy, dispersal and thus the persistence of robins through the landscape. The dominant role of the remnant perimeter to area ratio variable suggests that

Eastern Yellow Robins are sensitive to edge effects. Previous research has indicated that the Eastern Yellow Robin is area-sensitive based on a minimum area threshold (not found in remnants < 20 ha, Barrett 1995) and the association with large remnants (detected significantly more frequently in remnants > 200 ha, Major *et al.* 2001). However, regression modelling in the present study found no selection based on remnant area. Remnant area sensitivity and edge sensitivity are probably highly correlated (Brand and George 2001), though the relationship between the two is complex. Area and edge ratio are clearly correlated, although this relationship is weakened in large remnants with highly variable remnant perimeter to area ratios due to their shape. None of the studies mentioned above incorporated a measure of remnant perimeter to area ratio, and it may well be that this ratio is a more important factor than remnant area in determining remnant occupancy and the effect of habitat fragmentation on Eastern Yellow Robins.

Nest predation rates are elevated in edge habitat, and represent a major factor contributing to edge sensitivity (Ambuel and Temple 1983; Wilcove 1985; Yahner 1988; Paton 1994; Huhta *et al.* 1999; Luck *et al.* 1999b; Saracco and Collazo 1999; Chalfoun *et al.* 2002). In Australia, edge habitat is characterised by bird communities dominated by large aggressive and predatory species such as the Noisy Miner (*Manorina melanocephala*) and Pied Currawong (*Strepera graculina*) (Catterall *et al.* 1991; Paton 1994; Luck *et al.* 1999a; Ford *et al.* 2001), and there is evidence to suggest that nest predation and aggressive interspecific competition is a contributing factor in explaining edge sensitivity in some Australian woodland birds (Paton 1994; Ford *et al.* 2001), with some small insectivorous birds avoiding foraging in remnant edges due to the

presence of such large aggressive species (Catterall *et al.* 1991). Indeed, in a remnant examined as part of the present study (Imbota Nature Reserve), Debus (2006c) noted that Eastern Yellow Robins effectively exhibited an edge sensitivity, as manifested by always nesting at least 40 m from the woodland edge.

More importantly however, remnant edge habitat in agricultural landscapes is typically subjected to many degradation processes, such as grazing, nutrient input, altered microclimates and invasions by introduced plants (Murcia 1995; Ford *et al.* 2001). Grazing at remnant edges simplifies vegetation structure through a reduction in recruitment of tree saplings and shrubs (Yates *et al.* 2000a; Yates *et al.* 2000b), and a decrease in cover of leaf litter and logs (Abensperg-Traun *et al.* 1996; Belsky and Blumenthal 1997). In addition, the increased nutrients associated with stock grazing (nitrogen) and agricultural activities (phosphorus) at remnant edges (e.g., Weathers *et al.* 2001), result in an increased density of exotic perennial weeds (Yates *et al.* 2000b); habitat attributes believed to adversely effect the foraging behaviour of the Eastern Yellow Robin (Marchant 1987).

5.5.2 Territory habitat selection

Habitat selection at the landscape scale is closely related to habitat selection at the level of the territory. Eastern Yellow Robins select territories during the breeding season that have a high density of sapling and subcanopy trees, and shrubs. This result is similar to Debus (2006c) who found that Eastern Yellow Robins choose to nest in sites with many saplings and shrubs. Also Eastern Yellow Robin fledglings survived better where there was a dense understorey.

The ecologically similar Western Yellow Robin (*Eopsaltria griseogularis*), selected territories in sites with high shrub density, which was attributed to selection associated with more productive soils (Cousin 2004). Degradation of edges, especially by grazing, affects habitat quality by the removal of sapling trees, subcanopy trees and shrubs. Consequently, it appears likely that Eastern Yellow Robins avoid edges, i.e., sites with high perimeter to area ratio; because they do not establish territories close to edges due to the scarcity of saplings, subcanopy trees and shrubs.

5.5.3 Influence on foraging microhabitat selection

As a ground-foraging insectivore, the Eastern Yellow Robin foraging microhabitat is represented by areas with a high cover of leaf litter and logs and a low cover of ground vegetation (Chapter 3). Invariably, the ground ecosystem is most affected by edge effects, with increased solar radiation and winds near edges (Hobbs 1993; Matlack 1993) resulting in the desiccation of leaf litter. Epigeic invertebrates, on which Eastern Yellow Robins feed, are prone to such desiccation and may become less abundant and diverse in edge habitats (Burgess *et al.* 1999; Brand and George 2001; Mazerolle and Hobson 2003). Van Wilgenburg *et al.*, (2001) found that Araneae, Coleopteran, Dipteran, Hemipteran and Lepidopteran orders were 1.7 times more abundant in leaf litter of interior habitats than in leaf litter at remnant edges. Furthermore, more weeds at remnant edges bring about a change in habitat structure (Ford *et al.* 2001), resulting in a reduction in detectability of epigeic invertebrates and predators (Whittingham and Evans 2004), that together with a decrease in leaf litter cover and volume of logs and microclimatic changes, ultimately reduces food or foraging opportunities and thus foraging efficiency (Abensperg-Traun *et al.*

1996; Bromham *et al.* 1999; Abensperg-Traun *et al.* 2000; Ford *et al.* 2001; Van Wilgenburg *et al.* 2001). As such, remnants with a high remnant perimeter to area ratio may not possess appropriate foraging microhabitat and sufficient foraging resources for ground-foraging robins such as the Eastern Yellow Robin. Furthermore, as Eastern Yellow Robins also utilise sapling trees, subcanopy trees and logs as perching substrates from which they can scan and pounce onto the ground, the absence of these habitat attributes (especially in degraded edge habitat) has the potential to affect foraging efficiency and breeding success of the species (Recher 1991; Laven and Mac Nally 1998; Higgins and Peter 2002; Mac Nally *et al.* 2002).

5.5.4 Importance of recognising multiple spatial scales

Birds are known to select habitat on the basis of proximate factors at multiple spatial scales from features of remnant architecture in the landscape to vegetation structure at the territory scale, to the selection of foraging sites at the microhabitat scale (Anderson and Shugart 1974; George and Zack 2001; Lee *et al.* 2002). Habitat selection at the two spatial scales in the present study was, however, not mutually exclusive, with selection at the landscape scale for remnants with lower perimeter to area ratio (suggesting avoidance of edge habitat) representing a predictable selection at the territory scale for sites with a high density of sapling trees, subcanopy trees and shrubs, given the reduced recruitment of these vegetation structural attributes in edge habitat (Yates *et al.* 2000a; Yates *et al.* 2000b). This result reflects the potential 'bottom-up' influence on habitat selection in the Eastern Yellow Robin, with habitat selection at the finer (territory) spatial scale constraining that at the coarser (landscape) spatial scale (see Kristan 2006). Furthermore, given that foraging microhabitat

selection in the Eastern Yellow Robin during spring is characterised as sites with a high cover of leaf litter and logs and a low cover of ground vegetation (see Chapter 3), selection at the landscape scale for remnants with minimal edge habitat (in which foraging microhabitat integrity is maintained) may be constrained by selection for foraging microhabitat, thus giving further weight to the potential ‘bottom-up’ model of habitat selection in the Eastern Yellow Robin, with foraging microhabitat and territory scale selection constraining landscape scale selection.

5.5.5 Management and implications

Management for the conservation of this species should focus on retaining large remnants of native vegetation with minimum edge habitat. In addition, the protection and planting of linear corridors of vegetation may not provide appropriate habitat for the Eastern Yellow Robin, and a concerted effort should be made to plant around existing smaller remnants in a means that not only increases the size of the remnant, but also reduces the proportion of edge habitat.

Furthermore, there are far reaching implications if habitat selection in Eastern Yellow Robins is found to be best represented by a ‘bottom-up’ approach. Species management plans are traditionally based on habitat selection studies that are of limited spatial scope, focusing on management units operating at ‘manageable scales’ such as the regional or landscape scale. (see comments in Major *et al.* 2001). If habitat selection is governed by a ‘bottom-up’ model of habitat selection, then management plans based on coarse-scaled (regional or landscape scale) habitat selection studies of resident woodland birds need to be

considered with some degree of caution, taking into account, and/or incorporating, habitat selection studies at finer spatial scales.

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Appendix 5.1 Location and status of Eastern Yellow Robin occupancy in all 81 surveyed remnants.

All remnant locations presented according to Universal Transverse Mercator (UTM) easting and northing co-ordinates (56J UTM zone). 'Pr/Ab' refers to the presence (+) or absence (-) of EYRs from each respective remnant.

