CHAPTER 3: 'BOTTOM-UP' INFLUENCES ON THE FORAGING MICROHABITAT SELECTION OF THE EASTERN YELLOW ROBIN (Eopsaltria australis).

3.1 ABSTRACT

Foraging site selection in birds is influenced by many factors with selection varying temporally and spatially and governed by behavioural decisions maximising prey detection and capture, thus increasing foraging efficiency. However, is the selection of a specific foraging site constrained by selection at larger scales (i.e., foraging site selected after territories and patches have been selected)? Or does the selection of a specific foraging site constrain selection at larger spatial scales (i.e., selection of patches and territories governed by increased detectability of prey at the foraging site scale)? In the present study, foraging microhabitat selection was assessed in the Eastern Yellow Robin (*Eopsaltria australis*) at two spatial scales (microplot = pounce site, 0.3 m x 0.3 m and mesoplot = foraging area surrounding pounce site, 5 m x 5 m) and two temporal scales (winter and spring). Foraging microplots in winter harboured more logs, reflecting the favourable microclimate that logs provide for epigeic invertebrates compared to the surrounding ground substrate. During spring, higher temperatures reduced the affinity of epigeic invertebrates with logs and with a general increase in number of invertebrates, selection shifted to sites with a greater cover of leaf litter. Mesoplot selection in both seasons was characterised by sites with more leaf litter, less ground plant material, a denser canopy and more logs. These attributes are associated with an elevated abundance and increased detectability of epigeic prey. Mesoplots in which birds foraged contained a higher density of sapling and subcanopy trees during

winter. This reflects the important perching substrates they provide, thus maximising detectability of prey when they are less abundant than in spring. Eastern Yellow Robins apparently selected mesoplot where they searched for prey on the basis of characteristics of the microplot scale, i.e., where they pounced on prey.

3.2 INTRODUCTION

Habitat selection in birds is influenced by decisions and processes operating at multiple spatial and temporal scales. There is an inherent association between scales, with factors influencing habitat selection at large spatial scales taking place over long periods of time while decisions influencing selection at small spatial scales occurring over short periods of time (George and Zack 2001). For example, birds select foraging microhabitat on the basis of minute-by-minute behavioural decisions, which are influenced by many factors, such as the predominant foraging technique of the species, the selection of favourable microhabitats in which to search, and the detectability of invertebrate prey (Hutto 1990). Importantly, foraging microhabitat selection also alters seasonally (e.g., Cousin 2004b), primarily in response to changes in weather (Grubb 1975, 1978), and the flow-on effect of weather on the abundance and activity of prey (Lloyd 1963; Burgess *et al.* 1999; Kai and Corlett 2002). Understanding these seasonal influences is thus important in fully understanding ecological associations and foraging requirements (Hejl and Verner 1990).

In ground-foraging birds, such as the Australo-Papuan Robins (Petroicidae), foraging microhabitat selection is influenced by the composition of the ground substrate in the foraging site (Laven and Mac Nally 1998; Recher *et al.* 2002;

Cousin 2004b; Antos and Bennett 2006), although the vegetation structure surrounding the foraging site also plays an important role. Apart from the potential of foraging microhabitat representing a proximate cue reflecting invertebrate abundance (e.g., elevated abundance of prey associated with specific habitat attributes), these 'sit and wait' or 'ground-pouncing' robins (see Recher *et al.* 1985 for definition) also select foraging microhabitat with appropriate perches from which to launch their pounces onto the ground (see Cousin 2003; Antos and Bennett 2006). The selection of foraging microhabitat is thus influenced by structural attributes (such as perches) that maximise detectability of ground active (epigeic) invertebrate prey. Furthermore, selection is also governed by an avoidance of structural attributes reducing predator detection (Whittingham and Evans 2004; Jones *et al.* 2006).

While one can demonstrate the factors leading to foraging microhabitat selection, the ordered sequence of decisions leading to the selection of foraging microhabitat is not normally assessed. For example, does a ground-foraging bird select foraging microhabitat based on proximate habitat cues reflecting elevated invertebrate abundance, followed by opportunistic detection of prey within the selected microhabitat? This selection would represent a top-down approach with coarser spatial scale selection constraining finer spatial scale selection (see Kristan 2006). Or is the selection of foraging microhabitat determined by attributes merely enhancing the detectability of potential invertebrate prey at the pounce site scale? This form of selection suggests a 'bottom-up' approach, with coarser spatial scale selection constrained by finer spatial scale selection (see Kelly 1993; Kristan 2006). These questions reflect the growing importance of the recognition of scale and hierarchy in the

processes governing habitat selection (Schneider 2001). These questions reflect the need, not only for studies examining habitat selection at multiple spatial and temporal scales, but also to evaluate whether habitat choices at one scale are constrained by, or themselves constrain choices at other scales.

In the present study, I quantified foraging microhabitat selection at two spatial and two temporal scales in the Eastern Yellow Robin (*Eopsaltria australis*). As little research had been undertaken on specific foraging microhabitat selection of this species, I aimed to evaluate what habitat attributes influenced this selection. Furthermore, I also evaluated whether habitat choices at one scale were constrained or related to choices at other scales, thus evaluating whether selection across spatial scales operates in a 'top-down' or 'bottom-up' fashion.

3.3 METHODS

3.3.1 Study area

Study sites were located in remnant woodland and forested tracts on the New England Tablelands (30° 30' S, 151° 36' E) in a 70 km x 20 km area surrounding Armidale, New South Wales, Australia. The study area straddles the Great Dividing Range, with sites ranging from 730 m – 1,250 m above sea level. The vegetation of the study area varies in its species composition and degree of fragmentation, especially along its 70 km east-west axis. To the east of the Great Dividing Range, the vegetation is dominated by Eucalypt woodland, with New England Stringybark (*Eucalyptus caliginosa*) the dominant woodland tree species. Vegetation to the west of the range is dominated by 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*). The midstorey and understorey vegetation is varied throughout the study area and is dominated by *Acacia* spp. (Mimosaceae), *Cassinia* spp. (Asteraceae) and *Bursaria* spp. (Pittosporaceae). 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 extent of clearing however varies in its intensity, being more severe immediately surrounding and to the east of Armidale than to the west and north of Armidale, where the vegetation is less fragmented and more connected (see Figure 3.1), although the remaining vegetation throughout the whole region is strictly variegated (McIntyre and Barrett 1992).

The study area is characterised by a cool temperate climate, with the majority of rain falling in summer months. Winters are cold, dry and frosty, with occasional snowfalls. Annual rainfall averages 788 mm in Armidale, although varies across the study area according to local elevation and topographical changes.
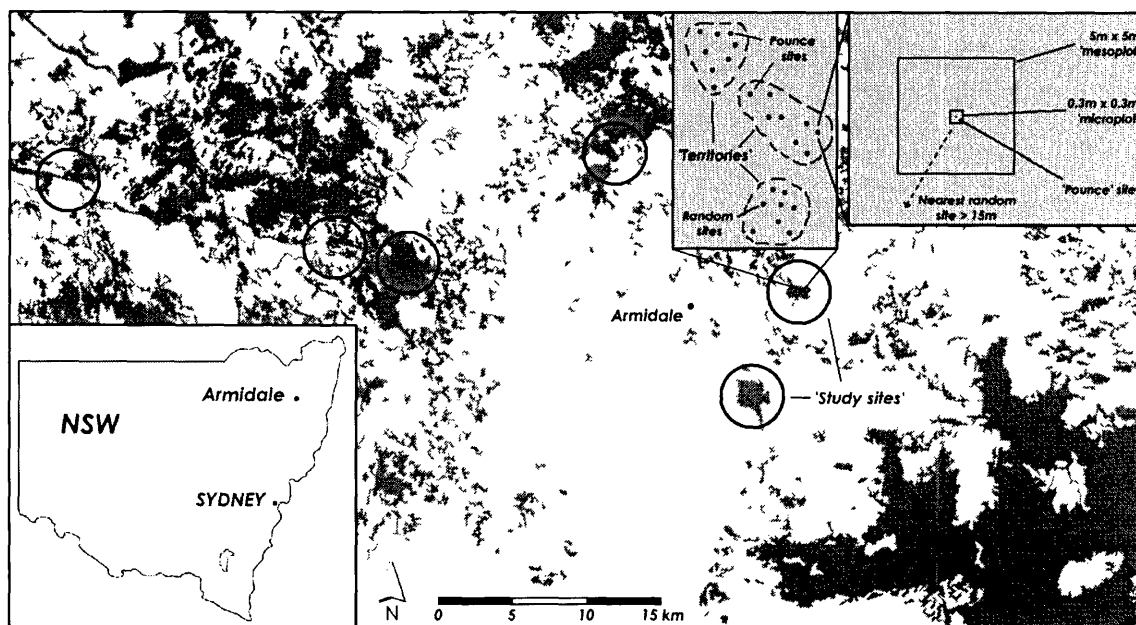
Figure 3.1 Location of the study area and the organisational (hierarchical) structure of the 'territories' within 'study sites' and the 'pounce/random' sites within 'territories'. Grey areas in main map denote wooded areas, with white areas denoting cleared areas.

3.3.2 Study species

The Eastern Yellow Robin (*Eopsaltria australis*) is a medium sized (20 g) Australo-Papuan robin belonging to the Petroicidae family (Higgins and Peter 2002). The species is found throughout the east coast of Australia, ranging from southeast South Australia to Cooktown in northern Queensland. Throughout its range, the Eastern Yellow Robin is found in a variety of habitats from eucalypt forests and woodlands to subtropical and temperate rainforest, with a preference throughout these habitats for a dense understorey (Higgins and Peter 2002). The Eastern Yellow Robin is predominantly a ground-pouncing bird, employing a sit and wait strategy from an elevated perch before pouncing onto the ground to capture prey (Recher and Holmes 1985; Ford *et al.* 1986; Holmes and Recher 1986b; Zanette *et al.* 2000). The Eastern Yellow Robin has shown a marked decline in distribution and abundance in many areas, especially in the woodlands of the wheat-sheep belt of NSW (Barrett *et al.* 1994;

Reid 1999). Previous research has suggested the area-sensitivity of the Eastern Yellow Robin in fragmented woodland, and is a response to reduced availability and poor quality of food, as well as reduced breeding success in small remnant patches of woodland (Doyle 1996; Zanette 2000; Zanette *et al.* 2000). The ground substrate is that part of the ecosystem that is most affected by the many effects of landuse such overgrazing, fire, weed invasion, firewood removal and altered microclimate (Hobbs 1993; Matlack 1993). As these robins rely on the ground substrate for foraging, it is imperative to understand the elements of ground microhabitat that the Eastern Yellow Robin selects.

3.3.3 Seasonal sampling

During winter 2004, I assessed foraging microhabitat selection in ten robin territories. This procedure was repeated in spring of 2004, although not all of the territories in this season were the same as those of winter. I undertook sampling in winter (24th May and 27th August 2004) and spring (24th September and 29th November 2004) to determine if there were any seasonal changes to foraging microhabitat selection of the robin. Winter and spring were chosen as seasons to examine this potential seasonal change, as they represented two contrasting seasons with different extremes in foraging pressures. Winter in the New England Tablelands is cold, with minimum temperatures regularly dipping below -5°C and maximum temperatures averaging 13°C, although sometimes as low as 6°C. One would thus expect that along with behavioural and physiological responses to winter climatic stresses, birds would also select foraging microhabitat in which their foraging is efficient; a process governed by proximate cues (such as habitat structure) in the surrounding environment (Smith and Shugart 1987; Bergin 1992). During spring, even though there is

usually an increase in invertebrate abundance (especially arboreal and aerial invertebrates, Ford *et al.* 1990), additional food is required to feed their young. As such, one would again expect birds to forage in microhabitats that increase their foraging efficiency.

Weather during the sampling period

The average daily maximum temperature during the winter 2004 data collection period was $13.9 \pm 0.3°C$ (mean $\pm$ S.E; range $5.5°C - 19.8°C$) and the average daily minimum temperature was $-1.0 \pm 0.5°C$ ($-9.3°C - 12.4°C$). The average daily maximum temperature during spring 2004 was $22.1 \pm 0.5°C$ ($13.8°C - 31.9°C$) and the average daily minimum temperature was $7.4 \pm 0.5°C$ ($-1.3°C - 17.2°C$). Rainfall during the winter 2004 data collection period totalled 102.2 mm. Rainfall during the spring 2004 data collection period totalled 188.6 mm, which included a six day period between 18th October and 23rd October when 103.2 mm of rain fell.

3.3.4 Foraging site sampling

At each territory, as soon as a robin was located, I waited at least 60 seconds before recording any foraging behaviour data, to reduce the potential of recording foraging behaviour in conspicuous locations disproportionally (Kleintjes and Dahlsten 1995), as well as reducing the influence of my presence. Collection of foraging data involved locating the exact location of ground-pounces. Pouncing was defined in this study as a robin flying down from a perch to take a prey organism from the ground (including leaf litter, ground vegetation, bare ground and occasionally logs), before returning to a perch (modified definition of Recher *et al.* 1985). Even though a pounce usually

resulted in the successful acquisition of prey, I made no assessment of foraging success, as the aim of the study was to assess foraging microhabitat site selection. Following collection of relevant data from a pounce site, I relocated the robin within the territory, and repeated the process until data from four pounces had been collected. I often took some time to relocate robins as they are quiet and subdued. Call playbacks were not used in the present study as I aimed to assess the selection of ground-pouncing sites while evoking minimal influence and playback could have influenced location of search areas. As robins were often located over 100 m from previous pounce sites, subsequent records were reasoned to be independent. To reduce the influence of aberrant foraging behaviours brought on by inclement weather, no data were collected on days with rain or strong winds.