<i>Remnant</i>	<i>easting</i>	<i>Northing</i>	<i>Pr/Ab</i>	<i>Remnant</i>	<i>easting</i>	<i>northing</i>	<i>Pr/Ab</i>
Imbota	376943	6616784	+	16 Inve	369524	6627715	-
East	399618	6622654	-	16 Mirr	362532	6628904	+
Yena	380512	6623387	+	17 Ach1	402227	6626123	-
Newholme	368252	6634623	+	17 Ach2	402205	6627735	-
Gwydir	332046	6631033	+	17 Ach3	402834	6626671	-
Corner	379438	6620148	-	17 Achi	401822	6626663	-
Woodlands	386767	6621721	-	17 Broo	382656	6627001	-
Gara	384580	6620283	-	17 Kara	391286	6632521	-
Snake	392851	6621756	-	17 Mimo	396811	6637068	-
Boorolong	362139	6632379	-	17 Petr	383243	6627799	-
08 Crow	317398	6648589	+	17 Pint	390622	6631499	-
08 Gr12	324029	6650254	+	17 Rock	383199	6628579	-
08 Merr	328410	6642046	+	17 Thal	387602	6629931	+
08 OldB	318101	6640123	+	17 Woo1	390886	6633627	-
08 Ston	319670	6641599	-	17 Wood	391458	6634334	-
09 Dulv	348903	6641901	-	20 Glen	326265	6620326	+
09 Gr11	332514	6639010	+	20 Retr	320692	6611927	+
10 Boor	363667	6643594	-	20 Roma	318595	6618367	-
10 Ebon	368207	6644114	-	22 Gree	359172	6618094	-
10 Olm1	359376	6640367	-	23 Alde	383186	6611803	-
10 Olm2	359007	6640224	-	23 lola	381583	6613891	-
10 Olmo	360404	6640671	-	23 Rive	385435	6619529	-
10 Pin2	379679	6642479	+	23 Sout	386158	6618334	-
10 Pine	378848	6642200	+	23 Treq	386827	6619524	-
10 Spri	376168	6644877	-	23 TSR1	381486	6619619	-
11 Inve	384336	6646652	-	26 Dan2	324156	6603888	+
11 Mare	381729	6649546	-	26 Dane	324965	6604587	+
11 Mojo	397775	6640620	+	26 Stab	323688	6604989	+
11 Rock	401479	6647668	-	27 Wilh	348969	6605521	+
11 Tarr	400784	6644650	-	28 Barl	358687	6610503	+
11 Wari	383374	6648020	-	28 Cree	372761	6599982	-
14 Carl	320384	6630431	+	28 Kelv	361893	6609507	-
14 Crow	320006	6633529	+	28 Mihi	375284	6601623	-
14 Nea1	320729	6632680	-	28 Nort	374481	6603449	-
14 Near	320430	6632370	-	28 Sum1	358105	6609049	+
14 OldK	319168	6631005	-	28 Summ	358857	6609381	+
14 OIK2	318916	6629754	-	28 Tive	379758	6609667	+
14 Sout	319891	6629639	+	29 Beve	384900	6600871	-
14 Tull	327131	6627402	+	29 Mor2	380483	6599124	-
15 Yarr	343245	6624724	+	29 More	381621	6598418	-
16 Brae	364344	6629867	-				

CHAPTER 6: FINE-SCALE HABITAT ATTRIBUTES CONSTRAIN HABITAT SELECTION OF THE SCARLET ROBIN (*Petroica multicolor*) AT COARSER SPATIAL SCALES: IMPORTANCE OF RECOGNISING 'BOTTOM-UP' HABITAT SELECTION.

6.1 ABSTRACT

Habitat selection in birds is generally assumed to be hierarchical, with habitat selection at a given spatial scale constrained by habitat selection at other spatial scales. For example, in a 'top-down' model of habitat selection a migratory bird selects a territory site only after having selected a favourable landscape. One would expect, however, that given the resident and sedentary nature of many Australian woodland birds, selection would operate in a 'bottom-up' manner, with habitat selection at fine spatial scales constraining that at coarser spatial scales. The present study aimed to determine whether such a model existed in the ground-foraging Scarlet Robin (*Petroica multicolor*) by examining habitat selection at the territory and landscape scales. At the landscape scale, modelling indicated robins primarily occupied large remnants. At the breeding territory scale, breeding territories contained a higher leaf litter and lower herbaceous plant cover compared to non territories. As small remnants are normally associated with degraded conditions such as a high cover of grasses and weeds (attributes that result in the reduced abundance and detectability of invertebrate prey), selection at the landscape scale is likely constrained by attributes selected for at the territory scale (high cover of leaf litter), which itself is governed by foraging microhabitat at smaller spatial scales. The present study thus suggests a 'bottom-up' model of habitat selection in the Scarlet Robin. The implications of such selection indicate that results from

coarse-scaled (regional or landscape) habitat selection studies of woodland birds (the ‘manageable scale’ at which many conservation and management plans are invariably formed) need to be considered with some degree of caution, taking into account habitat selection at finer spatial scales.

6.2 INTRODUCTION

Birds actively select habitat on the basis of factors operating at multiple spatial scales from landscape features through vegetation structure to foraging substrate (Anderson and Shugart 1974; Rotenberry and Wiens 1980; George and Zack 2001). Habitat selection also operates at multiple temporal scales in close association with spatial scales (George and Zack 2001), from minute-by-minute behavioral decisions governing foraging site selection, to seasonal changes in location and extent of breeding territories.

Habitat selection in birds is generally assumed to be hierarchical in nature (George and Zack 2001; Jones 2001). An inevitable consequence of such a hierarchical structure is that habitat selection at a given spatial scale is invariably constrained by habitat selection at other spatial scales (Wiens 1989; Kristan 2006). For example, a migratory bird may select a territory site only after having selected a favourable landscape or region (George and Zack 2001). Thus territory scale selection is constrained by landscape scale selection. This example exemplifies a ‘top-down’ model of habitat selection, with coarser spatial scales constraining selection at finer spatial scales. While this model of hierarchical habitat selection is particularly relevant to migratory species (Kristan 2006), one would expect that the majority of Australian woodland bird species, being resident and sedentary, would not respond in this ‘top-down’

manner. Instead, one would expect habitat selection in resident woodland birds to operate in a 'bottom-up' approach. For example, a dispersing woodland bird may move through a fragmented landscape assessing suitability of remnants, but base suitability on fine-scale attributes such as vegetation structure reflecting invertebrate abundance and diversity. In such an example, habitat selection at fine spatial scales constrains that at coarser spatial scales (Kristan 2006). There are far-reaching implications if habitat selection is indeed found to be best represented by a 'bottom-up' approach. Species management plans are traditionally based on habitat selection studies that are of limited spatial scope, focusing on management units operating at 'manageable scales' such as the regional or landscape scale (see comments in Major *et al.* 2001).

The present study aimed to determine whether a 'bottom-up' approach can be demonstrated for a representative resident and sedentary woodland bird species in the New England region of New South Wales, by examining habitat selection in a fragmented agricultural landscape at two spatial scales; territory and landscape. The ground-foraging insectivorous Scarlet Robin (*Petroica multicolor*) was chosen as the model species to assess potential 'bottom-up' hierarchical habitat selection. The scale at which a species most strongly interacts with its environment represents the spatial scale at which environmental variables affect it most strongly (Cushman and McGarigal 2004). Thus, given that the Scarlet Robin is a specialist ground-foraging insectivore, it would appear that this species may be constrained by fine-scaled habitat attributes associated with the ground substrate on which it feeds. As such, it provides a perfect opportunity to assess whether coarser-scaled (territory and

landscape scale) habitat selection is indeed constrained by specific fine-scaled environmental attributes, thus suggesting 'bottom-up' habitat selection.