'Microplot' site selection

Assessment of foraging microplot selection followed similar methodology to Cousin (2004b). Once a robin pounced, I assessed the ground substrate composition in a 0.3 m x 0.3 m 'microplot' directly surrounding the pounce site. The specific dimension of the microplot was used as any detected terrestrial prey would not likely have traversed further than 150 mm from the time and point of prey detection by the robin to prey acquisition. Within the microplot, I recorded the percentage composition of leaf litter, plant material, bare ground and log. Leaf litter included all bark, sticks and leaves, plant material included any grassy and herbaceous vegetation, bare ground included any area comprising of rock or sand, and logs were any dead fallen timber with a diameter larger than 50 mm and length larger than 800 mm. To ascertain which microplot variables were selected at pounce sites, I compared the ground

substrate composition at pounce sites to random microplot sites within the territory. Constraining the location of random microplot sites to within the territory is a more accurate method of determining selection, as it represents a true measure of availability (Jones 2001). At each pounce site, a single random microplot site was located between 15 m and 30 m away in a random direction according to a random number (between 15 and 30) and compass direction (eight cardinal directions) table. I collected data in the same way at random microplot sites as I had at pounce microplot sites.

'Mesoplot' site selection

To incorporate more of the vegetational structure surrounding the pounce site into an analysis of foraging microhabitat selection, I recorded structural elements in a 5 m x 5 m 'mesoplot'. This scale of assessment was chosen because the average distance from perch to prey of pouncing robins is generally within three metres (Recher *et al.* 2002). This scale was also chosen as the usual 0.04 ha scale so common in the literature often incorporates too much of the surrounding heterogeneity of the habitat (Beck and George 2000), thus masking the microhabitat elements important for foraging. Please note that any mention of 'microhabitat' collectively refers to the elements of both the 'microplot' and 'mesoplot'. Twelve habitat variables were initially measured within the mesoplot, including the distance from the pounce site to the nearest tree (> 1 m high), shrub (> 0.3 m high and 0.3 m wide) and log (diameter >50 mm and length larger than 800 mm). The number of sapling trees (1 m – 5 m), subcanopy trees (5 m – 10 m) and canopy trees (>10 m) were also counted within the mesoplot. Canopy cover was calculated as the percentage of points (from 25 points radiating out from the centre of the mesoplot) at which tree

canopy intersected cross-hairs as viewed through the end of a 30 cm vertically held ocular tube (Morrison *et al.* 1998). The percentage cover of shrubs, plant material (herbaceous vegetation < 0.3 m and grass) and bare ground within the mesoplot was estimated. Finally, I recorded an index of leaf litter (estimated as one of nine indices of abundance between sparse and dense, Cousin 2004a) and log abundance (estimated as one of five indices between absent and abundant). Just as with microplot assessment, I compared foraging mesoplot sites and random mesoplot sites within the territory, collecting data at the random mesoplot sites in the same way as at pounce mesoplot sites. The random mesoplot sites were centered on the location of the random microplot sites (see Figure 3.1).

3.3.5 Invertebrate sampling

I sampled invertebrates to determine whether selection for foraging microhabitat was tied to invertebrate biomass. Eastern Yellow Robins are primarily sit and wait predators, so the majority of prey consumed is represented by epigeic invertebrates that they detect and subsequently pounce onto from an elevated perch. As a result, I utilised pitfall trapping as the method to record invertebrate abundance. While a number of studies indicate the limited value of pitfall trapping for assessing invertebrate community composition (Greenslade 1964), others suggest their applicability and reliability in studies aimed at assessing the abundance of epigeic invertebrates (Fichter 1941; Williams 1959; Pik *et al.* 1999; Magagula 2003), such as the present study. Following collection of all microplot and mesoplot data, I buried a 90 mm PVC sleeve 130 mm into the ground at the exact locations of the pounce sites and at the random sites. Seven days later, I placed a 425 ml (90 mm x 110 mm) cup within the PVC

sleeves, such that the lip of the cup was flush with the ground. Approximately 100 ml of anti-freeze (30% ethylene glycol) was poured into the cup, which acted as a collecting fluid and preservative. A couple of drops of household detergent were also added to the fluid to function as a surfactant. Traps were not set until seven days after the initial digging in of the PVC sleeve, in order to alleviate the impact of any 'settling-in' disturbance to the leaf litter and soil fauna (Abbott *et al.* 1984).

Pitfalls were left set for 14 days, after which I collected their contents and stored them in 70% ethanol. All trapped invertebrates larger than 4 mm were then counted and sorted to ordinal level. The only exception to this sorting protocol was the separation of the Formicidae family from the rest of the Hymenoptera order (herein, Formicidae is referred to as order for ease of explanation), as well as the separation of all larvae into their own group. While Eastern Yellow Robins have been recorded consuming a large diversity of invertebrates, only the four main epigeic invertebrate dietary orders (based on personal observations and those presented in Ford 1985) collected in this study were further assessed; namely the Formicidae, Araneae, Hemiptera and Coleoptera.

3.3.6 Variable reduction

The microplot and mesoplot variables were initially reduced in number following a combination of correlation analysis and Principal Component Analysis (PCA). Of the four microplot variables, bare ground was omitted as it was dominated by zero values. The percentage cover of leaf litter and plant material in the microplot was significantly negatively correlated ($r = -0.844$, $df = 159$, $p < 0.001$), so these variables were replaced with a new composite variable (denoted as

'litter substrate') computed as principal component scores from a PCA. Larger values of the new litter substrate variable indicated a high percentage cover of leaf litter and an associated lower percentage cover of plant material. As analysis of foraging microhabitat selection was undertaken separately for both seasons, the values of the new 'litter substrate' microplot variable were computed by PCAs undertaken on each seasons' microplot data. The percent total variance explained by the new composite substrate variable in winter and spring equated to 91.8% and 92.5% respectively.

For mesoplot variable reduction, when two variables were significantly correlated with each other, I retained the more ecologically meaningful variable for further analysis. Thus, the distance to shrub and distance to log variables were omitted as they were significantly correlated with percentage cover of shrubs (% shrub; $r = -0.427$, $df = 158$, $p < 0.001$) and index of log abundance ($r = -0.433$, $df = 158$, $p < 0.001$) respectively. Just as in the microplot variable reduction, the percentage bare ground variable was omitted as it was dominated by zero values and was weakly correlated with a number of other disparate variables. Because there was a positive correlation between the number of sapling trees and number of subcanopy trees variables ($r = 0.277$, $df = 158$, $p < 0.001$), these variables were combined into a single variable, the number of sapling and subcanopy trees. As a result of the close association of six of the mesoplot variables (distance to tree, number of canopy trees, canopy cover, % plant, leaf litter and logs), as determined by correlation analysis and grouping in preliminary PCAs, these variables were grouped into a single composite variable denoted as 'woodiness'. With the new 'woodiness' variable, larger values represent denser woodland with a denser canopy, denser leaf

litter, less plant material on the ground, and more logs. Lower values represent more open woodland with sparser leaf litter, more plant material on the ground, a less dense canopy and fewer logs. As with the computation of the microplot substrate variable values, the values of the new 'woodiness' mesoplot variable were computed by PCAs undertaken on each seasons' mesoplot data. The percent total variance explained by the new composite woodiness variable in winter and spring equated to 47.9% and 44.1% respectively.

3.3.7 Analysis

The habitat elements influencing foraging microhabitat selection of robins as well as the association of invertebrate abundance with pounce sites was analysed 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 designed to analyse nested or hierarchically structured data (Raudenbush and Bryk 2002). Hierarchical structure is widespread in many ecological investigations, 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, pounce and random sites sampled from a given territory will tend to be more homogeneous than pounce and random sites sampled randomly from all study sites across the landscape. As foraging microhabitat from a given territory shares similar site-specific characteristics (e.g., topography, species assemblages, biotic effects), these sampled microhabitats 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. In the present study, the data was structured at three hierarchical levels; pounce and random sites within territories within study sites (see Figure 3.1). As such a 3-level hierarchical linear modelling approach was attempted on the data. Specifically, due to the binary response variable (pounce or random), a hierarchical generalised linear modelling (HGLM) procedure was undertaken, 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 analysis of the data, it was shown that structuring the data at the third level (study sites) and even the second level (territory) was ineffective, as determined by the results of a variance component test in HLM6. This pattern of no hierarchical structure was observed in the foraging microplot, foraging mesoplot and invertebrate association components of this study, so I undertook all analyses using binary logistic regression analysis. Testing for hierarchical structure is a necessary and important step before undertaking analysis based on non-hierarchical structured data using analyses such as linear and logistic regression.

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:

$$\Delta_i = AIC_i - minAIC$$

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).

3.4 RESULTS

3.4.1 Microplot selection

At the microplot scale, during winter and spring, robins pounced in areas with higher percentage composition of leaf litter and logs than random sites within the territory (Figure 3.2).
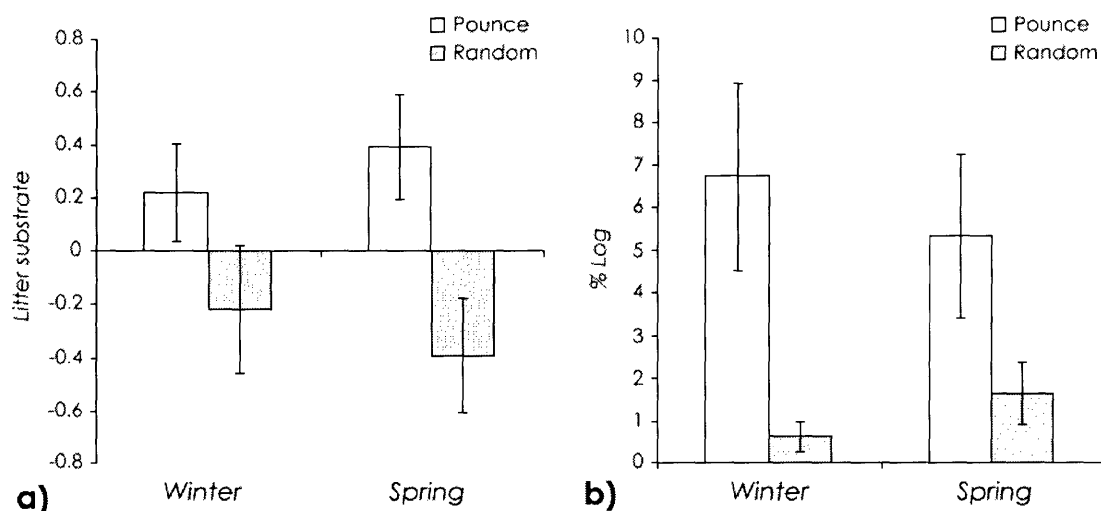
Figure 3.2 a) the average litter substrate composition (see section 3.3.6) and b) the average percentage composition of logs in pounce and random microplots in winter and spring. All graphs show the average ± standard error.

The results of logistic regression modelling indicate that the univariate model with percentage composition of logs was the best model describing microplot scale selection of robins in winter, with pounce sites exhibiting a higher percentage composition of logs than random sites (see Table 3.1). In addition, a nearly equally weighted bivariate model (Akaike weight of 0.4767 compared to 0.5180 for the univariate log model) including litter substrate and logs was also produced. Examination of the regression coefficient confidence intervals indicates that the univariate log model had strong explanatory power on account of the confidence intervals not including zero. Furthermore, only the percentage composition of logs in the bivariate model had any explanatory power, with the confidence interval for the litter substrate including zero.

During spring, the bivariate model with litter substrate and logs was the best model describing microplot scale selection by robins, with pounce sites exhibiting a greater index of litter substrate and percentage composition of logs

than random sites. Although of considerably less Akaike weight, the univariate litter substrate model also described microplot scale selection. In contrast to winter, examination of the regression coefficient confidence intervals indicates that only the litter substrate variable had any strong explanatory power; both in the bivariate model and the univariate model.

Table 3.1 Results of logistic regression analysis for variables influencing microplot selection surrounding Eastern Yellow Robin pounce sites in winter and spring of 2004.

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. † = Coefficients for which the 95% confidence interval does not include zero.

Response variable	Predictor variable(s)	ΔAIC_c	Akaike weight	Model variable(s)	Coefficient	Std err	Confidence interval
Winter microplot	Log	0	0.5180	Log	0.173	0.076	0.0240, 0.3220†
	Litter substrate + Log	0.1659	0.4767	Litter substrate	0.207	0.178	-0.1419, 0.5559
				Log	0.168	0.077	0.0171, 0.3189†
Spring microplot	Litter substrate + Log	0	0.5647	Litter substrate	0.437	0.180	0.0842, 0.7898†
				Log	0.054	0.038	-0.0205, 0.1285
	Litter substrate	0.8761	0.3644	Litter substrate	0.454	0.179	0.1032, 0.8048†

Examination of the multi-model inference procedure for the two predictor variables reflects the results of the logistic regression modelling, and indicates the importance of each microplot variable in different seasons (Table 3.2).

Table 3.2 Multi-model inference weight of evidence for predictor variables contributing to microplot response variable models for winter and spring.

	Weight of evidence	
Predictor	*Winter*	*Spring*
Litter substrate	0.4820	0.9290
Log	0.9947	0.6356

During winter, the percentage composition of logs explained almost all of the difference in microplot composition between pounce and random sites. During spring, it was litter substrate that contributed almost all of the difference in microplot composition between pounce and random sites. In both seasons however, the importance of the second predictor variable was still quite high, with the percentage composition of log in spring contributing a weighting of 0.6356.