6.3 METHODS

6.3.1 Study area

Study territories and landscapes were located in remnant woodland and forested tracts on the New England Tablelands (30° 30' S, 151° 30' E) in a 60 km x 65 km area surrounding Armidale, New South Wales, Australia (Figure 6.1). The western edge of the study area straddles the Great Dividing Range, with sites ranging from 800 m – 1250 m above sea level. Vegetation throughout the study area varies in its species composition, with New England Stringybark (*Eucalyptus caliginosa*) the dominant woodland tree species. The midstorey and understorey vegetation is varied throughout the study area, although is dominated by *Acacia* spp., *Cassinia* spp. and *Bursaria* spp. As a result of extensive clearing of much of this native vegetation for sheep and cattle grazing by early last century, only 20% of the original vegetation remains (Barrett *et al.* 1994). The size of remnants in the study area varies from 0.69 ha to a continuous belt of vegetation to the south-east of the study area (including Oxley Wild Rivers National Park), which incorporates hundreds of thousands of hectares. The degree of connectivity of vegetation in the study area varies considerably, with remnants to the west of the study area more connected and variegated than remnants directly surrounding Armidale where the extent of vegetation clearance has been more severe, although it is still effectively variegated. Variegated landscapes are characterised by a mosaic of forest, open woodland and scattered trees (Lord and Norton 1990; McIntyre and Barrett 1992; Bennett 1999). The implications of such findings are of great

consequence, in that the permeability of variegated landscapes by dispersing individuals is potentially different to that in fragmented systems (see Bennett and Ford 1997; Graham and Blake 2001). Specifically, the potential perception of a species to identify intervening variegated habitat as a continuation of remnant habitat represents an important component to take into account when examining the results of landscape scale selection (see Chapter 1).

The study area is characterised by a cool temperate climate, with the majority of rain falling in summer months. Maximum temperatures average 26.3°C in the warmest month (January), with temperatures rarely exceeding 35°C. Minimum temperatures average 12.5°C in January, and rarely drop below 7°C. Winters are particularly cold, dry and frosty, with occasional snowfalls. Maximum temperatures average 12.3°C in the coldest month (July), although occasionally drop to 5°C, with minimum temperatures averaging -0.3°C and regularly dropping to below -5°C. Annual rainfall averages 788 millimetres in Armidale, although it varies across the study area according to local elevation and topographical changes.

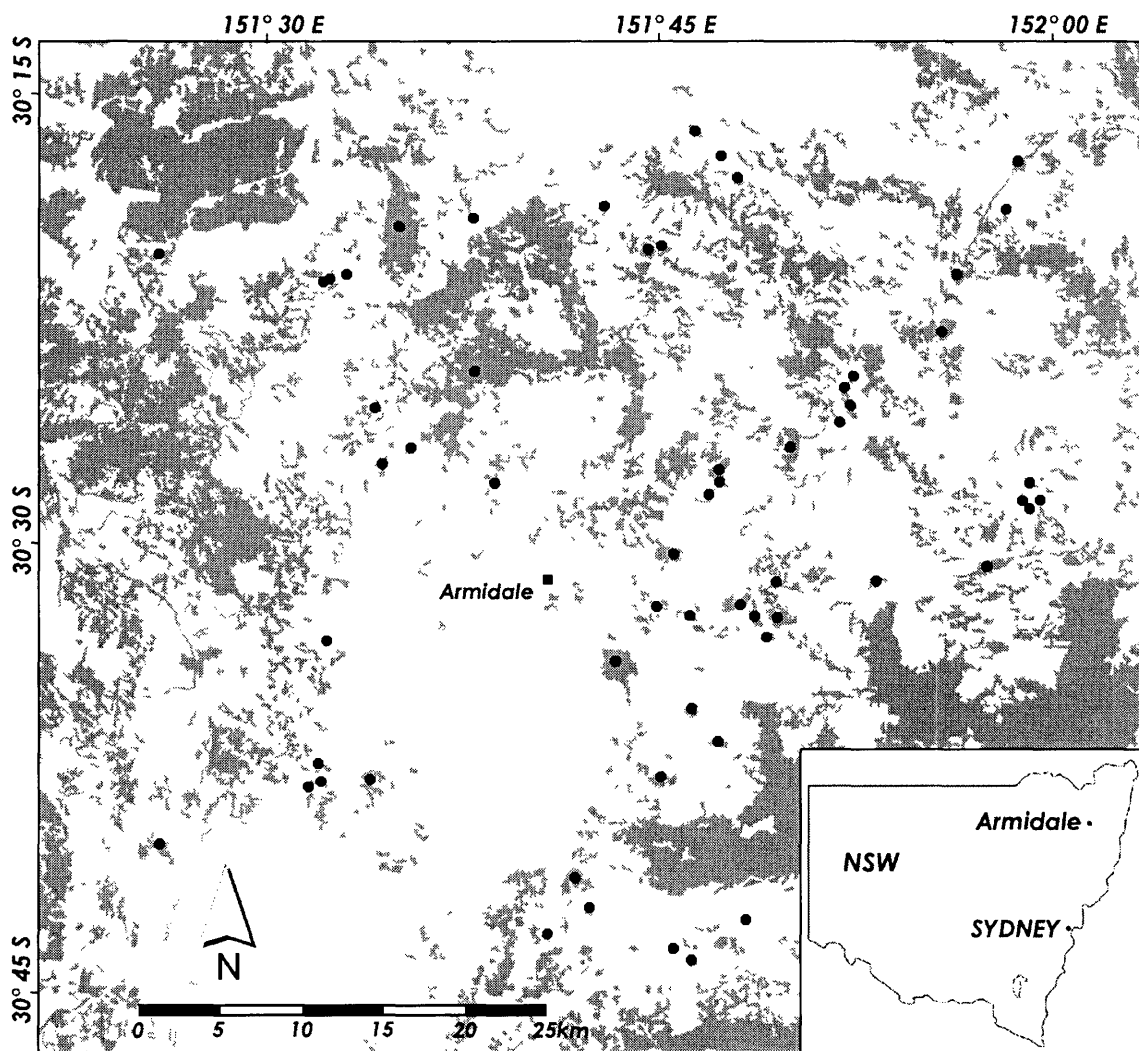


Figure 6.1 Map of the study area showing the location of the 59 sampled remnants (black dots at the approximate centre of the remnant). Grey areas in map denote wooded areas, with white areas denoting cleared areas. Lat and long co-ordinates presented according to the Australian Geodetic Datum 1966 (AGD66).

6.3.2 Study species

The Scarlet Robin (*Petroica multicolor*) is a small sized (13 g) ground-foraging insectivorous Australo-Papuan robin (Petroicidae). In Australia, it is found throughout the southwest and southeast of the continent south of 25°S latitude, although it is also widely distributed on islands in the southwest Pacific including the Solomon Islands, Fiji, Samoa and Norfolk Island (Higgins and Peter 2002). In Australia, it primarily inhabits eucalypt forest and woodland with an open understorey, although it occasionally inhabits mallee vegetation, wetland

vegetation and pine plantations (Higgins and Peter 2002). Although relatively common in some areas, in others, populations have declined. In the southwest of Australia, the *campbelli* subspecies, although not listed as threatened (Garnett and Crowley 2000), is continuing to disappear from even quite large remnants (Saunders and Ingram 1995). In the wheatbelt of NSW, although the Scarlet Robin is not listed as one of the 20 declining species by Reid (1999), Australo-Papuan robins (Petroicidae) as a group, and ground-foragers as a foraging guild, are over-represented as declining species. Furthermore, robins have been identified as 'focal' species which are most sensitive to fragmentation and degradation of habitat in agricultural landscapes (Lambeck 1997; Watson *et al.* 2001), with Watson *et al.* (2003) identifying the Scarlet Robin as being significantly affected by remnant size and habitat complexity.

6.3.3 Landscape scale sampling

Higgins and Peter (2002) indicate that most records of Scarlet Robins in NSW are located from coastal regions to the western slopes of the Great Divide. In the present greater study area, Scarlet Robins were rarely found west of the Gwydir River (per. obs.), so all sampled remnants were thus restricted to locations to the east of the Gwydir River. Within the study area, characteristics of landscape elements associated with occupied remnants were compared to unoccupied remnants. I sampled 59 remnants for the presence of robins between July and October 2005. Remnants sampled represented a variety of sizes (average 124.6 ha; 20 remnants < 20 ha, 27 remnants between 20 – 100 ha, eleven remnants between 100 – 1000 ha and two remnants > 1000 ha) and were chosen from the landscape based on a combination of assessment of 1:25,000 maps and ArcView GIS 3.2a™ digitised maps. Remnants had to be of

a small enough size to ensure that the whole remnant could be accurately assessed for the presence of robins. I made an effort to select remnants that exhibited varying degrees of isolation from surrounding remnants and forested areas. I sampled the remnants by traversing through all remnants and looking and listening for individuals of the species. As this species is generally sedentary and occupies year-round territories (pers. obs., Higgins and Peter 2002), I assumed that if an individual was seen, it was a resident in the remnant rather than a transient individual. As I undertook this study during the breeding season, I also used playback of recorded calls in every remnant to determine presence of the species, and if present, was always met by at least one scolding individual. Once an individual or pair of robins was located in a remnant, I ceased searching to reduce the impact on any breeding activities. I deemed a remnant unoccupied only if a systematic assessment for robins with the aid of call playback failed to locate any robins. This assessment involved me traversing the whole remnant by walking transects not separated by more than 50 – 75 m until the whole remnant was surveyed or an individual was located. In combination with playback, I believed this methodology would accurately determine the presence of robins within the remnant. All landscape scale variables were calculated from GIS digitised maps and data presented in ArcView GIS 3.2a™.