3.4.2 Mesoplot selection

At the mesoplot scale, robins pounced in areas with a higher degree of woodiness in both seasons, although the number of sapling and subcanopy trees was also higher in pounce sites in winter (Figure 3.3).
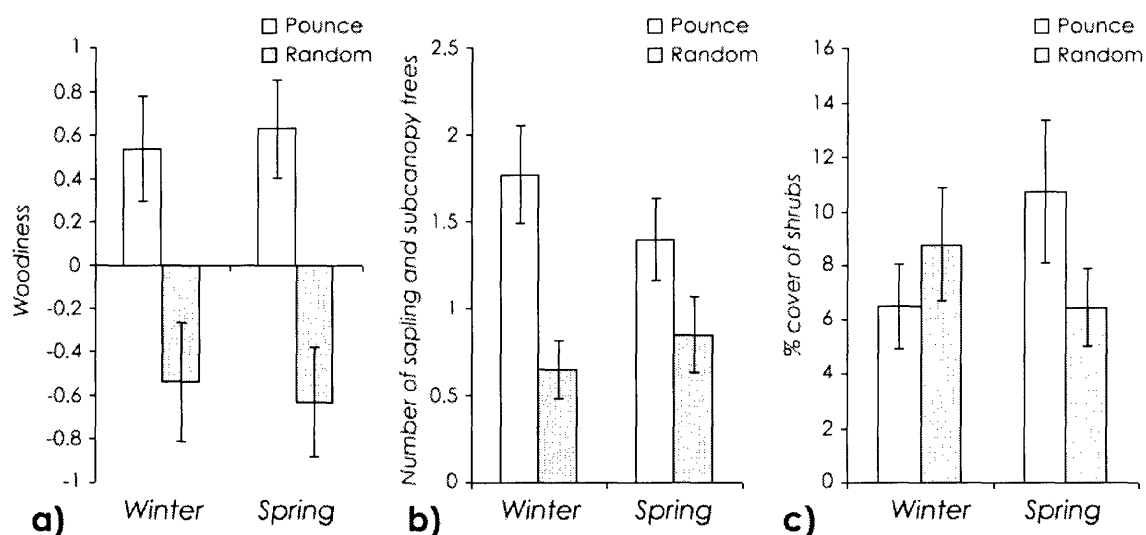
Figure 3.3 a) the average degree of woodiness, b) the number of sapling and subcanopy trees and c) the percentage cover of shrubs in pounce and random mesoplots in winter and spring. All graphs show mean ± std. err.

The results of the logistic regression modelling indicate that during winter, the bivariate model incorporating woodiness and number of sapling and subcanopy trees was best at describing mesoplot scale selection of robins, with mesohabitat surrounding pounce sites exhibiting a higher degree of woodiness and a higher density of sapling and subcanopy trees than random sites (Table 3.3). This bivariate model had strong explanatory power on account of the regression coefficient confidence intervals for both variables not including zero.

During spring, the pattern of mesoplot scale selection was more complicated, with four models selected. The univariate model with degree of woodiness was the highest weighted model (Akaike weight = 0.3343), with two bivariate models incorporating woodiness and percentage cover of shrubs, and woodiness and the number of sapling and subcanopy trees respectively. The Akaike weight of the former bivariate model (0.3158) was higher than the latter (0.1791). Finally, a trivariate model incorporating woodiness, number of sapling and subcanopy trees and the percentage cover of shrubs was selected. All models indicated

that the mesoplot habitat variables were positively associated with pounce sites, with pounce sites having a higher degree of woodiness, and a higher density of shrubs and sapling and subcanopy trees. Examination of the regression coefficient confidence intervals however, indicates that only the degree of woodiness had any explanatory power in all of the models, with confidence intervals not including zero (see Table 3.3).

Table 3.3 Results of logistic regression analysis for variables influencing mesoplot selection surrounding Eastern Yellow Robin pounce sites in winter and spring of 2004.

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. Woodiness = index of woodiness in mesoplot, Sap sub = number of sapling and subcanopy trees in mesoplot, Shrub = percentage cover of shrubs in mesoplot. [†] = Coefficients for which the 95% confidence interval does not include zero.

Response variable	Predictor variable(s)	ΔAIC_c	Akaike weight	Model variable(s)	Coefficient	Std err	Confidence interval
Winter mesoplot	Woodiness + Sap sub	0	0.5596	Woodiness	0.340	0.162	0.0225, 0.6575[†]
				Sap sub	0.484	0.191	0.1096, 0.8584[†]
Spring mesoplot	Woodiness	0	0.3343	Woodiness	0.577	0.180	0.2242, 0.9298[†]
	Woodiness + Shrub	0.1139	0.3158	Woodiness	0.589	0.185	0.2264, 0.9516[†]
				Shrub	0.029	0.021	-0.0122, 0.0702
	Woodiness + Sap sub	1.2479	0.1791	Woodiness	0.547	0.182	0.1903, 0.9037[†]
				Sap sub	0.169	0.180	-0.1838, 0.5218
	Woodiness + Sap sub + Shrub	1.4035	0.1657	Woodiness	0.565	0.188	0.1965, 0.9335[†]
				Sap sub	0.170	0.179	-0.1808, 0.5208
				Shrub	0.029	0.022	-0.0141, 0.0721

Examination of the multi-model inference procedure for the three predictor variables indicates a shift in weight of evidence between seasons from the number of sapling and subcanopy trees to woodiness (Table 3.4)

Table 3.4 Multi-model inference weight of evidence for predictor variables contributing to mesoplot response variable models for winter and spring.

Woodiness = index of woodiness in mesoplot, Sap sub = number of sapling and subcanopy trees in mesoplot, Shrub = percentage cover of shrubs in mesoplot.

	Weight of evidence	
Predictor	*Winter*	*Spring*
Woodiness	0.7914	0.9940
Sap sub	0.9567	0.3449
Shrub	0.2591	0.2519

During winter, the density of sapling and subcanopy trees explained almost all of the difference in mesoplot composition between pounce and random sites, with the degree of woodiness also showing a comparatively high weighting (Table 3.4). In contrast, during spring, the degree of woodiness was the dominant variable explaining differences in mesoplot selection at pounce and random sites, with the other two variables not contributing much to the difference. The percentage cover of shrubs was equally lowly weighted in both seasons, indicating its lack of importance in selection of foraging mesohabitat.

3.4.3 Invertebrate association

A total of 6,608 invertebrates from the Formicidae, Araneae, Hemiptera and Coleoptera orders were trapped and sorted from both seasons; 770 in winter and 5,318 in spring. The average abundance of all invertebrate orders per trap was higher in spring than winter (Figure 3.4).
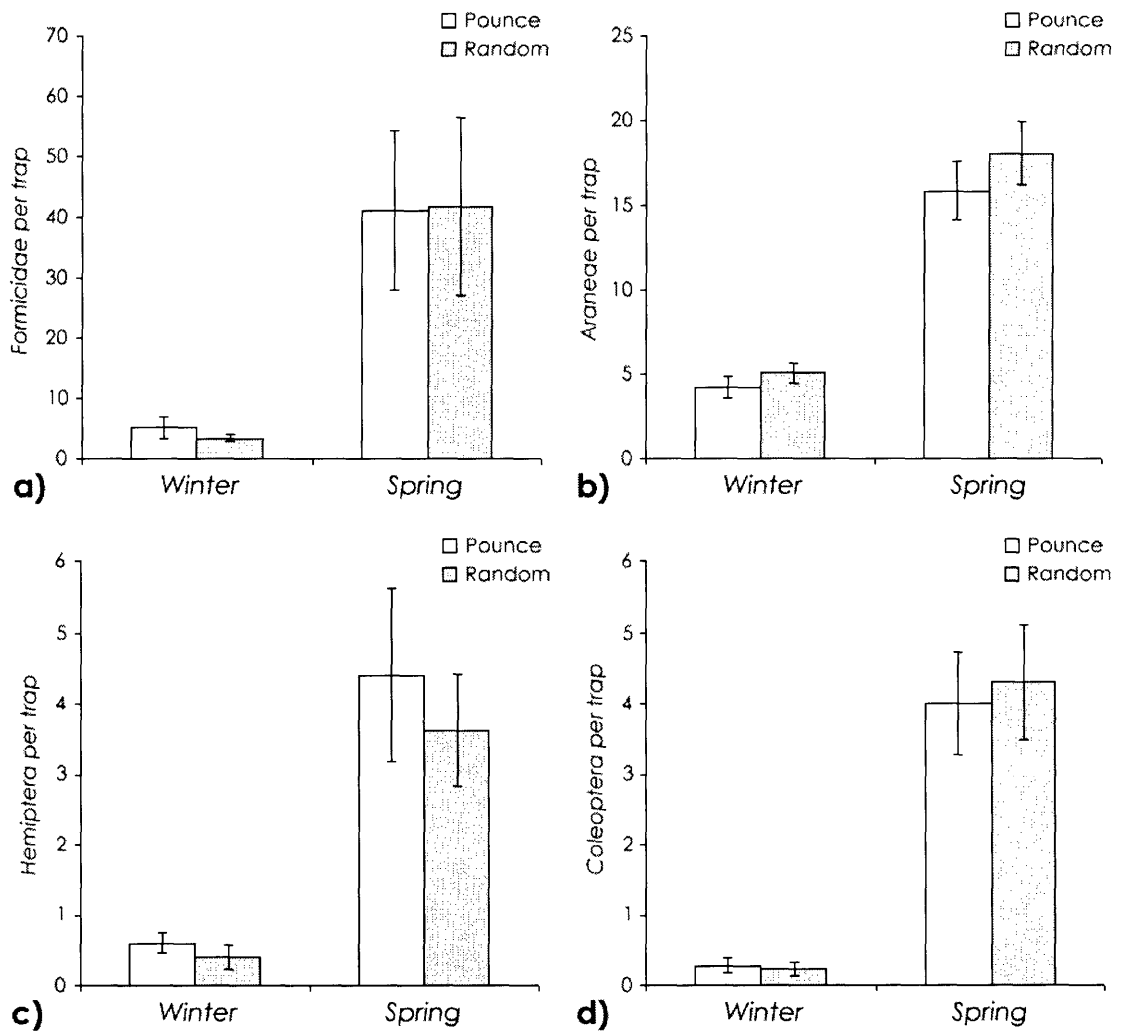
Figure 3.4 The average abundance of a) Formicidae, b) Araneae c) Hemiptera and d) Coleoptera at pounce sites and random sites in winter and spring. All graphs show mean ± std. err.

The results of the logistic regression modelling indicate that during winter, the univariate model incorporating Araneae abundance was best at distinguishing pounce sites from random sites, with fewer Araneae trapped at pounce sites than at random sites, although the Akaike weight for this was low (0.1416). Three univariate invertebrate models and bivariate models were also selected although the Akaike weights for all of these models were low (ranging from 0.0703 to 0.1368). None of the models had any strong explanatory power on

account of their regression coefficient confidence intervals all including zero. During spring, the results were similar, with the abundance of Araneae best distinguishing pounce site invertebrate abundance from random sites. Similarly, three univariate models (in a different order of weighting from winter), and a bivariate model were selected, all with low Akaike weights. Like the winter logistic regression modelling, none of the spring models had strong explanatory power, with all model predictor variable regression coefficient confidence intervals including zero (Table 3.5).

Table 3.5 Results of logistic regression analysis for invertebrate orders associated with Eastern Yellow Robin pounce sites in winter and spring of 2004. 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. [†] = Coefficients for which the 95% confidence interval does not include zero.

Response variable	Predictor variable(s)	ΔAIC_c	Akaike weight	Model variable(s)	Coefficient	Std err	Confidence interval
Winter invertebrates	Araneae	0	0.1416	Araneae	-0.059	0.060	-0.1766, 0.0586
	Formicidae	0.0700	0.1368	Formicidae	0.030	0.035	-0.0386, 0.0986
	Hemiptera	0.1600	0.1308	Hemiptera	0.215	0.243	-0.2613, 0.6913
	Coleoptera	0.8620	0.0921	Coleoptera	0.139	0.375	-0.5960, 0.8740
	Formicidae + Hemiptera	1.2659	0.0752	Formicidae	0.032	0.036	-0.0386, 0.1026
				Hemiptera	0.230	0.243	-0.2463, 0.7063
	Araneae + Hemiptera	1.3199	0.0732	Araneae	-0.060	0.060	-0.1776, 0.0576
				Hemiptera	0.215	0.243	-0.2613, 0.6913
	Formicidae + Araneae	1.3999	0.0703	Formicidae	0.028	0.036	-0.0426, 0.0986
				Araneae	-0.054	0.060	-0.1716, 0.0636
Spring invertebrates	Araneae	0	0.1633	Araneae	-0.015	0.020	-0.0542, 0.0242
	Hemiptera	0.1520	0.1513	Hemiptera	0.022	0.036	-0.0486, 0.0926
	Coleoptera	0.5000	0.1271	Coleoptera	-0.009	0.047	-0.1011, 0.0831
	Formicidae	0.5320	0.1251	Formicidae	0	0.003	-0.0059, 0.0059
	Araneae + Hemiptera	1.4941	0.0773	Araneae	-0.019	0.021	-0.0602, 0.0222
				Hemiptera	0.030	0.038	-0.0445, 0.1045

Examination of the multi-model inference procedure for the four predictor variables indicates a lack of weight of evidence of all orders in winter (Table 3.6).

Table 3.6 Multi-model inference weight of evidence for predictor variables contributing to invertebrate order (and Formicidae family of the Hymenoptera order) abundance differences between pounce and random sites for winter and spring.

	Weight of evidence	
Predictor	*Winter*	*Spring*
Formicidae	0.5792	0.3791
Araneae	0.4348	0.2756
Hemiptera	0.4333	0.7857
Coleoptera	0.3347	0.4055

In spring, the multi-model inference procedure indicates the specific importance of Hemipteran abundance, with a reasonably high weighting of 0.7857. All other orders had low weights.

3.5 DISCUSSION

3.5.1 Foraging microhabitat selection

During winter, Eastern Yellow Robins pounced at the microplot scale in sites with a high percentage composition of logs. They foraged at the mesoplot scale in sites with a high density of sapling and subcanopy trees, as well as areas with a high degree of woodiness: reflecting the importance of more leaf litter, less ground plant material, a denser canopy and more logs. During winter, the abundance of epigeic invertebrates was much lower than during spring (Figure 3.4). Robins possibly pounced near to logs because they provide a favourable microclimate for epigeic invertebrates, which are known to shelter in accumulations of leaf litter and microhabitats surrounding logs (Fager 1968; Taylor 1990; Lindenmayer *et al.* 2002). Hence, robins are more likely to detect

epigeic invertebrates near logs. At the mesoplot scale, robins may chose to forage in sites with a high density of sapling and subcanopy trees because they provide perches from which robins can scan the ground. Again, this choice may influence the likelihood of detecting epigeic invertebrates (see Chavez-Ramirez *et al.* 1994).