In order to determine aspects characterising remnants occupied by robins and the landscapes surrounding occupied remnants, six variables were recorded. I recorded the size of remnants to determine if any minimum area thresholds existed for this species, as has been suggested for other robins such as the Eastern Yellow Robin (20 ha, *Eopsaltria australis*, Barrett 1995) and Hooded

Robin (100 ha, *Melanodryas cucullata*, Watson *et al.* 2001). The perimeter of remnants was also noted in order to calculate a remnant perimeter (m) to remnant area (ha) ratio. This measure is effectively an index of core habitat area, with higher values indicating sites with a higher degree of edge habitat compared to core habitat. Although some of the landscape area is effectively variegated (Lord and Norton 1990; McIntyre and Barrett 1992) rather than fragmented, the boundaries of surveyed remnants still closely aligned that provided in the ArcView GIS digitised maps. Furthermore, any discrepancy in extent or location of edge was so minimal so as to make no difference to the final measure of remnant size or remnant perimeter.

The influence of landscape scale factors on remnant occupation is not mutually exclusive from those factors governing remnant scale selection, with species such as the ecologically similar Eastern Yellow Robin (*Eopsaltria australis*) more likely to occupy small remnants only if larger forest tracts are nearby (Barrett 1995). As such, I calculated a number of variables within a 10 km x 10 km (10,000 ha) area surrounding occupied and unoccupied remnants. The percentage cover of wooded areas within the 10 km x 10 km area was calculated as a measure of vegetation extent within the immediate vicinity of the remnant. I calculated this measure (independently of spatial configuration) as total habitat cover in a landscape can often have a greater effect on species persistence than spatial configuration (Villard *et al.* 1999). I assessed the degree of connectivity of the vegetation within the 10 km x 10 km landscape area through the calculation of an average inter-remnant distance measure. This measure was developed during the course of the study and is calculated as the average distance between remnants in eight cardinal compass directions from

the centre of the occupied remnant in the 10 km x 10 km landscape area (see section 5.3.3 and Figure 5.2 for detailed information). Although not taking into account functional connectivity (see Uezu *et al.* 2005), I devised the method as it represents a standardised method for calculation of the interception of wooded or forested areas within and to the edge of a 10 km x 10 km area for an idealised dispersing individual along linear vectors radiating from the central occupied remnant. Given the variegated nature of some of the landscape, the permeability of the linear vectors between remnants to a dispersing individual varies according to the characteristics of the inter-remnant matrix (see Chapter 1).

The isolation of remnants was calculated as a single measure of distance to nearest large remnant. The criteria selected for justifying a 'large remnant' was based loosely on a number of calculations including the area needed to maintain an effective population size (see Barrowclough and Shields 1984; Couvet 2002). Thus, the distance to nearest remnant larger than 2,000 hectares was also included as a subjective estimate of the remnant size of a self-sustaining source population.

6.3.4 Territory scale variables

Habitat selection at the territory scale was assessed by determining those habitat attributes that distinguished occupied territories from unoccupied territories. Twenty territories and their paired non-territories were assessed in eight study sites that were themselves located in the study remnants presented in the landscape scale sampling section (section 6.3.2).

I assessed territory scale selection by examining habitat attributes along a single 100 m x 5 m transect in each territory. Territory boundaries were approximated by noting any territorial behaviour of robins, and reactions to call playback. Transects were located along the central axis of known territories, and where possible, intersected the location of any nests to maximise idealised territory habitat. Sampling in any given territory was never carried out while females were brooding eggs or while there were nestlings, to avoid potential predation by known nest predators such as Pied Currawongs (*Strepera graculina*), Grey Shrike-thrush (*Colluricincla harmonica*) and Grey Butcherbirds (*Cracticus torquatus*) (Debus 2006a, 2006b). In those sites where nests were not located, the approximate boundary of territories was designated according to areas used by an individual or pair of robins followed for at least 30 minutes. Territory transects were then located within the centre of the territory boundaries. Non-territories were located no less than 300 m from territories, and were only considered non-territories if an individual or pair of robins was not detected within 45 minutes using call playback. The location of non-territories was mapped in relation to the location of territory sites using ArcView GIS 3.2a™, with approximately 300 – 400 m separating territories from non-territories.

Along the length of the transect, I counted the number of sapling and subcanopy trees (1 m – 10 m), canopy trees (>10 m) and shrubs (> 0.3 m high and 0.3 m wide). I estimated the cover of herbs (herbaceous vegetation < 0.3 m and grass) and leaf litter as one of five measures of abundance between sparse and dense in 10 m sections along the 100 m transect. This was then averaged, to give a final measure for the territory. I also calculated log volume using the

line intercept method for downed wood (Harmon and Sexton 1996). I used this method as it is particularly easy to undertake in the field and is not labour intensive, especially as the lengths of logs are not required to be measured. Instead, only the diameter of every log (fallen timber with diameter > 50 mm and length > 800 mm) that intersected the centre line of the 100 m transect was measured. If a log was noticeably tapered however, an average diameter was recorded. The formula used to calculate the volume of logs per unit area ($\text{m}^3 \text{m}^{-2}$) using the line transect intercept method is:

$$V = 9.869 * \sum(d^2 / 8L)$$

Where d is the log diameter (m), and L is the transect length (m).

One of the criticisms of the line transect method is that it excludes dead standing trees, resulting in an underestimate of total woody debris. However, the aim of the present method was to calculate a coarse approximate volume of fallen logs as these are elements of the woody debris in the habitat that are most utilised by robins such as the Scarlet Robin as perching and foraging substrates (e.g., see Laven and Mac Nally 1998).

6.3.5 Variable reduction

Before analysis, I reduced the number of landscape and territory variables following a combination of correlation analysis and Principal Component Analysis (PCA).

Landscape scale variables

I eliminated the measure of remnant perimeter from further analysis as it was highly correlated with remnant size ($r = 0.983$, $df = 58$, $p < 0.001$). I retained remnant size as I deemed it more of an ecologically meaningful variable than remnant perimeter. The final variables utilised in further landscape scale analysis included remnant size, remnant perimeter to area ratio, average inter-remnant distance (see section 5.3.3), percentage of 10 km x 10 km landscape area wooded and the distance to nearest remnant larger than 2000 ha.

Territory scale variables

For the territory scale analysis, the index of herb cover and the index of leaf litter abundance were significantly negatively correlated ($r = -0.334$, $df = 38$, $p = 0.035$), so I replaced these variables with a new composite ground substrate variable computed as principal component scores from a PCA. Larger values of the new ground substrate variable indicated a high index of herb cover and an associated low index of leaf litter abundance. The percent total variance explained by the new composite ground substrate variable was 66.7%. The final variables utilised in further territory scale analysis included the number of canopy trees, number of sapling and subcanopy trees, number of shrubs, volume of logs and an index of ground substrate.

6.3.6 Analysis

Landscape scale

The presence or absence of robins in each remnant represented the dependent variable and was scored as 1 or 0 respectively. The independent variables

mentioned in the landscape scale variable section were used to investigate the influence of the remnant and landscape factor variables on the binary dependent variable. As such, I undertook a binary (or binomial) logistic regression analysis.

Territory scale

I initially analysed the habitat elements characterising territory scale selection of robins using a hierarchical linear modelling (HLM) procedure using the HLM6 program (Raudenbush *et al.* 2005). Hierarchical linear modelling (HLM) is a form of regression analysis that is designed to analyse nested or hierarchically structured data (Raudenbush and Bryk 2002). Hierarchical structure is widespread in many ecological systems, with many studies failing to adequately address such structure. One of the fundamental assumptions underlying traditional multiple or logistic regression analysis is that observations are independent (Raudenbush and Bryk 2002). In ecological studies, this assumption is frequently violated. For example, habitat attributes of territories and non-territories sampled within a given remnant will tend to be more homogeneous than territories and non-territories sampled randomly from all study sites across the landscape. As habitat attributes of territories and non-territories from a given remnant share similar site-specific characteristics (e.g., topography, species assemblages, biotic effects), these territories are not fully independent. If this assumption of independence is violated, estimates of regression coefficients and associated standard errors are erroneous and can lead to falsely inferred conclusions. As such, it is imperative to first attempt to analyse data taking into account hierarchical structure. In the present study, the data was structured at two hierarchical levels; territories and non-territories

within study remnants. As such, I attempted a 2-level hierarchical linear modelling approach on the data. Specifically, due to the binary response variable (territory or non-territory), I undertook a hierarchical generalised linear modelling (HGLM) procedure using the HLM6 program (Raudenbush *et al.* 2005). See Raudenbush and Bryk (2002) for a detailed explanation of hierarchical linear modelling, its component statistics and its application.