Robins also forage in sites with a high index of woodiness. Woody site have much leaf litter and many logs, both of which may contain more invertebrates. In addition, robins may detect invertebrates more easily in leaf litter than in dense herbaceous vegetation. Woody sites also have a dense canopy, which may maintain slightly higher temperatures on the ground in winter (Smith and Shugart 1987), allowing epigeic invertebrates to become active (Wachob 1996), and so that foraging robins are more likely to detect them. The importance of logs at the microplot scale is repeated at the mesoplot scale in the selection of woody sites. The composite woodiness variable has also been shown to be positively associated with an elevated abundance of some invertebrate orders (see Table 2.4 in Chapter 2), so selection for woodiness at the mesoplot scale may reflect the elevated abundance of invertebrates associated with this variable. However, I believe that detectability represents the primary factor governing selection of foraging microhabitat, with selection for sapling and subcanopy perches at the mesoplot scale in winter constrained by selection increasing detectability of epigeic invertebrates associated with logs at the microplot scale. The similarities in invertebrate community composition between pounce and random sites in winter supports the suggestion that selection of foraging sites is based more on microhabitat attributes increasing detectability rather than selection for specific invertebrate prey.

During spring, robins pounced at the microplot scale in sites with a high cover of leaf litter, with selection at the mesoplot for sites with a higher degree of woodiness. The shift in microplot selection from logs in winter to litter substrate in spring reflects the increased abundance of epigeic invertebrates in the leaf litter (see Figure 3.4), as influenced by the warmer spring conditions, reducing the affinity of invertebrates with logs. Although Eastern Yellow Robins are still predominantly ground-foraging in spring, they also forage in other habitat stratum (pers. obs.). This is due in part to an increase in the abundance of aerial and arboreal prey during spring compared to winter (Recher *et al.* 1983; Ford *et al.* 1990), and as a result, sapling and subcanopy selection becomes less important as hawking, snatching (see Recher *et al.* 1985 for definitions) and other foraging manoeuvres become more prevalent. Woodiness becomes the most important foraging mesohabitat variable and reflects the higher diversity and abundance of epigeic invertebrate prey associated with this composite variable (see Chapter 2), as well as the greater detectability associated with a higher cover of leaf litter and low density of shrubs. Again, the absence of a difference in invertebrate community composition between pounce and random sites suggests foraging site selection governed by selection of microhabitat attributes maximising the detectability of epigeic invertebrate prey, rather than selection for specific invertebrate prey.

3.5.2 Importance of recognising multiple spatial and temporal scales

Interestingly, in neither season was a high density of shrubs seen as an important mesohabitat variable. This result is surprising given that an elevated shrub density is an important structural attribute correlated with increased

breeding success of Eastern Yellow Robins (Debus 2006a). Furthermore, shrubs represent important attributes governing habitat selection of the Eastern Yellow Robin at larger spatial scales such as at the territory and landscape scales (see Chapter 5 and Debus 2006b). Results of the present study suggests there exists an important interaction between vegetation structure and foraging success (Robinson and Holmes 1982), with shrubs representing a hindrance to the detectability of epigeic invertebrates (see also Holmes and Recher 1986a; Robinson 1992; Bakermans and Rodewald 2006). A dense understorey structure may represent an important habitat attribute only at larger spatial scales such as at the territory scale influencing breeding success (Debus 2006a). This result emphasises the importance of examining habitat selection at multiple spatial and temporal scales, as habitat structural attributes play different roles and represent different degrees of importance at different spatial and temporal scales.

3.5.3 'Bottom-up' decisions influence habitat selection

Selection for structural attributes at the foraging mesoplot scale increasing the detectability of invertebrates at the microplot scale indicates the potential for finer spatial scale selection constraining coarser spatial scale selection. Habitat selection in birds is believed to be represented by a hierarchical process (George and Zack 2001; Battin and Lawler 2006), with processes governing selection at one spatial scale influencing those at other spatial scales (Cushman and McGarigal 2004). Traditionally, habitat selection studies are often limited in their spatial scope, focusing on management units operating at 'manageable scales' such as the landscape or territory scale. The problem with this approach is that it is often very limiting; assuming a 'top-down' hierarchical model of

habitat selection (e.g., Li *et al.* 2002; McLoughlin *et al.* 2002), focusing on species responses to large spatial scales (e.g., dispersal capabilities, remnant occupation, habitat associations based on coarse-scaled GIS mapping), while rejecting elements governing smaller spatial scale selection such as foraging microhabitat requirements. While such top-down habitat selection models best represent the hierarchical decisions facing a migratory species (i.e., firstly selecting a region in which to settle, followed by favourable vegetation type, and then an appropriate nesting and foraging site, George and Zack 2001), the majority of Australian woodland birds are resident and sedentary. Cushman and McGarigal (2004) state that the scale at which a species most strongly interacts with its environment corresponds to the spatial scale at which environmental variables affect it most. As a ground-foraging insectivore, the Eastern Yellow Robin interacts most strongly with the foraging microhabitat scale presented in the present study. As such, one could predict that habitat selection at coarser spatial scales may be influenced or constrained by selection operating at the foraging microhabitat scale.

The present study suggests that results from coarse-grained 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, and recognising the potential for a 'bottom-up' model governing hierarchical habitat selection.

3.6 REFERENCES

Abbott I, Van Heurck P, Wong L (1984) Responses to long-term fire exclusion: physical, chemical and faunal features of litter and soil in a Western Australian forest. *Australian Forestry* **47**, 237 - 242.

Antos MJ, Bennett AF (2006) Foraging ecology of ground-feeding woodland birds in temperate woodlands of southern Australia. *Emu* **106**, 29 - 40.

Bakermans MH, Rodewald AD (2006) Scale-dependent habitat use of Acadian Flycatcher (*Empidonax virescens*) in central Ohio. *The Auk* **123**, 368 - 382.

Barrett GW, Ford HA, Recher HF (1994) Conservation of woodland birds in a fragmented rural landscape. *Pacific Conservation Biology* **1**, 245 - 256.

Battin J, Lawler JJ (2006) Cross-scale correlations and the design and analysis of avian habitat selection studies. *The Condor* **108**, 59 - 70.

Beck MJ, George TL (2000) Song post and foraging site characteristics of breeding varied thrushes in northwestern California. *The Condor* **102**, 93 - 103.

Bergin TM (1992) Habitat selection by the Western Kingbird in western Nebraska: a hierarchical analysis. *The Condor* **94**, 903 - 911.

Burgess ND, Ponder KL, Goddard J (1999) Surface and leaf-litter arthropods in the coastal forests of Tanzania. *African Journal of Ecology* **37**, 355 - 365.

Burnham KP, Andersen DR (2001) Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* **28**, 111 - 119.

Burnham KP, Anderson DR (2002) 'Model selection and multimodel inference. A practical information-theoretic approach (second edn).' (Springer Science+Business Media, Inc: New York)

Chavez-Ramirez F, Gawlik DE, Prieto FG, Slack RD (1994) Effects of habitat structure on patch use by Loggerhead Shrikes wintering in a natural grassland. *The Condor* **96**, 228 - 231.

Cousin JA (2003) Foraging ecology and habitat selection of the Western Yellow Robin (*Eopsaltria griseogularis*) in a Wandoo woodland, Western Australia: conservation ecology of a declining species. MSc thesis, Edith Cowan University.

Cousin JA (2004a) Habitat selection of the Western Yellow Robin (*Eopsaltria griseogularis*) in a Wandoo woodland, Western Australia. *Emu* **104**, 229 - 234.

Cousin JA (2004b) Pounce site characteristics of the Western Yellow Robin *Eopsaltria griseogularis*: the importance of assessing foraging microhabitat. *Pacific Conservation Biology* **10**, 21 - 27.

Cushman SA, McGarigal K (2004) Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. *Ecological Applications* **14**, 1090 - 1105.

Debus SJS (2006a) Breeding and population parameters of robins in a woodland remnant in northern New South Wales, Australia. *Emu* **106**, 147 - 156.

Debus SJS (2006b) Breeding-habitat and nest-site characteristics of Scarlet Robins and Eastern Yellow Robins near Armidale, New South Wales. *Pacific Conservation Biology* **12**, 261 - 271.

Doyle P (1996) Habitat fragmentation and food availability: consequences for the Eastern Yellow Robin *Eopsaltria australis*. BSc (Hons) thesis, University of New England.

Fager EW (1968) The community of invertebrates in decaying old wood. *Journal of Animal Ecology* **37**, 121 - 142.

Fichter E (1941) Apparatus for the comparison of soil surface arthropod populations. *Ecology* **22**, 338 - 339.

Ford HA (1985) The bird community in eucalypt woodland and eucalypt dieback in the northern tablelands of New South Wales. In 'Birds of eucalypt forests and woodlands: Ecology, conservation, management'. (Eds A Keast, HF Recher, H Ford and D Saunders) pp. 333 - 340. (Royal Australasian Ornithologists Union and Surrey Beatty & Sons: Chipping Norton, NSW)

Ford HA, Huddy L, Bell H (1990) Seasonal changes in foraging behaviour of three passerines in Australian *Eucalyptus* woodland. *Studies in Avian Biology* **13**, 245 - 253.

Ford J, Noske S, Bridges L (1986) Foraging of birds in eucalypt woodland in north-eastern New South Wales. *Emu* **86**, 168 - 179.

George TL, Zack S (2001) Spatial and temporal considerations in restoring habitat for wildlife. *Restoration Ecology* **9**, 272 - 279.

Greenslade PJM (1964) Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* **33**.

Grubb TC (1975) Weather-dependent foraging behavior of some birds wintering in a deciduous woodland. *The Condor* **77**, 175 - 182.

Grubb TC (1978) Weather-dependent foraging rates of wintering woodland birds. *The Auk* **95**, 370 - 376.

Hejl SJ, Verner J (1990) Within-season and yearly variations in avian foraging locations. *Studies in Avian Biology* **13**, 202 - 209.

Higgins PJ, Peter JM (2002) 'Handbook of Australian, New Zealand and Antarctic Birds. Volume 6. Pardalotes to Shrike-thrushes.' (Oxford University Press: Melbourne)

Hobbs RJ (1993) Effects of landscape fragmentation on ecosystem processes in the Western Australian wheatbelt. *Biological Conservation* **64**, 193 - 201.

Holmes RT, Recher HF (1986a) Determinants of guild structure in forest bird communities: an intercontinental comparison. *The Condor* **88**, 427 - 439.

Holmes RT, Recher HF (1986b) Search tactics of insectivorous birds foraging in an Australian eucalypt forest. *The Auk* **103**, 515 - 530.

Hutto RL (1990) Measuring the availability of food resources. *Studies in Avian Biology* **13**, 20 - 28.

Jones J (2001) Habitat selection studies in avian ecology: a critical review. *The Auk* **118**, 557 - 562.

Jones KA, Krebs JR, Whittingham MJ (2006) Interaction between seed crypsis and habitat structure influence patch choice in a granivorous bird, the chaffinch *Fringilla coelebs*. *Journal of Avian Biology* **37**, 413 - 418.

Kai KH, Corlett RT (2002) Seasonality of forest invertebrates in Hong Kong, South China. *Journal of Tropical Ecology* **18**, 637 - 644.

Kelly JP (1993) The effect of nest predation on habitat selection by Dusky Flycatchers in limber pine-juniper woodland. *The Condor* **95**, 83 - 93.

Kleintjes PK, Dahlsten DL (1995) Within-season trends in the foraging behavior of the Mountain Chickadee. *Wilson Bulletin* **107**, 655 - 666.

Kristan WB (2006) Sources and expectations for hierarchical structure in bird-habitat associations. *The Condor* **108**, 5 - 12.

Laven NH, Mac Nally R (1998) Association of birds with fallen timber in box-ironbark forest of central Victoria. *Corella* **22**, 56 - 60.

Li X, Li D, Li Y, Ma Z, Zhai T (2002) Habitat evaluation for crested ibis: A GIS-based approach. *Ecological Research* **17**, 565 - 573.

Lindenmayer DB, Claridge AW, Gilmore AM, Michael D, Lindenmayer BD (2002) The ecological roles of logs in Australian forests and the potential impacts of harvesting intensification on log-using biota. *Pacific Conservation Biology* **8**, 121 - 140.

Lloyd M (1963) Numerical observations on movements of animals between beech litter and fallen branches. *Journal of Animal Ecology* **32**, 157 - 163.

Magagula CN (2003) Changes in carabid beetle diversity within a fragmented agricultural landscape. *African Journal of Ecology* **41**, 23 - 30.

Matlack GR (1993) Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* **66**, 185 - 194.

McIntyre S, Barrett GW (1992) Habitat variegation, an alternative to fragmentation. *Conservation Biology* **6**, 146 - 147.

McLoughlin PD, Case RL, Gau RJ, Cluff HD, Mulders R, Messier F (2002) Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia* **132**, 102 - 108.

Morrison ML, Marcot BG, Mannan RW (1998) 'Wildlife habitat relationships; concepts and applications.' (The University of Wisconsin Press: Madison, USA)

Pik AJ, Oliver I, Beattie AJ (1999) Taxonomic sufficiency in ecological studies of terrestrial invertebrates. *Australian Journal of Ecology* **24**, 555 - 562.

Raudenbush SW, Bryk AS (2002) 'Hierarchical linear models: applications and

data analysis methods.' (Sage Publications, Inc.: Thousand Oaks,

California)

Raudenbush SW, Bryk AS, Congdon R (2005) HLM for Windows (version 6.02)

[Computer software]. Scientific Software International, Inc., Lincolnwood,

IL.

Recher HF, Davis WE, Calver MC (2002) Comparative foraging ecology of five

species of ground-pouncing birds in western Australian woodlands with

comments on species decline. *Ornithological Science* **1**, 29 - 40.