Following preliminary HGLM analysis of the data, it was shown that structuring the data at the second level (remnant scale) was ineffective, as determined by the results of a variance component test in HLM6. As a result, I undertook all analyses using binary logistic regression analysis, as in the landscape scale analysis mentioned previously.

I examined log-likelihood values calculated by the logistic regression procedure for each model, and calculated a modified second-order Akaike's Information Criterion, AIC_c . The AIC_c values are used instead of the first-order AIC when the number of parameters is relatively large compared to sample size (i.e., $n/K < 40$, Burnham and Anderson 2002) and is calculated as:

$$AIC_c = -2\log(L) + 2K + 2K(K+1)/(n-K-1)$$

Where $\log(L)$ = log likelihood of model

K = total number of parameters in the model

n = sample size

From these AIC_c values, models were ranked by rescaling the AIC_c values such that the model with the minimum information criteria had a value of 0:

$$\Delta_i = AIC_i - \min AIC$$

I then calculated normalised Akaike weights (w_i) as they are useful as the 'weight of evidence' in favour of model i being the best model in the set of models.

$$w_i = \exp(-\Delta_i / 2) / \sum \exp(-\Delta_i / 2)$$

The Akaike weights sum to one, with the model showing the strongest support having the largest weight. For each response variable, I chose the model with the greatest Akaike weight for further analysis. In addition, Burnham and Anderson (2001) suggest that models with Δ_i values less than two still have substantial support, so I also included these models. I assessed adequacy of the final selected models by examining the regression coefficients and their 95% confidence intervals. If the regression coefficient confidence intervals included zero, then it indicated that the relationship between the response variable and the predictor variable(s) was too variable to be certain of a definite positive or negative association.

Rather than focusing on a 'best model' approach, I assessed the importance of predictor variables across all models (Burnham and Anderson 2002). I undertook this in the present study by the multi-model inference procedure. This procedure was achieved by summing the Akaike weights for all models

containing a given predictor variable. The final sum represents a weight of evidence for that variable across all models. This process is particularly important in those circumstances when there is a number of almost equally well supported models (Burnham and Andersen 2001).

6.4 RESULTS

6.4.1 Landscape scale selection

The 59 surveyed remnants varied in size from 4.6 ha to 2,404.0 ha, with an average size of 124.6 ha. Scarlet Robins occupied 32 (54.2%) of the 59 surveyed remnants, with the average size of these occupied remnants approximately 209.2 ± 84.5 ha; mean \pm standard error (Figure 6.2a) and of unoccupied remnants approximately 24.4 ± 5.1 ha.

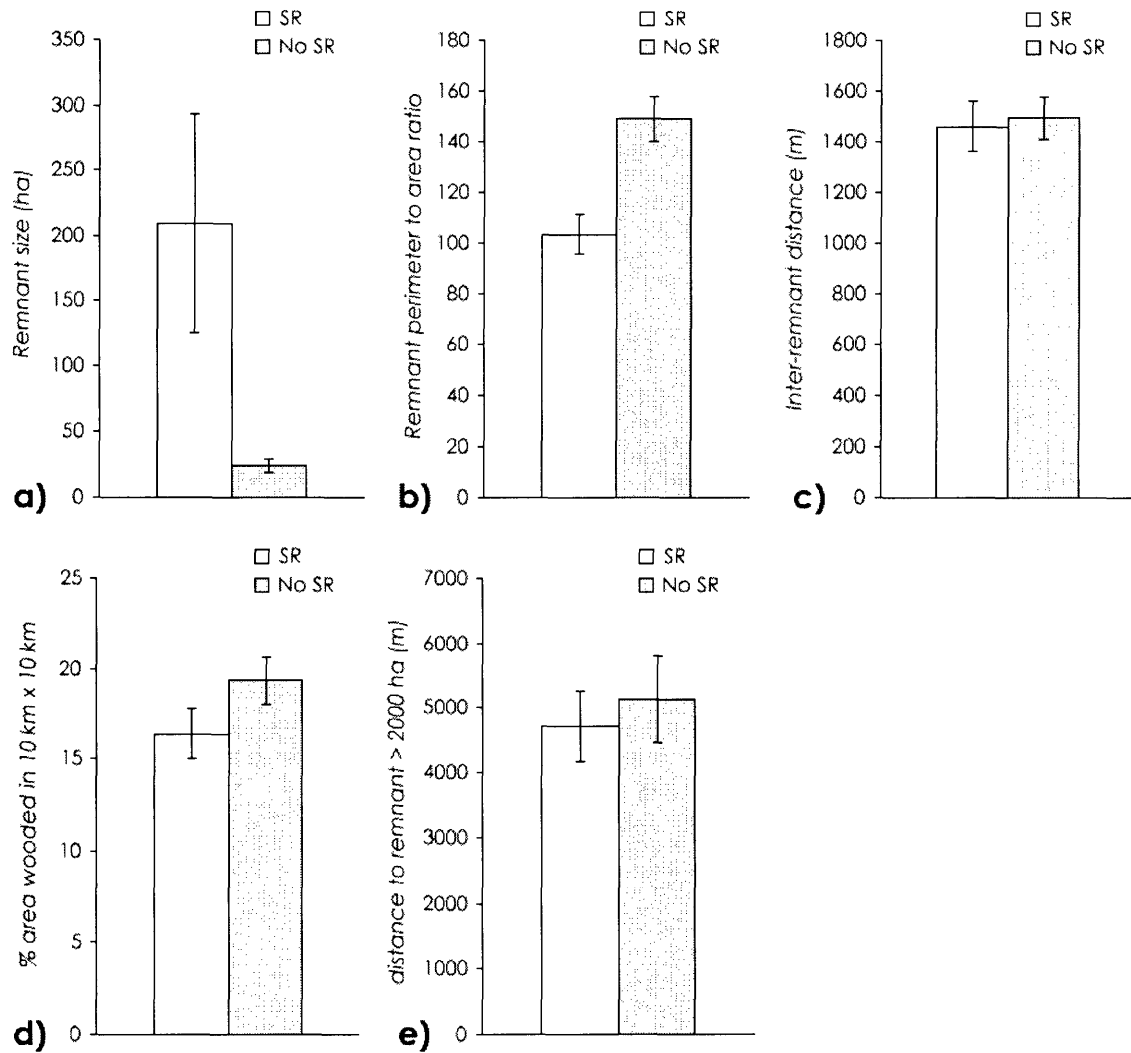


Figure 6.2 a) the average size of remnants occupied by Scarlet Robins (SR: n = 32) and unoccupied by Scarlet Robins (No SR: n = 27), b) the remnant perimeter to area ratio of occupied and unoccupied remnants, c) the average inter-remnant distance in 10 km x 10 km area surrounding occupied and unoccupied remnants, d) the % area of 10 km x 10 km area wooded surrounding occupied and unoccupied remnants and e) the distance to nearest remnant larger than 2000 ha from occupied and unoccupied remnants. All graphs show the average \pm standard error.

Scarlet Robins occupied remnants as small as 6.9 ha, although 28 of the 32 occupied remnants (87.5%) were larger than 20 ha. The largest unoccupied remnant was 123.9 ha, although the remnant was surrounded by a 10 km x 10 km landscape that had the smallest percentage area wooded (5.2%) of all 59 surveyed landscapes. The remnant perimeter to area ratio of occupied remnants was much lower (103.4 ± 7.8) than that of unoccupied remnants

(149.0 ± 9.0 ; fig 6.2b), while the percentage of wooded area surrounding occupied remnants was somewhat lower ($16.4 \pm 1.4\%$) than that surrounding unoccupied remnants ($19.3 \pm 1.3\%$; fig 6.2d). The average inter-remnant distance was similar in 10 km x 10 km landscapes surrounding occupied and unoccupied remnants ($1,459.6 \pm 100.0$ m and $1,496.3 \pm 84.7$ m respectively; fig 6.2c), as was the distance to remnant larger than 2000 ha ($4,707.2 \pm 539.2$ m and $5,131.6 \pm 666.6$ m respectively; fig 6.2e).