Recher HF, Gowing G, Kavanagh R, Shields J, Rohan-Jones W (1983) Birds,

resources and time in a tablelands forest. *Proceedings of the Ecological

Society of Australia* **12**, 101 - 123.

Recher HF, Holmes RT (1985) Foraging ecology and seasonal patterns of

abundance in a forest avifauna. In 'Birds of Eucalypt Forests and

Woodlands: Ecology, Conservation, Management'. (Eds A Keast, HF

Recher, H Ford and D Saunders) pp. 79 - 96. (Royal Australasian

Ornithologists Union and Surrey Beatty & Sons: Chipping Norton, NSW)

Recher HF, Holmes RT, Schulz M, Shields J, Kavanagh R (1985) Foraging

patterns of breeding birds in eucalypt forest and woodland of

southeastern Australia. *Australian Journal of Ecology* **10**, 399 - 419.

Reid JW (1999) 'Threatened and declining birds in the New South Wales sheep-

wheat belt: diagnosis, characteristics and management.' Report to NSW

National Parks and Wildlife Service, Sydney.

Robinson D (1992) Habitat use and foraging behaviour of the Scarlet Robin and

the Flame Robin at a site of breeding-season sympatry. *Wildlife

Research* **19**, 377 - 395.

Robinson SK, Holmes RT (1982) Foraging behaviour of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology* **63**, 1918 - 1931.

Schneider DC (2001) The rise of the concept of scale in ecology. *Bioscience* **51**, 545 - 553.

Smith TM, Shugart HH (1987) Territory size variation in the Ovenbird: the role of habitat structure. *Ecology* **68**, 695 - 704.

Taylor RJ (1990) Occurrence of log-dwelling invertebrates in regeneration and old-growth wet sclerophyll forest in southern Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **124**, 27 - 34.

Wachob DG (1996) The effect of thermal microclimate on foraging site selection by wintering mountain chickadees. *The Condor* **98**, 114 - 122.

Whittingham MJ, Evans KL (2004) The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* **146 (supp ii)**, 210 - 220.

Williams G (1959) The seasonal and diurnal activity of the fauna sampled by pitfall traps in different habitats. *Journal of Animal Ecology* **28**, 1 - 13.

Zanette L (2000) Fragment size and the demography of an area-sensitive songbird. *Journal of Animal Ecology* **69**, 458 - 470.

Zanette L, Doyle P, Trémont SM (2000) Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* **81**, 1654 - 1666.

CHAPTER 4: FORAGING SITE SELECTION CONSTRAINS HABITAT SELECTION AT COARSER SPATIAL SCALES IN THE SCARLET ROBIN (Petroica multicolor).

4.1 ABSTRACT

Foraging microhabitat selection in birds is influenced by many factors such as risk of predation, habitat structure and food availability, which vary spatially and temporally. Given that habitat selection is assumed to operate in a hierarchical manner, foraging microhabitat selection has the potential to influence selection at coarser spatial scales, although this has rarely been studied in resident, sedentary species. The present study aimed to determine how the ground-foraging Scarlet Robin (Petroica multicolor) selects its microhabitat at two spatial scales (microplot, 0.3 m x 0.3 m; mesoplot, 5 m x 5 m) and two temporal scales (winter and spring), and whether selection constrains or is constrained by selection at other spatial scales. Robins selected sites with a high cover of leaf litter in winter, and selected sites with a sparse cover of shrubs at the mesoplot scale in spring, but selected microplot sites at random. While the number of epigeic invertebrates trapped during spring was greater than that during winter, there was no difference in invertebrate communities between foraging sites and random sites in either season. Robins select foraging microhabitat in which epigeic invertebrate prey are highly detectable in both seasons, though not necessarily more abundant. Scarlet Robins probably choose the location of their territories after choosing foraging sites that have a high cover of leaf litter, because they detect their prey most effectively at such sites. The present study therefore suggests the potential of finer spatial scale

selection (i.e., foraging site selection as governed by detectability of epigeic invertebrates) influencing selection at coarser spatial scales.

4.2 INTRODUCTION

Foraging microhabitat selection by birds, and factors leading to such selection is often difficult to evaluate, especially in highly mobile species that search for prey over large areas (e.g., raptors, see Wakeley 1978). In ground-foraging insectivores however, an accurate assessment can be made of foraging microhabitat selection, based on the knowledge of exact locations of foraging sites, and the microhabitat attributes associated with them. Habitat structure plays a critical role in foraging microhabitat selection of ground-foraging insectivorous birds, because it may reflect invertebrate abundance (e.g., elevated abundance of prey associated with specific habitat attributes), may hinder detectability of prey (e.g., dense shrub layer obscures view of ground), and may reduce predator detection and hence increase risk of predation (Whittingham and Evans 2004; Jones *et al.* 2006). Importantly, this role of habitat structure varies, for instance because the climate influences the abundance, location, activity and detectability of prey (Wolda 1990; Keane and Morrison 1999). Few researchers have studied the ordered sequence of decisions leading to the selection of foraging microhabitat. For example, does a ground-foraging bird select foraging microhabitat based on habitat cues that indicate that invertebrates are abundant, and then detect prey opportunistically within the selected microhabitat? Or is the selection of foraging microhabitat surrounding a foraging site merely a consequence of initial selection of the foraging microplot, as influenced by the detectability of invertebrate prey at the foraging site? These questions reflect the growing importance of the recognition

of scale, and hierarchy in the processes governing habitat selection (Schneider 2001).

Habitat selection in birds is generally assumed to be hierarchical in nature (George and Zack 2001; Jones 2001). If this assumption holds, one can assume that foraging microhabitat selection, being at the small end of the spatial scale spectrum, has the potential to either constrain coarser-scaled selection, or instead, be constrained by all coarser-scale selection. Cushman and McGarigal (2004) state that the scale at which a species most strongly interacts with its environment corresponds to the spatial scale at which environmental variables affect it most. For example, a migratory bird species may be expected to interact most strongly with coarse-scaled attributes, with initial selection of a favourable landscape or region, followed by the selection of a favourable territory scale site in which to settle constraining eventual selection at finer spatial scales for foraging microhabitat within that territory. Such a model of habitat selection is best described as a 'top-down' approach, with coarser spatial scale selection constraining that at finer spatial scales (Battin and Lawler 2006; Kristan 2006). However, for a non-migratory specialist ground-foraging insectivore, one would expect that the most important interaction scale would be represented by foraging microhabitat, with selection for coarser scales (e.g., territory or remnant occupation in fragmented landscapes) constrained by the availability of favourable foraging microhabitats. Such a model of habitat selection exemplified by foraging microhabitat scale influencing or constraining selection at coarser spatial scales, is best described as a 'bottom-up' model of habitat selection (Kristan 2006). Interestingly, while relatively few studies demonstrate more selectivity at smaller spatial scales or

'bottom-up' models of habitat selection (although see Kelly 1993; Sodhi *et al.* 1999), the literature abounds with examples of habitat selection models governed by a 'top-down' approach (e.g., McLoughlin *et al.* 2002). Management decisions are invariably formed on such 'top-down' models based on attributes operating at 'manageable scales' such as the regional or landscape scale, which are themselves not very objective or accurate (see comments in Li *et al.* 2002).

In the present study, I quantified foraging microhabitat selection at two spatial and two temporal scales in the Scarlet Robin (*Petroica multicolor*) to evaluate whether habitat choices at one scale are constrained or related to choices at other scales. As the species is sedentary and also a ground-foraging insectivore, I was particularly interested in evaluating whether selection across spatial scales operates in a 'top-down' or 'bottom-up' fashion.

4.3 METHODS

4.3.1 Study area

Study sites were located in remnant woodland and forested tracts on the New England Tablelands (30° 32' S, 151° 46' E) in a 35 km x 20 km area surrounding Armidale, New South Wales, Australia. The study area sits atop the eastern edge of the Great Dividing Range, with sites ranging from 1,000 m – 1,250 m above sea level. The vegetation of the study area varies in its species composition, with vegetation dominated by eucalypt woodland, with New England Stringybark (*Eucalyptus caliginosa*) the dominant woodland tree species. The midstorey and understorey vegetation varies throughout the study area and is dominated by *Acacia* spp. (Mimosaceae), *Cassinia* spp.

(Asteraceae) and *Bursaria* spp. (Pittosporaceae). 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). However, rather than a fragmented landscape typified by a 'isolated remnants in a sea of farmland', the remaining vegetation is referred to as variegated (McIntyre and Barrett 1992), characterised by a landscape represented by a mosaic of forest, open woodland and scattered trees (McIntyre and Barrett 1992; Bennett 1999).

The study area is characterised by a cool temperate climate, with the majority of rain falling in summer months. Winters are cold, dry and frosty, with occasional snowfalls. Annual rainfall averages 788 mm in Armidale, although it varies across the study area according to local elevation and topographical changes.
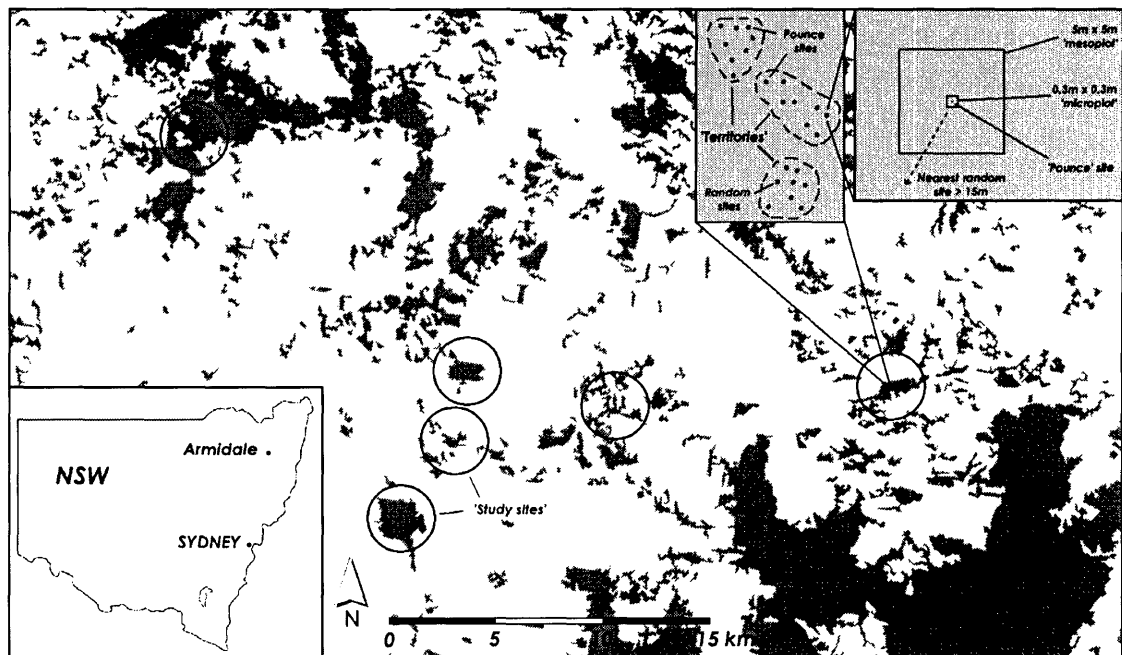

Figure 4.1 Location of the study area and the organisational (hierarchical) structure of the 'territories' within 'study sites' and the 'pounce/random' sites within 'territories'. Grey areas in main map denote wooded areas, with white areas denoting cleared areas.

4.3.2 Study species

The Scarlet Robin (*Petroica multicolor*) is a small (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, their 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 sheep-wheat belt of NSW, although the Scarlet Robin is not listed as one of the 20 declining species by Reid (1999), robins (Petroicidae) as a group, and ground-foragers as a foraging guild are over-represented as declining species. The ground ecosystem is most affected by numerous interrelated anthropogenic impacts such as overgrazing, fire, weed invasion, firewood removal and altered microclimate (Hobbs 1993; Matlack 1993). As robins rely on the ground as a foraging resource, we need to understand the elements of ground microhabitat that the Scarlet Robin selects.

4.3.3 Seasonal sampling

During winter 2004, I assessed foraging microhabitat selection in nine robin territories. This procedure was repeated in spring 2004, although not all of the

territories in this season were the same as those in winter. I undertook sampling in winter (24th May and 27th August 2004) and spring (24th September and 29th November 2004) to determine if Scarlet Robins changed their foraging microhabitat seasonally. Winter and spring were chosen as seasons to examine this potential seasonal change, as they represented two contrasting seasons with different extremes in foraging pressures. Winter in the New England Tablelands is characterised by cold conditions with minimum temperatures regularly dipping below -5°C and maximum temperatures averaging 13°C, although sometimes as low as 6°C. One would thus expect that along with behavioural and physiological responses to winter climatic stresses, there would also be selection for foraging microhabitat that increases foraging efficiency; a process governed by proximate cues (such as habitat structure) in the surrounding environment (Smith and Shugart 1987; Bergin 1992). During spring, even though there is usually an increase in invertebrate abundance (especially arboreal and aerial invertebrates, Ford *et al.* 1990), additional food is required to feed their young. As such, one would also expect selection for foraging microhabitat that increases foraging efficiency.

Weather during the sampling period

The average daily maximum temperature during the winter 2004 data collection period was 13.9 ± 0.3°C (mean ± S.E; range 5.5°C – 19.8°C) and the average daily minimum temperature was -1.0 ± 0.5°C (-9.3°C – 12.4°C). The average daily maximum temperature during spring 2004 was 22.1 ± 0.5°C (13.8°C – 31.9°C) and the average daily minimum temperature was 7.4 ± 0.5°C (-1.3°C – 17.2°C). Rainfall during the winter 2004 data collection period totalled 102.2 mm. Rainfall during the spring 2004 data collection period totalled 188.6 mm, which

included a six day period between 18th October and 23rd October when 103.2 mm of rain fell.

4.3.4 Foraging site sampling

At each territory, as soon as a robin was located, I allowed a minimum of 60 seconds to elapse before recording any foraging behaviour data to reduce the potential of recording foraging behaviour in conspicuous locations disproportionally (Kleintjes and Dahlsten 1995) as well as reducing the influence of my presence. Collection of foraging data involved locating the exact location of ground-pounces. Pouncing was defined in this study as a robin flying down from a perch to take a prey organism from the ground (including leaf litter, ground vegetation, bare ground and occasionally logs), before returning to a perch (modified definition of Recher *et al.* 1985). Even though a pounce usually resulted in the successful acquisition of prey, I made no assessment of foraging success, as the aim of the study was to assess foraging microhabitat site selection. Following collection of relevant data from a pounce site, I relocated the robin within the territory, and repeated the process until data from four pounces had been collected. Relocation of the robins often took some time on account of their quiet and subdued nature. Call playbacks were not used in the present study as I aimed to assess the selection of ground-pouncing sites while evoking minimal influence and playback would have influenced location of search areas. In addition, as robins were often located over 100 metres from previous pounce sites, subsequent records were reasoned to be independent. To reduce the influence of aberrant foraging behaviours brought on by inclement weather, no data were collected on days with rain or strong winds.

'Microplot' site selection

Assessment of foraging microplot selection followed similar methodology to Cousin (2004b). Once a Scarlet Robin pounced, I assessed the ground substrate composition in a 0.3 m x 0.3 m 'microplot' directly surrounding the pounce site. The specific dimension of the microplot was used as any detected terrestrial prey would not likely have traversed further than 150 mm from the time and point of prey detection by the robin to prey acquisition. Within the microplot, I recorded the percentage composition of leaf litter, plant material, bare ground and log. Leaf litter included all bark, sticks and leaves, plant material included any grassy and herbaceous vegetation, bare ground included any area comprising of rock or sand, and logs were any dead fallen timber with a diameter larger than 50 mm and longer than 800 mm. I compared microhabitat at pounce sites, and compared them with that at random microplot sites within the territory. Constraining the location of random microplot sites within the territory is a more accurate method of determining selection, as it represents a true measure of availability (Jones 2001). At each pounce site, a single random microplot site was located between 15 m and 30 m away in a random direction according to a random number (between 15 and 30) and compass direction (eight cardinal directions) table. I collected data in the same way at random microplot sites as I had at pounce microplot sites.

'Mesoplot' site selection

To incorporate more of the vegetational structure surrounding the pounce site into an analysis of foraging microhabitat selection, I recorded structural elements in a 5 m x 5 m 'mesoplot'. This scale of assessment was chosen

because the average distance from perch to prey of pouncing robins is generally within three metres (Recher *et al.* 2002). This scale was also chosen because the 0.04 ha scale so commonly sampled in the literature often incorporates too much of the surrounding heterogeneity of the habitat (Beck and George 2000), thus masking the microhabitat elements important for foraging. Please note that any mention of 'microhabitat' collectively refers to the elements of both the 'microplot' and 'mesoplot'. Twelve habitat variables were collected within the mesoplot, including the distance from the pounce site to the nearest tree (> 1 m high), shrub (> 0.3 m high and 0.3 m wide) and log (diameter >50 mm and length larger than 800 mm). The number of sapling trees (1 m – 5 m), subcanopy trees (5 m – 10 m) and canopy trees (>10 m) were also counted within the mesoplot. Canopy cover was calculated as the percentage of points (from 25 points radiating out from the centre of the mesoplot) at which tree canopy intersected cross-hairs as viewed through the end of a 30 cm vertically held ocular tube (Morrison *et al.* 1998). The percentage cover of shrubs, plant material (herbaceous vegetation < 0.3 m and grass) and bare ground within the mesoplot was estimated. Finally, I recorded an index of leaf litter (estimated as one of nine indices of abundance between sparse and dense, Cousin 2004a) and log abundance (estimated as one of five indices between absent and abundant). Just as with microplot assessment, I compared pounce mesoplot sites and random mesoplot sites within the territory, with collection of all data at random mesoplot sites the same as that collected at pounce mesoplot sites. The random mesoplot sites were located at the same location surrounding the random microplot sites (see Figure 4.1).

4.3.5 Invertebrate sampling

I undertook invertebrate sampling to determine whether selection for foraging microhabitat was tied to invertebrate biomass. Scarlet Robins are primarily sit and wait predators, so the majority of prey consumed is represented by active epigeic invertebrates that they detect and subsequently pounce onto from an elevated perch. As a result, I utilised pitfall trapping as the method to record invertebrate availability (i.e., abundance and activity). While a number of studies indicate the limited value of pitfall trapping for assessing invertebrate community composition (Greenslade 1964), others suggest their applicability and reliability in studies aimed at assessing the abundance of epigeic invertebrates (Fichter 1941; Williams 1959; Pik *et al.* 1999; Magagula 2003), such as the present study. Following collection of all microplot and mesoplot data, I buried a 90 mm PVC sleeve 130 mm into the ground at the exact locations of the pounce sites and at the random sites. Seven days later, I placed a 425 mL (90 mm x 110 mm) cup within the PVC sleeves, such that the lip of the cup was flush with the ground. Approximately 100 mL of anti-freeze (30% ethylene glycol) was poured into the cup, which acted as a collecting fluid and preservative. A couple of drops of household detergent were also added to the fluid to function as a surfactant. Traps were not set until seven days after the initial digging in of the PVC sleeve, in order to alleviate the impact of any 'settling-in' disturbance to the leaf litter and soil fauna (Abbott *et al.* 1984).

Pitfalls were left set for 14 days, after which I collected their contents and stored them in 70% ethanol. All trapped invertebrates larger than 4 mm were then counted and sorted to ordinal level. The only exception to this sorting protocol

was the separation of the Formicidae family from the rest of the Hymenoptera order (herein, Formicidae is referred to as order for ease of interpretation), as well as the separation of all larvae into their own group. While Scarlet Robins have been recorded consuming a large diversity of invertebrates, only the four main epigeic invertebrate dietary orders (based on personal observations and that presented in Huddy 1979; Ford 1985) collected in this study were further assessed; namely the Formicidae, Araneae, Hemiptera and Coleoptera.

4.3.6 Variable reduction

The microplot and mesoplot variables were initially reduced in number following a combination of correlation analysis and Principal Component Analysis (PCA). Of the four microplot variables, bare ground was omitted as it was dominated by zero values. The percentage cover of leaf litter and plant material in the microplot was significantly negatively correlated ($r = -0.848$, df = 143, $p < 0.001$), so these variables were replaced with a new composite variable (denoted as 'litter substrate') computed as principal component scores from a PCA. Larger values of the new litter substrate variable indicated a high percentage cover of leaf litter and an associated lower percentage cover of plant material. As analysis of foraging microhabitat selection was to be undertaken separately for both seasons, the values of the new 'litter substrate' microplot variable were computed by PCAs undertaken on each seasons' microplot data. The percent total variance explained by the new composite substrate variable in winter and spring equated to 92.1% and 92.9% respectively.

For mesoplot variable reduction, when two variables were significantly correlated with each other, I retained the more ecologically meaningful variable

for further analysis. Thus, the distance to shrub and distance to log variables were omitted as they were significantly correlated with percentage cover of shrubs (% shrub; r = -0.465, df = 142, p < 0.001) and index of log abundance (r = -0.611, df = 142, p < 0.001) respectively. Just as in the microplot variable reduction, the percentage bare ground variable was omitted as it was dominated by zero values and was weakly correlated with a number of other disparate variables. Because of the positive correlation between the number of sapling trees and number of subcanopy trees variables (r = 0.277, df = 142, p < 0.001), these variables were combined into a single number of sapling trees and subcanopy trees variable. As a result of the close association of six of the mesoplot variables (distance to tree, number of canopy trees, canopy cover, % plant, leaf litter and logs), as determined by correlation analysis and grouping in preliminary PCAs, these variables were grouped into a single composite variable denoted as 'woodiness'. With the new 'woodiness' variable, larger values represent denser woodland with a denser leaf litter, less plant material on the ground, a denser canopy, and more logs. Lower values represent more open woodland with sparser leaf litter, more plant material on the ground, a sparser canopy and fewer logs. As with the computation of the microplot substrate variable values, the values of the new 'woodiness' mesoplot variable were computed by PCAs undertaken on each seasons' mesoplot data. The percent total variance explained by the new composite woodiness variable in winter and spring equated to 51.9% and 55.2% respectively.

4.3.7 Analysis

The habitat elements influencing foraging microhabitat selection of robins as well as the association of invertebrate abundance with pounce sites was

analysed 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 designed to analyse nested or hierarchically structured data (Raudenbush and Bryk 2002). Hierarchical structure is widespread in many ecological investigations, 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, pounce and random sites sampled from a given territory will tend to be more homogeneous than pounce and random sites sampled randomly from all study sites across the landscape. As foraging microhabitat from a given territory shares similar site-specific characteristics (e.g., topography, species assemblages, biotic effects), these sampled microhabitats 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. In the present study, the data was structured at three hierarchical levels; pounce and random sites within territories within study sites (see Figure 4.1). As such a 3-level hierarchical linear modelling approach was attempted on the data. Specifically, due to the binary response variable (pounce or random), a hierarchical generalised linear modelling (HGLM) procedure was undertaken, 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 analysis of the data, it was shown that structuring the data at the third level (study sites) and even the second level (territory) was ineffective, as determined by the results of a variance component test in HLM6. This pattern of no hierarchical structure was observed in the foraging microplot, foraging mesoplot and invertebrate association components of this study, so I undertook all analyses using binary logistic regression analysis. Testing for hierarchical structure is a necessary and important step before undertaking analysis based on non-hierarchical structured data using analyses such as linear and logistic regression.

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:

$$\Delta_i = AIC_i - minAIC$$

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).

4.4 RESULTS

4.4.1 Microplot selection

At the microplot scale, during winter and spring, robins pounced in areas with higher percentage composition of leaf litter than random sites within the territory (Figure 4.2a). The percentage composition of logs was similar between pounce and random sites in winter, with more logs associated with pounce sites than random sites in spring.
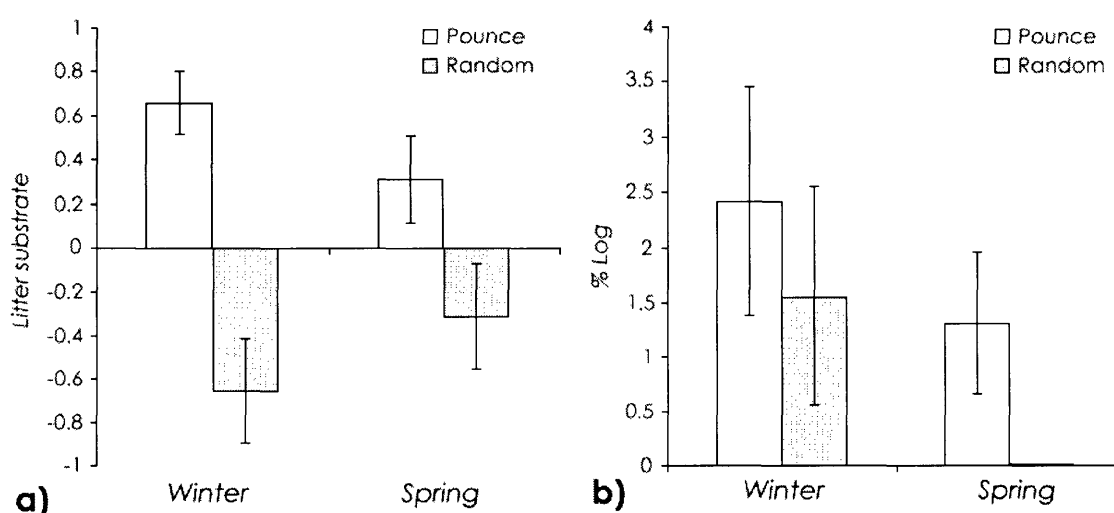

Figure 4.2 a) the average litter substrate composition (see section 4.3.6) and b) the average percentage composition of logs in pounce and random microplots in winter and spring. All graphs show the average ± standard error.

The results of logistic regression modelling indicate that the univariate model with litter substrate composition was the best model describing microplot scale selection of Scarlet Robins in winter, with pounce sites exhibiting a higher index of leaf litter than random sites (see Table 4.1). In addition, a bivariate model including litter substrate and logs was also produced, albeit of lower Akaike weight (0.3135 compared to 0.6864 for the univariate model). Examination of the regression coefficient confidence intervals indicates that only the litter

substrate variable had good explanatory power in both models based on the confidence intervals not including zero.

During spring, the bivariate model with litter substrate and logs was the best model describing microplot scale selection by robins, with pounce sites exhibiting a greater index of litter substrate and percentage composition of logs than random sites. The univariate log model was also selected as approximating the microplot scale selection data. However, neither model in spring had good explanatory power on account of the regression coefficient confidence intervals including zero.

Table 4.1 Results of logistic regression analysis for variables influencing microplot selection surrounding Scarlet Robin pounce sites in winter and spring of 2004.

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. † = Coefficients for which the 95% confidence interval does not include zero.

Response variable	Predictor variable(s)	ΔAIC_c	Akaike weight	Model variable(s)	Coefficient	Std err	Confidence interval
Winter microplot	Litter substrate	0	0.6864	Litter substrate	0.907	0.246	0.4248, 1.3892†
	Litter substrate + Log	1.5670	0.3135	Litter substrate	0.920	0.248	0.4339, 1.4061†
				Log	0.035	0.046	-0.0552, 0.1252
Spring microplot	Litter substrate + Log	0	0.5668	Litter substrate	0.321	0.189	-0.0494, 0.6914
				Log	2.667	98.817	-191.0143, 196.3483
	Log	0.8750	0.3660	Log	2.731	99.226	-191.7520, 197.2140

Examination of the multi-model inference procedure for the two predictor variables reflects the results of the logistic regression modelling, and indicates the importance of each microplot variable in different seasons (Table 4.2).

Table 4.2 Multi-model inference weight of evidence for predictor variables contributing to microplot response variable models for winter and spring.