The results of the logistic regression modelling indicated that five models were selected that best distinguished landscape elements characterising occupied remnants from unoccupied remnants (Table 6.1). The best model was a univariate model (Akaike weight of 0.1679) incorporating remnant size, with remnants occupied by Scarlet Robins being of greater size than unoccupied remnants. This univariate model had good explanatory power due to the regression coefficient confidence intervals for remnant size not including zero. A trivariate model incorporating remnant size, inter-remnant distance and percentage cover of wooded areas in 10 km x 10 km landscapes was also selected as best approximating the data (Akaike weight of 0.1565). The response of remnant size was the same as in the univariate model, with occupied remnants of larger size than unoccupied remnants. The average inter-remnant distance was smaller in landscapes surrounding remnants occupied by robins, while the percentage cover of wooded areas in 10 km x 10 km landscapes around occupied remnants was lower than that around unoccupied remnants. Only remnant size had any good explanatory power in this trivariate model due to the regression coefficients not including zero. An almost equally weighted bivariate model (Akaike weight of 0.1484) was also selected and

incorporated remnant size and percentage cover of wooded areas in 10 km x 10 km landscapes. This model did not have good explanatory power due to the regression coefficients of the two variables including zero. A quadrivariate model incorporating remnant size, inter-remnant distance, percentage cover of wooded areas in 10 km x 10 km landscapes and distance to nearest remnant > 2000 ha was also selected as best approximating the data, although the Akaike weight (0.0679) was considerably lower than previously mentioned models. Only the remnant size and percentage cover of wooded areas in 10 km x 10 km landscapes variables had any explanatory power in this model, with the response of these variables the same as in previous models. The final model chosen was a bivariate model incorporating remnant size and inter-remnant distance (Akaike weight of 0.0668), with only the former variable having good explanatory power in this model (Table 6.1).

Table 6.1 Results of logistic regression modelling for landscape attributes associated with remnant occupancy by Scarlet Robins.

Final models for each response variable were chosen based on those candidate models with ΔAIC_c values less than 2.0. Akaike weights are calculated from the relative likelihood values as determined by ΔAIC_c values. Rem size = remnant size, Inter-rem = inter-remnant distance, Per area = percentage cover of wooded areas in 10 km x 10 km landscape, Dist 2000 = distance to nearest remnant > 2000 ha. † = Coefficients for which the 95% confidence interval does not include zero.

Predictor variable(s)	ΔAIC_c	Akaike weight	Model variable(s)	Coefficient	Std err	Confidence interval
Rem size	0	0.1679	Rem size	0.034	0.012	0.0105, 0.0575 [†]
Rem size + Inter-rem + Per area	0.1405	0.1565	Rem size	0.035	0.013	0.0095, 0.0605 [†]
			Inter-rem	-0.001	0.001	-0.0030, 0.0010
			Per area	-0.119	0.065	-0.2464, 0.0084
Rem size + Per area	0.2461	0.1484	Rem size	-0.001	0.001	-0.0030, 0.0010
			Per area	-0.119	0.065	-0.2464, 0.0084
Rem size + Inter-rem + Per area + Dist 2000	1.8098	0.0679	Rem size	0.035	0.013	0.0095, 0.0605 [†]
			Inter-rem	-0.001	0.001	-0.0030, 0.0010
			Per area	-0.132	0.067	-0.2633, -0.007 [†]
			Dist 2000	0	0	0.0000, 0.0000
Rem size + Inter-rem	1.8421	0.0668	Rem size	0.034	0.012	0.0105, 0.0575 [†]
			Inter-rem	-0.067	0.049	-0.1630, 0.0290

Examination of the multimodel inference procedure for the five predictor variables indicates the dominant role of remnant size in distinguishing remnant and landscape elements associated with occupied sites from those of unoccupied sites, with a weight of evidence of 0.9902 (Table 6.2). This was followed by the percentage cover of wooded areas in 10 km x 10 km landscape and inter-remnant distance with weights of evidence of 0.5777 and 0.4288 respectively. The remaining two predictor variables (remnant perimeter to area ratio and distance to nearest remnant > 2000 ha) had a similar smaller weighting.

Table 6.2 Multi-model inference weight of evidence (WoE) for predictor variables contributing to landscape scale selection response variable models.

Rem size = remnant size, EA ratio = remnant perimeter to area ratio, Inter-rem = inter-remnant distance, Per area = percentage cover of wooded areas in 10 km x 10 km landscape, Dist 2000 = distance to nearest remnant > 2000 ha.

<i>Predictor</i>	<i>WoE</i>
Rem size	0.9902
EA ratio	0.2633
Inter-rem	0.4288
Per area	0.5777
Dist 2000	0.2661

6.4.2 Territory scale selection

Habitat attributes across all the territories and non-territories varied considerably throughout the study area. The number of canopy trees in 100 m x 5 m transects varied from two to 27 (a projected density of canopy trees between 40/ha and 540/ha), with the number of sapling and subcanopy trees ranging from six to 59 (a projected density of sapling and subcanopy trees between 120/ha and 1,180/ha). There was a large range of densities in numbers of shrubs per transect; between one and 127 (a projected density of

shrubs between 20/ha and 2,540/ha). Scarlet Robin territories were characterised by a high density of canopy trees (Figure 6.3a), a small density of shrubs (Figure 6.3c), a high volume of logs (Figure 6.3d), and low values of the ground substrate index (Figure 6.3e), while the density of sapling and subcanopy trees (Figure 6.3b) varied little between territories and non-territories, albeit slightly higher in non-territories.

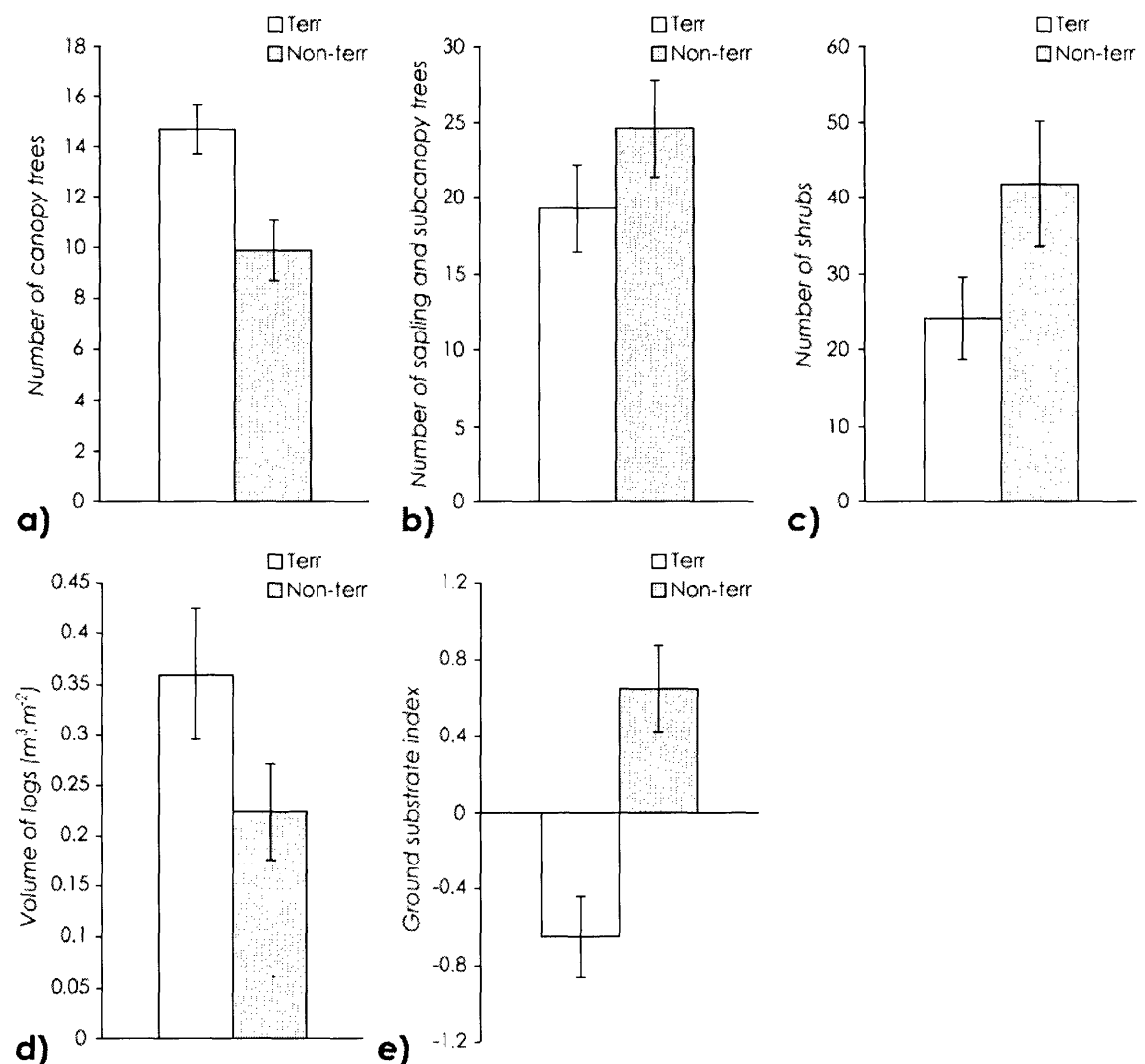


Figure 6.3 a) the number of canopy trees in 100 m x 5 m transects in Scarlet Robin territories (Terr: n = 20) and non-territories (Non-terr: n = 20), b) the number of saplings and subcanopy trees in territory and non-territory transects, c) the number of shrubs in territory and non-territory transects, d) the volume of logs in territory and non-territory transects and d) the index of ground substrate cover in territory and non-territory transects. All graphs show the average \pm standard error.

The results of logistic regression modelling indicated that six models were selected that best distinguished habitat attributes characterising robin territories from non-territories (Table 6.3). The best of these models was a bivariate model (Akaike weight of 0.1509) incorporating number of canopy trees and ground substrate index, with territories characterised by a higher density of canopy trees and a lower index of ground substrate (i.e., more leaf litter and less herbaceous plants) than non-territories. Only the ground substrate variable in this model had good explanatory power due to the regression coefficient confidence intervals not including zero (Table 6.3). A trivariate model incorporating number of shrubs, volume of logs and index of ground substrate was also selected, with Scarlet Robin territories characterised by lower densities of shrubs, a higher volume of logs and a smaller ground substrate index. Only the ground substrate variable had good explanatory power, with the regression coefficient confidence intervals for the number of shrubs and the volume of logs including zero. The remaining four logistic regression models incorporated the index of ground substrate, volume of logs, number of canopy trees and number of shrubs in various combinations of univariate, bivariate and trivariate models (Table 6.3), although only the index of ground substrate had good explanatory power in all of the models due to the regression coefficients not including zero. The response of the ground substrate index in each of the logistic regression models was the same, with territories having a lower index value (i.e., more leaf litter and less herbaceous plants) than non-territories.

Table 6.3 Results of logistic regression modelling for habitat attributes associated with territories of Scarlet Robins.

Final models for each response variable were chosen based on those candidate models with ΔAIC_c values less than 2.0. Akaike weights are calculated from the relative likelihood values as determined by ΔAIC_c values. Can trees = number of canopy trees, Shrub = number of shrubs, Log = volume of logs, Ground = ground substrate index. † = Coefficients for which the 95% confidence interval does not include zero.

Predictor variable(s)	ΔAIC_c	Akaike weight	Model variable(s)	Coefficient	Std err	Confidence interval
Can trees + Ground	0	0.1509	Can trees	0.1720	0.1040	-0.0318, 0.3758
			Ground	-1.2870	0.5000	-2.2670, -0.3070 [†]
Shrub + Log + Ground	0.1218	0.1420	Shrub	-0.0290	0.0180	-0.0643, 0.0063
			Log	385.7360	222.7480	-50.8501, 822.3221
			Ground	-1.4930	0.5370	-2.5455, -0.4405 [†]
Ground	0.7481	0.1038	Ground	-1.4800	0.4990	-2.4580, -0.5020 [†]
Log + Ground	0.8180	0.1002	Log	247.3390	178.3950	-102.3152, 596.9932
			Ground	-1.4590	0.5060	-2.4508, -0.4672 [†]
Can trees + Log + Ground	0.9498	0.0938	Can trees	0.1550	0.1040	-0.0488, 0.3588
			Log	234.8060	189.5550	-136.7218, 606.3338
			Ground	-1.2890	0.5110	-2.2906, -0.2874 [†]
Shrub + Ground	1.2900	0.0792	Shrub	-0.0200	0.0160	-0.0514, 0.0114
			Ground	-1.4410	0.5020	-2.4249, -0.4571 [†]

Examination of the multi-model inference procedure for the five predictor variables indicates the dominant importance of the ground substrate index in distinguishing Scarlet Robin territory habitat characteristics from non-territories (Table 6.4). Three of the remaining predictor variables (volume of logs, number of canopy trees and shrubs) had similar intermediate weightings, with the number of sapling and subcanopy trees exhibiting a low weighting, reflecting an absence of its importance in any of the logistic regression models.

Table 6.4 Multi-model inference weight of evidence (WoE) for predictor variables contributing to territory scale selection response variable models.

Can trees = number of canopy trees, Sap sub = number of sapling and subcanopy trees, Shrub = number of shrubs, Log = volume of logs, Ground = ground substrate index.

<i>Predictor</i>	<i>WoE</i>
Can trees	0.4568
Sap sub	0.2160
Shrub	0.4137
Log	0.4950
Ground	0.9799

6.5 DISCUSSION

6.5.1 Importance of remnant specific landscape attributes

Remnant size was the principal variable governing whether a remnant was occupied by Scarlet Robins in the study area. This indicates that attributes of the remnant itself rather than the surrounding landscape are more important in discerning habitat selection of the Scarlet Robin in the present study area (see also Major *et al.* 2001). The prevalence of remnant size as a predictor of remnant occupation suggests that Scarlet Robins are area-sensitive. It must be noted that robins were still located in remnants as small as 6.9 ha, indicating no minimum area requirement, as has been suggested for other species of robins

in the area (e.g., 20 ha for Eastern Yellow Robin *Eopsaltria australis*, Barrett 1995). Area-sensitivity, as defined in the present study, refers to a tendency for robins to occupy large remnants more often than small remnants (Winter and Faaborg 1999). Area-sensitivity in some studies is attributed to a sampling artifact rather than a true response to area. Horn *et al.* (2000) suggest that proportional sampling or equal-effort sampling techniques do not accurately assess area-sensitivity. As a result, I believe that the method I employed of covering a remnant until I detected robins or until I had completely sampled it means that the distribution of the species is a true measure of area-sensitivity, and is not compromised by any sampling artifact. Furthermore, the area-sensitivity response in the present study mirrors the study of Barrett *et al.* (1994) who showed that Scarlet Robins, in a similar region to the present study, were more common in large remnants (>400 ha) compared to small remnants (defined as 6 – 20 ha).

Although one can ascertain that an area-sensitive response likely exists, there is still uncertainty about the factors leading to this response, especially the extent that small spatial scale factors (e.g., altered microhabitats) or large spatial scale factors (e.g., isolation of remnants with suitable habitat) influence the expression of area-sensitivity (Winter and Faaborg 1999). For example, in small remnants, birds can experience high rates of nest predation (Wilcove 1985), whether as an exclusive result of remnant size (Keyser *et al.* 1998; Chalfoun *et al.* 2002), or the result of increased edge habitat in small remnants favouring nest predators (Paton 1994; Luck *et al.* 1999; Saracco and Collazo 1999). Predation is the major reason for the very low nest success of Scarlet Robins, which may mean the species cannot maintain populations within small

remnants. Debus (2006a) recorded nest success at only 9% for Scarlet Robins in Imbota Nature Reserve, one of the remnants examined in the present study. Ford *et al.* (2001) show Scarlet Robins as having the lowest nesting success rate (10%) of 25 selected Australian passerine species (see Robinson 1990). Large, aggressive species, such as Noisy Miners (*Manorina melanocephala*), are often abundant in small remnants in south-eastern Australia. They may exclude small insectivores, such as the Scarlet Robin (Loyn 1987; Watson *et al.* 2000; Major *et al.* 2001; Mac Nally and Horrocks 2002; Mac Nally *et al.* 2002).