	Weight of evidence	
Predictor	*Winter*	*Spring*
Litter substrate	0.9999	0.6340
Log	0.3136	0.9327

During winter, the litter substrate variable explained all of the difference in microplot composition between pounce and random sites. During spring, the percentage composition of log contributed almost all of the difference in microplot composition between pounce and random sites.

4.4.2 Mesoplot selection

At the mesoplot scale, robins pounced in areas with a higher degree of woodiness especially in winter (Figure 4.3a). There did not appear to be any difference in the selection of mesoplots in relation to the number of sapling and subcanopy trees (Figure 4.3b). The percentage cover of shrubs in the mesoplot was only notably different in spring, with pounce mesoplots harbouring fewer shrubs than random sites (Figure 4.3c).
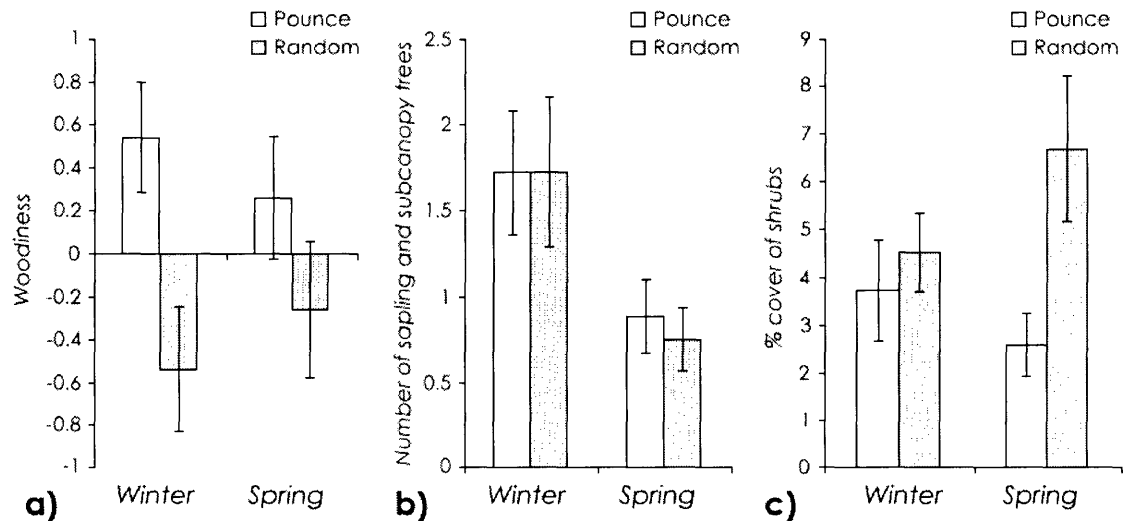
Figure 4.3 a) the average degree of woodiness, b) the number of sapling and subcanopy trees and c) the percentage cover of shrubs in pounce and random mesoplots in winter and spring. All graphs show mean ± std. err.

The results of the logistic regression modelling indicate that during winter, the univariate model incorporating woodiness was best at describing mesoplot scale selection of Scarlet Robins, with mesohabitat surrounding pounce sites exhibiting a higher degree of woodiness than random sites (Table 4.3). This univariate model had good explanatory power on account of the regression coefficient confidence intervals not including zero. The bivariate model incorporating woodiness and number of sapling and subcanopy trees was also selected, although only the woodiness variable in this model had good explanatory power as a result of the regression coefficient confidence intervals not including zero.

During spring, the pattern of mesoplot scale selection was explained by three models. The univariate model with percentage cover of shrubs was the best model describing mesoplot selection (Table 4.3). The bivariate model incorporating woodiness and percentage cover of shrubs, as well the bivariate model incorporating number of sapling and subcanopy trees and percentage

cover of shrubs were also selected as best approximating the data. Only the percentage cover of shrubs had good explanatory power in all three models, with the regression coefficient confidence intervals of the shrub variable in each not including zero (Table 4.3), with mesohabitat surrounding pounce sites harbouring a lower density of shrubs than that surrounding random sites.

Table 4.3 Results of logistic regression analysis for variables influencing mesoplot selection surrounding Scarlet Robin pounce sites in winter and spring of 2004.

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. Woodiness = index of woodiness in mesoplot, Sap sub = number of sapling and subcanopy trees in mesoplot, Shrub = percentage cover of shrubs in mesoplot. † = Coefficients for which the 95% confidence interval does not include zero.

Response variable	Predictor variable(s)	ΔAIC_c	Akaike weight	Model variable(s)	Coefficient	Std err	Confidence interval
Winter mesoplot	Woodiness	0	0.4880	Woodiness	0.500	0.172	0.1629, 0.8371†
	Woodiness + Sap sub	1.2770	0.2577	Woodiness	0.540	0.178	0.1911, 0.8889†
				Sap sub	-0.104	0.112	-0.3235, 0.1155
Spring mesoplot	Shrub	0	0.4883	Shrub	-0.106	0.050	-0.2040, -0.0080†
	Woodiness + Shrub	1.8310	0.1955	Woodiness	0.083	0.142	-0.1953, 0.3613
				Shrub	-0.099	0.050	-0.1970, -0.0010†
	Sap sub + Shrub	1.9650	0.1828	Sap sub	0.096	0.207	-0.3097, 0.5017
				Shrub	-0.107	0.050	-0.2050, -0.0090†

Examination of the multi-model inference procedure for the three predictor variables indicates a shift in weight of evidence between seasons of degree of woodiness and percentage cover of shrub variables (Table 4.4).

Table 4.4 Multi-model inference weight of evidence for predictor variables contributing to mesoplot response variable models for winter and spring.

Woodiness = index of woodiness in mesoplot, Sap sub = number of sapling and subcanopy trees in mesoplot, Shrub = percentage cover of shrubs in mesoplot.

	Weight of evidence	
Predictor	*Winter*	*Spring*
Woodiness	0.9940	0.3096
Sap sub	0.3449	0.2801
Shrub	0.2519	0.9324

During winter, the degree of woodiness explained almost all of the difference in mesoplot composition between pounce and random sites. The numbers of sapling and subcanopy trees as well as the percentage cover of shrubs showed a relatively low weighting in winter. In spring however, there was a notable shift from selection governed by the degree of woodiness to the percentage cover of shrubs in the mesoplot. The weighting of the number of sapling and subcanopy trees variable in spring was also low as in winter (Table 4.4) and indicated its lack of importance in the selection of foraging mesohabitat.

4.4.3 Invertebrate association

A total of 5,051 invertebrates from the Formicidae, Araneae, Hemiptera and Coleoptera orders were trapped and sorted from both seasons; 1,282 in winter and 3,769 in spring. The average abundance of invertebrates of each order per trap at pounce and random sites was greater in spring than in winter (Figure 4.4).
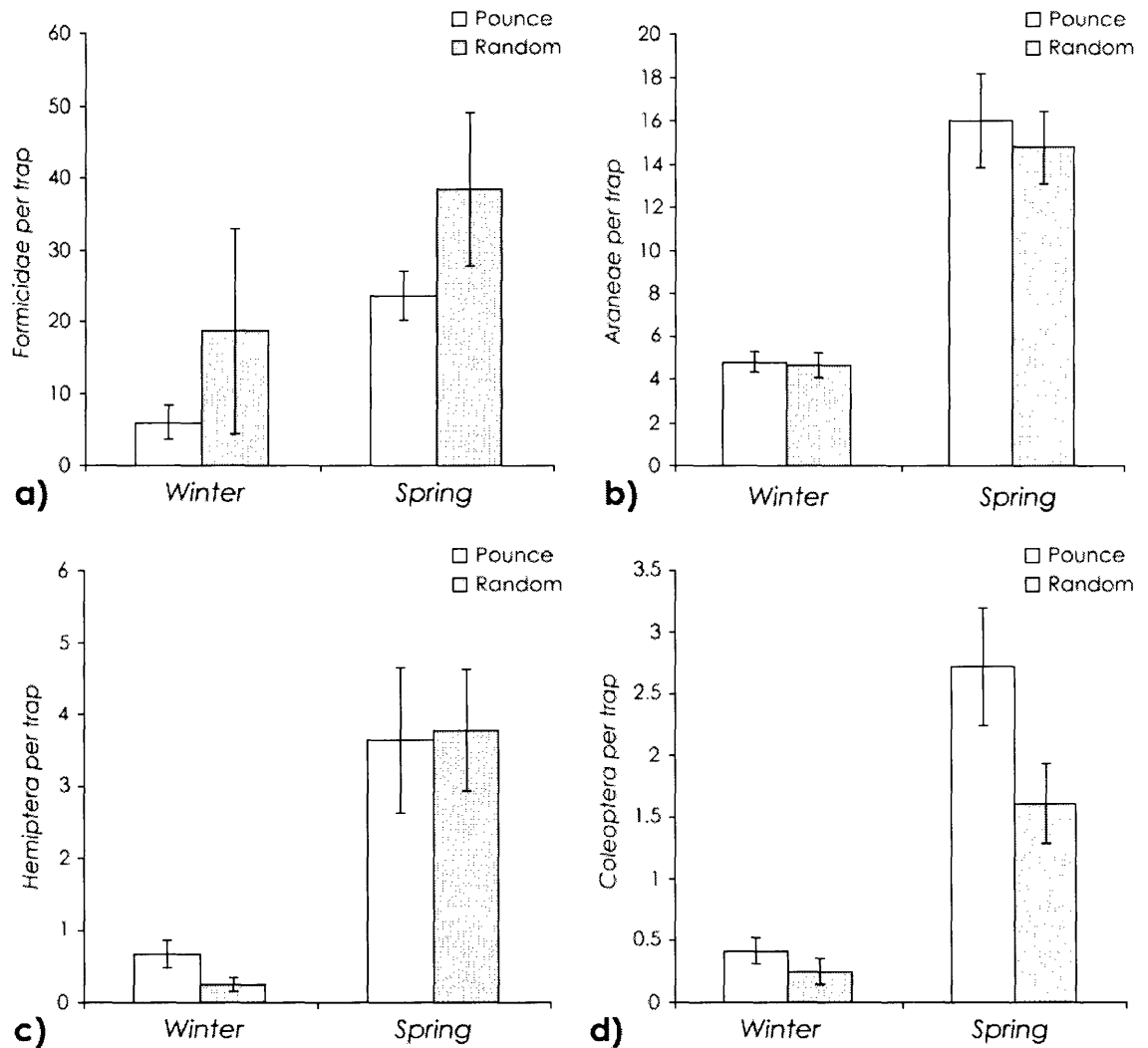
Figure 4.4 The average abundance of a) Formicidae, b) Araneae c) Hemiptera and d) Coleoptera at pounce sites and random sites in winter and spring. All graphs show mean ± std. err.

The results of the logistic regression modelling indicate that during winter, the univariate model incorporating Hemiptera abundance was best at delineating pounce sites from random sites, with the abundance of Hemiptera higher at pounce sites compared to random sites (Table 4.5). Two bivariate models were also selected including a model incorporating Hemiptera and Coleoptera as well as Formicidae and Hemiptera. Neither the univariate model nor the two bivariate models had good explanatory power on account of the regression coefficient confidence intervals for all variables including zero.

In spring, the univariate model incorporating Coleoptera was the best at delineating pounce sites from random sites. In addition to this model, two bivariate models (a Formicidae and Coleoptera model and a Hemiptera and Coleoptera model) as well as another univariate model (incorporating Formicidae) were also selected. Like the winter logistic regression modelling, none of the spring models had good explanatory power, with all variable regression coefficient confidence intervals including zero (Table 4.5). Compared to the microplot and mesoplot logistic regression models, the Akaike weight of all selected models was considerably lower; never rising higher than 0.2521 for the univariate Hemiptera model in winter (Table 4.5).

Table 4.5 Results of logistic regression analysis for invertebrate orders (and Formicidae family of the Hymenoptera order) associated with Scarlet Robin pounce sites in winter and spring of 2004.

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. [†] = Coefficients for which the 95% confidence interval does not include zero.

Response variable	Predictor variable(s)	ΔAIC_c	Akaike weight	Model variable(s)	Coefficient	Std err	Confidence interval
Winter invertebrates	Hemiptera	0	0.2521	Hemiptera	0.612	0.340	-0.0544, 1.2784
	Hemiptera + Coleoptera	0.9830	0.1542	Hemiptera	0.605	0.337	-0.0555, 1.2655
				Coleoptera	0.416	0.389	-0.0346, 1.1784
	Formicidae + Hemiptera	1.5350	0.1170	Formicidae	-0.004	0.006	-0.0158, 0.0078
				Hemiptera	0.594	0.339	-0.0704, 1.2584
Spring invertebrates	Coleoptera	0	0.2377	Coleoptera	0.196	0.107	-0.0137, 0.4057
	Formicidae + Coleoptera	0.8950	0.1519	Formicidae	-0.006	0.006	-0.0178, 0.0058
				Coleoptera	0.183	0.108	-0.0287, 0.3947
	Hemiptera + Coleoptera	1.8370	0.0949	Hemiptera	-0.027	0.046	-0.1172, 0.0632
				Coleoptera	0.213	0.113	-0.0085, 0.4345
	Formicidae	1.9060	0.0916	Formicidae	-0.008	0.006	-0.0198, 0.0038

Examination of the multi-model inference procedure for the three predictor variables indicates a shift in weight of evidence between Hemiptera and Coleoptera (Table 4.6).

Table 4.6 Multi-model inference weight of evidence for predictor variables contributing to invertebrate order (and Formicidae family of the Hymenoptera order) abundance differences between pounce and random sites for winter and spring.

| | Weight of evidence | |
Predictor	Winter	Spring
Formicidae	0.3791	0.5235
Araneae	0.2756	0.2871
Hemiptera	0.7857	0.3165
Coleoptera	0.4055	0.7412

The results of the multi-model inference procedure indicates the high weighting of Hemiptera during winter (Table 4.6), with Formicidae, Araneae and Coleoptera having similar lower weighting. In spring, the multi-model inference procedure indicates the specific importance of Coleoptera abundance, with a high weighting of 0.7412, and lower values for the other groups.

4.5 DISCUSSION

4.5.1 Spatiotemporal shift in foraging microhabitat selection

During winter, Scarlet Robins chose foraging microhabitat that had disproportionately more leaf litter than random sites. This was evident at the microplot scale (selection for litter substrate) and the mesoplot scale (selection for woodiness). In winter, the abundance of epigeic invertebrates (measured by an index of activity, Wachob 1996) is much lower than during spring (Chapter 2 and see Figure 4.4). Therefore, robins would be expected to select foraging microhabitat where prey was abundant and detectable. Epigeic invertebrates

are potentially more detectable in leaf litter than amongst herbaceous plants and grasses. As such, pounce site selection at the microplot scale may represent opportunistic detection of mobile prey, rather than actual selectivity for this ground substrate attribute. Selection of foraging mesohabitat with a high index of woodiness further reflects the importance of the increased detectability of invertebrates associated with the leaf litter component of the composite woodiness variable during winter. Furthermore, canopy elements of the woodiness variable in winter influence detectability by the buffered ground substrate microclimate, whereby additional foliage cover maintains understorey temperatures by reducing the extremes of minimum temperature (Smith and Shugart 1987), favouring the retention and activity of epigeic invertebrates during this season. In a study on Mountain Chickadees in the United States, Wachob (1996) found that in addition to food availability, foraging sites during winter were selected according to favourable thermal microclimates. Although detectability appears to be the primary mechanism driving the association of pounce site selection with the degree of woodiness, a positive association has been shown to exist between woodiness and the abundance of some invertebrate orders (see Table 2.4 in Chapter 2), so selection is probably influenced by the detectability of invertebrates in that component of the foraging microhabitat that has an already elevated abundance of invertebrates. This would explain the absence of a discernible difference in invertebrate abundance between pounce and random sites in winter, with selection of pounce sites based more on foraging microhabitat attributes increasing detectability rather than selection for specific invertebrate prey.

During spring, there was no apparent selection for attributes at the microplot scale, with selection at the mesoplot scale governed by sites with a low density of shrubs. An absence of importance of ground substrate attributes in either the microplot or mesoplot scales during spring can be attributed to a number of factors. Although Scarlet Robins are still predominantly ground-foraging in spring, they also forage in other habitat strata (Robinson 1992; Recher and Davis 1998). This is due, in part, to the elevated abundance of arboreal and aerial invertebrates during this season (Recher *et al.* 1983; Ford *et al.* 1990), with hawking and snatching (see Recher *et al.* 1985 for definitions) becoming prevalent foraging manoeuvres. Secondly, there are higher numbers and a higher rate of activity of epigeic invertebrates during spring given the warmer conditions of this season, so detectability increases amongst all elements of the microhabitat, not just that associated with the ground substrate. Furthermore, selection for sites at the mesoplot scale with a low density of shrubs reflects the favourable foraging opportunities provided by this open structure in allowing unobstructed views of the ground to scan for epigeic prey (Holmes and Recher 1986; Robinson 1992). Reducing the risk of predator detection may also represent an important consideration in the selection of foraging sites during spring, when robins are feeding mates and nestlings (Whittingham and Evans 2004; Jones *et al.* 2006). As foraging microhabitat selection in spring, as in winter, appears to be governed by attributes maximising the detectability of epigeic invertebrate prey, the absence of a difference in invertebrate abundance between pounce and random sites reflects the role of detectability rather than specific invertebrate prey governing pounce site selection in spring.

4.5.2 Foraging microhabitat selection governing coarser scale selection

Although foraging microhabitat selection appears to be influenced by detectability of epigeic invertebrate prey, selection for specific microhabitat attributes differed according to the season, indicating the importance of assessing habitat selection at multiple spatial and temporal scales. In understanding the importance of spatial and temporal variability in foraging microhabitat selection, it is important to recognise that habitat selection in birds is believed to be represented by a hierarchical process (George and Zack 2001; Battin and Lawler 2006), with processes governing selection at one spatial scale influencing those at other spatial scales (Cushman and McGarigal 2004). In the present study, it appears that epigeic invertebrate detectability at a small spatial scale constrains selection for microhabitat up to the mesohabitat scale. Given that leaf litter is an important component governing habitat selection in the Scarlet Robin at the territory scale (see Chapter 6), it is possible that habitat selection at even larger spatial scales are constrained by selection at finer spatial scales such as at the foraging microhabitat scale. Unfortunately, due to time and budgetary constraints, it is often not possible to incorporate all spatial scales into habitat selection models and conservation management plans. As a result, habitat selection studies are often limited in their spatial scope, focusing on management units operating at 'manageable scales' such as the regional or landscape scale. This approach is limiting in that it assumes a 'top-down' approach to habitat selection (e.g., McLoughlin *et al.* 2002); focusing on responses operating at large spatial scales (e.g., remnant occupation, territory scale habitat attributes). Such models of habitat selection studies assume that hierarchical selection at coarser scales constrain that at finer scales (Battin and Lawler 2006; Kristan 2006).

In the present study, rather than a 'top-down' model of hierarchical habitat selection, the results suggest a potential 'bottom-up' model of habitat selection, with finer scale selection processes constraining selection at coarser scales. This is no surprise when taking into account the resident and sedentary nature of the Scarlet Robin (Higgins and Peter 2002). Cushman and McGarigal (2004) state that the scale at which a species most strongly interacts with its environment corresponds to the spatial scale at which environmental variables affect it most. As a ground-foraging insectivore, the foraging microhabitat scale presented in this study is the most important interaction scale. As such, one could predict that habitat selection at coarser spatial scales may be influenced or constrained by selection operating at the foraging microhabitat scale.

The present study suggests that results from coarse-grained 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, and recognising the potential for a 'bottom-up' process governing hierarchical habitat selection.

4.6 REFERENCES

Abbott I, Van Heurck P, Wong L (1984) Responses to long-term fire exclusion: physical, chemical and faunal features of litter and soil in a Western Australian forest. *Australian Forestry* 47, 237 - 242.

Barrett GW, Ford HA, Recher HF (1994) Conservation of woodland birds in a fragmented rural landscape. *Pacific Conservation Biology* 1, 245 - 256.

Battin J, Lawler JJ (2006) Cross-scale correlations and the design and analysis of avian habitat selection studies. *The Condor* 108, 59 - 70.

Beck MJ, George TL (2000) Song post and foraging site characteristics of breeding varied thrushes in northwestern California. *The Condor* 102, 93 - 103.

Bennett AF (1999) 'Linkages in the landscape. The role of corridors and connectivity in wildlife conservation.' (IUCN: Gland, Switzerland)

Bergin TM (1992) Habitat selection by the Western Kingbird in western Nebraska: a hierarchical analysis. *The Condor* 94, 903 - 911.

Burnham KP, Andersen DR (2001) Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* 28, 111 - 119.

Burnham KP, Anderson DR (2002) 'Model selection and multimodel inference. A practical information-theoretic approach (second edn).' (Springer Science+Business Media, Inc: New York)

Cousin JA (2004a) Habitat selection of the Western Yellow Robin (*Eopsaltria griseogularis*) in a Wandoo woodland, Western Australia. *Emu* 104, 229 - 234.

Cousin JA (2004b) Pounce site characteristics of the Western Yellow Robin *Eopsaltria griseogularis*: the importance of assessing foraging microhabitat. *Pacific Conservation Biology* 10, 21 - 27.

Cushman SA, McGarigal K (2004) Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. *Ecological Applications* **14**, 1090 - 1105.

Fichter E (1941) Apparatus for the comparison of soil surface arthropod populations. *Ecology* **22**, 338 - 339.

Ford HA (1985) The bird community in eucalypt woodland and eucalypt dieback in the northern tablelands of New South Wales. In 'Birds of eucalypt forests and woodlands: Ecology, conservation, management'. (Eds A Keast, HF Recher, H Ford and D Saunders) pp. 333 - 340. (Royal Australiasian Ornithologists Union and Surrey Beatty & Sons: Chipping Norton, NSW)

Ford HA, Huddy L, Bell H (1990) Seasonal changes in foraging behaviour of three passerines in Australian *Eucalyptus* woodland. *Studies in Avian Biology* **13**, 245 - 253.

Garnett ST, Crowley GM (2000) 'The Action Plan for Australian Birds.' (Environment Australia: Canberra)

George TL, Zack S (2001) Spatial and temporal considerations in restoring habitat for wildlife. *Restoration Ecology* **9**, 272 - 279.

Greenslade PJM (1964) Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* **33**.

Higgins PJ, Peter JM (2002) 'Handbook of Australian, New Zealand and Antarctic Birds. Volume 6. Pardalotes to Shrike-thrushes.' (Oxford University Press: Melbourne)

Hobbs RJ (1993) Effects of landscape fragmentation on ecosystem processes in the Western Australian wheatbelt. *Biological Conservation* **64**, 193 - 201.

Holmes RT, Recher HF (1986) Determinants of guild structure in forest bird communities: an interncontinental comparison. *The Condor* **88**, 427 - 439.

Huddy L (1979) Social behaviour and feeding ecology of Scarlet Robins (*Petroica multicolor*). BSc (honours) thesis, University of New England.

Jones J (2001) Habitat selection studies in avian ecology: a critical review. *The Auk* **118**, 557 - 562.

Jones KA, Krebs JR, Whittingham MJ (2006) Interaction between seed crypsis and habitat structure influence patch choice in a granivorous bird, the chaffinch *Fringilla coelebs*. *Journal of Avian Biology* **37**, 413 - 418.

Keane JJ, Morrison ML (1999) Temporal variation in resource use by Black-throated Gray Warblers. *The Condor* **101**, 67 - 75.

Kelly JP (1993) The effect of nest predation on habitat selection by Dusky Flycatchers in limber pine-juniper woodland. *The Condor* **95**, 83 - 93.

Kleintjes PK, Dahlsten DL (1995) Within-season trends in the foraging behavior of the Mountain Chickadee. *Wilson Bulletin* **107**, 655 - 666.

Kristan WB (2006) Sources and expectations for hierarchical structure in bird-habitat associations. *The Condor* **108**, 5 - 12.

Li X, Li D, Li Y, Ma Z, Zhai T (2002) Habitat evaluation for crested ibis: A GIS-based approach. *Ecological Research* **17**, 565 - 573.

Magagula CN (2003) Changes in carabid beetle diversity within a fragmented agricultural landscape. *African Journal of Ecology* **41**, 23 - 30.

Matlack GR (1993) Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* **66**, 185 - 194.

McIntyre S, Barrett GW (1992) Habitat variegation, an alternative to fragmentation. *Conservation Biology* **6**, 146 - 147.

McLoughlin PD, Case RL, Gau RJ, Cluff HD, Mulders R, Messier F (2002) Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia* **132**, 102 - 108.

Morrison ML, Marcot BG, Mannan RW (1998) 'Wildlife habitat relationships; concepts and applications.' (The University of Wisconsin Press: Madison, USA)

Pik AJ, Oliver I, Beattie AJ (1999) Taxonomic sufficiency in ecological studies of terrestrial invertebrates. *Australian Journal of Ecology* **24**, 555 - 562.

Raudenbush SW, Bryk AS (2002) 'Hierarchical linear models: applications and data analysis methods.' (Sage Publications, Inc.: Thousand Oaks, California)

Raudenbush SW, Bryk AS, Congdon R (2005) HLM for Windows (version 6.02) [Computer software]. Scientific Software International, Inc., Lincolnwood, IL.

Recher HF, Davis WE (1998) The foraging profile of a wandoo woodland avifauna in early spring. *Australian Journal of Ecology* **23**, 514 - 527.

Recher HF, Davis WE, Calver MC (2002) Comparative foraging ecology of five species of ground-pouncing birds in western Australian woodlands with comments on species decline. *Ornithological Science* **1**, 29 - 40.

Recher HF, Gowing G, Kavanagh R, Shields J, Rohan-Jones W (1983) Birds, resources and time in a tablelands forest. *Proceedings of the Ecological Society of Australia* **12**, 101 - 123.

Recher HF, Holmes RT, Schulz M, Shields J, Kavanagh R (1985) Foraging patterns of breeding birds in eucalypt forest and woodland of southeastern Australia. *Australian Journal of Ecology* **10**, 399 - 419.

Reid JW (1999) 'Threatened and declining birds in the New South Wales sheep-wheat belt: diagnosis, characteristics and management.' Report to NSW National Parks and Wildlife Service, Sydney.

Robinson D (1992) Habitat use and foraging behaviour of the Scarlet Robin and the Flame Robin at a site of breeding-season sympatry. *Wildlife Research* **19**, 377 - 395.

Saunders DA, Ingram J (1995) 'Birds of Southwestern Australia; An atlas of changes in distribution and abundance of the wheatbelt fauna.' (Surrey Beatty & Sons Pty Ltd.: Chipping Norton, NSW)

Schneider DC (2001) The rise of the concept of scale in ecology. *Bioscience* **51**, 545 - 553.

Smith TM, Shugart HH (1987) Territory size variation in the Ovenbird: the role of habitat structure. *Ecology* **68**, 695 - 704.

Sodhi NS, Paszkowski CA, Keehn S (1999) Scale-dependent habitat selection by American redstarts in aspen-dominated forest fragments. *Wilson Bulletin* **111**, 70 - 75.

Wachob DG (1996) The effect of thermal microclimate on foraging site selection by wintering mountain chickadees. *The Condor* **98**, 114 - 122.

Wakeley JS (1978) Factors affecting the use of hunting sites by Ferruginous Hawks. *Condor* **80**, 316 - 326.

Whittingham MJ, Evans KL (2004) The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* **146 (supp ii)**, 210 - 220.

Williams G (1959) The seasonal and diurnal activity of the fauna sampled by pitfall traps in different habitats. *Journal of Animal Ecology* **28**, 1 - 13.

Wolda H (1990) Food availability for an insectivore and how to measure it. *Studies in Avian Biology* **13**, 38 - 43.