Typically, small remnants are degraded (Barrett *et al.* 1994; Seddon *et al.* 2003). They are often on private land, and are more intensely managed and thus modified through inappropriate fire regimes, collection of firewood, grazing by domestic stock and weed invasion (Bennett 1999). Although there was no remnant perimeter to area effect in the present study (as proportion of edge habitat varies greatly according to remnant shape), small remnants invariably contain proportionately more edge habitat, and thus edge effects are more pronounced (e.g., reduced breeding success, change in vegetation structure etc.)(Saunders *et al.* 1991; Matlack 1993; Paton 1994; Murcia 1995; Luck *et al.* 1999; Ford *et al.* 2001; Major *et al.* 2001). Barrett *et al.* (1994) lists the Scarlet Robin in the New England region as a common species dependent on healthy woodland. They categorise the Scarlet Robin as a species absent from small, degraded patches; restricted to remnants where grazing, logging, understorey clearing and removal of fallen timber is limited. Importantly, for small insectivorous birds like Scarlet Robins, studies have also indicated reduced availability and poor quality food in small remnant patches in fragmented landscapes (Doyle 1996; Burke and Nol 1998; Zquette 2000; Zquette *et al.*

2000) as a result of the primary influence that habitat modifications have in simplifying ground microhabitat (Major *et al.* 1999), thus bringing about a decline in invertebrate abundance and diversity (Recher 1991; Hobbs 1993; Matlack 1993; Arnold and Weeldenburg 1998; Bromham *et al.* 1999; York 1999; Abensperg-Traun *et al.* 2000; Antos and Bennett 2006).

6.5.2 The role of ground substrate in territory selection

In the present study, robins selected breeding territories that had a low ground substrate index, i.e., they had more leaf litter and less herbaceous plant cover than areas not selected. This agrees with previous research suggesting the species was associated with drier habitats harbouring a sparse shrub and sapling layer and relatively open ground layer (Robinson 1992; Debus 2006a). Robins may select for high leaf litter and low plant cover within their territories to maximise foraging efficiency. This is because invertebrate prey were more abundant or more detectable where there was much leaf litter but little ground vegetation (see Chapter 2). Robins may well use a high cover of leaf litter as a proximate cue when they select their territory.

Disturbances that increase the extent and density of vegetation on the ground (such as nutrient enrichment or weed invasion) result in habitat that is not selected by robins because food is less abundant and detectable (Recher *et al.* 2002). Conversely, burnt habitat continues to be occupied by Scarlet Robins in the short-term (Wooller and Calver 1988; Garnett and Crowley 2000), even though the abundance and diversity of epigeic invertebrates initially declines (Abbott 1984; York 1999). Prey may be more conspicuous though until regrowth becomes denser (Smith 1985). In addition, the more open burnt

habitat may impose a reduced predation risk on birds foraging on the ground (Whittingham and Evans 2004; Jones *et al.* 2006).

6.5.3 A case exemplifying ‘bottom-up’ habitat selection

Habitat selection in birds is generally assumed to be hierarchical in nature (George and Zack 2001; Jones 2001), and there is an inherent association between scales, with adjacent spatial scales exhibiting a greater influence than disparate spatial scales (Cushman and McGarigal 2004). Unfortunately, due to time and budgetary constraints, habitat selection studies are often limited in their spatial scope, focusing on management units operating at the landscape scale (see comments in Major *et al.* 2001). The problem with this approach is that it is often very limiting, in that it assumes a ‘top-down’ approach to habitat selection (e.g., McLoughlin *et al.* 2002).

‘Top-down’ habitat selection is a hierarchical, sequential process, whereby a bird flies over or through a landscape and decides where to settle based on the habitat it encounters. Following this selection, it proceeds to select finer-scaled or finer-grained habitat attributes, as constrained by its initial coarse-scaled selection (Kristan 2006). Assumptions associated with such ‘top-down’ habitat selection focus on species responses at the largest spatial scales (e.g., dispersal capabilities, patch size), while underestimating or, at worst, rejecting elements governing smaller spatial scale selection. Such habitat selection assumptions best characterise a migratory species (Kristan 2006), whereby hierarchical selection at coarser scales constrain that at finer scales (Battin and Lawler 2006; Kristan 2006). This approach to habitat selection is not as

applicable in Australia, as the majority of the threatened woodland and forest birds are, to a great degree, resident and sedentary.

In the present study, selection at the territory scale by Scarlet Robins is governed by ground substrate attributes representing microhabitats associated with a higher detectability and abundance of invertebrates (see Chapter 2 and 4). Such selection may effectively constrain occupation of remnants at the landscape scale, as small remnants are avoided due to their degraded habitat (especially the ground substrate) rather than simply because they are small (Barrett *et al.* 1994). Habitat selection in the Scarlet Robin may therefore be best represented by a 'bottom-up' approach rather than a 'top-down' approach so commonly assumed, and from which management decisions are invariably formed (e.g., Hall and Mannan 1999). 'Bottom-up' habitat selection suggests that selection for coarse-scaled attributes (e.g., landscape scale selection) is constrained by fine-scaled attributes (e.g., foraging microhabitat). This mode of habitat selection implies that an individual may move from remnant to remnant within a landscape, but ultimately assesses suitability of the remnant based on finer scaled habitat attributes such as ground substrate in its role as a proximate cue for invertebrate prey resources. This is however dependent on its willingness and ability to sample a range of remnants and locations within remnants, as well as its ability to assess habitat quality. In this regard, Forbes and Kaiser (1994) discuss the 'information barrier' that a dispersing bird faces, with a Scarlet Robin having to balance the potential benefit in sampling distant remnants with the cost (i.e., energetic cost, predatory risk etc.) of traversing the landscape to assess its quality. In this regard, prevalence for Scarlet Robins to occupy larger remnants may reflect the favourable foraging attributes in large

remnants compared to small remnants. Conversely, this prevalence for Scarlet Robins in larger remnants, may reflect the extirpation of populations in small remnants due to their potentially limited foraging resources (Doyle 1996; Burke and Nol 1998; Zañette *et al.* 2000), and the high nest predation rates and low breeding success reported for the species (Debus 2006a). This would, however, require long-term knowledge of the metapopulation dynamics of the species and factors influencing dispersal behaviour.

The implications of such ‘bottom-up’ habitat selection indicates that results from coarse-scaled (regional or landscape scale) habitat selection studies of resident woodland birds need to be considered with some degree of caution, taking into account, and/or incorporating, habitat selection studies at finer spatial scales.

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Appendix 6.1 Location and status of Scarlet Robin occupancy in all 59 surveyed remnants.

All remnant locations presented according to Universal Transverse Mercator (UTM) easting and northing co-ordinates (56J UTM zone). 'Pr/Ab' refers to the presence (+) or absence (-) of robins from each respective remnant.

<i>Remnant</i>	<i>easting</i>	<i>northing</i>	<i>Pr/Ab</i>	<i>Remnant</i>	<i>easting</i>	<i>northing</i>	<i>Pr/Ab</i>
Imbota	376943	6616784	+	17 Achi	401822	6626663	-
East	399618	6622654	+	17 Broo	382656	6627001	-
Yena	380512	6623387	+	17 Kara	391286	6632521	+
Newholme	368252	6634623	+	17 Mimo	396811	6637068	+
Corner	379438	6620148	+	17 Petr	383243	6627799	-
Woodlands	386767	6621721	+	17 Pint	390622	6631499	-
Gara	384580	6620283	+	17 Rock	383199	6628579	-
Snake	392851	6621756	-	17 Thal	387602	6629931	+
Boorolong	362139	6632379	-	17 Woo1	390886	6633627	-
09 Dulv	348903	6641901	+	17 Wood	391458	6634334	-
10 Boor	363667	6643594	+	22 Gree	359172	6618094	+
10 Ebon	368207	6644114	-	23 Alde	383186	6611803	-
10 Olm1	359376	6640367	-	23 lola	381583	6613891	+
10 Olm2	359007	6640224	-	23 Rive	385435	6619529	+
10 Olmo	360404	6640671	-	23 Sout	386158	6618334	+
10 Pin2	379679	6642479	+	23 Treq	386827	6619524	+
10 Pine	378848	6642200	+	23 TSR1	381486	6619619	+
10 Spri	376168	6644877	-	27 Wilh	348969	6605521	+
11 Inve	384336	6646652	+	28 Barl	358687	6610503	+
11 Mare	381729	6649546	-	28 Cree	372761	6599982	-
11 Mojo	397775	6640620	+	28 Kelv	361893	6609507	-
11 Rock	401479	6647668	+	28 Mihi	375284	6601623	-
11 Tarr	400784	6644650	+	28 Nort	374481	6603449	+
11 Wari	383374	6648020	-	28 Sum1	358105	6609049	+
16 Brae	364344	6629867	-	28 Summ	358857	6609381	+
16 Inve	369524	6627715	+	28 Tive	379758	6609667	+
16 Mirr	362532	6628904	-	29 Beve	384900	6600871	-
17 Ach1	402227	6626123	-	29 Mor2	380483	6599124	-
17 Ach2	402205	6627735	-	29 More	381621	6598418	-
17 Ach3	402834	6626671	+				