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Winter bird communities in the northern Negev: species dispersal patterns, habitat use and implications for habitat conservation

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Abstract. Bird habitat conservation may require different management strategies for different seasonal bird assemblages. We studied habitat use by winter birds in forest and scrubland habitat patches in the northern Negev, Israel. Our goal was to assess whether differences in responses to landscape and habitat structure between breeding and non-breeding seasons require changes in future conservation plans that have been suggested for the Negev breeding bird community. We evaluated habitat and area effects on bird abundance and distribution and tested whether species habitat use during winter involves niche shifts. Compared with breeding birds, a larger proportion of winter bird species occupied both scrubland and forest. As in summer, forest bird species responded to habitat structure, whereas scrubland species were associated with both habitat structure and area. Resident birds disperse into habitats in which they were not present during summer. Consequently, for several species, the correlation between bird densities and environmental factors showed a better fit at the landscape rather than at the habitat scale. In addition, rather than niche shift, birds actually extended their niche breadth. Nest site selection may constrain bird distribution into a realized niche, smaller than their fundamental niche. Despite the scale differences in habitat use, the similar species diversity patterns between seasons suggest that both winter and summer birds would benefit from conservation of scrub patches larger than 50 ha, and enrichment of foliage layers within the planted forests.

Introduction

Studies on breeding bird conservation in patchy habitats have shown a positive correlation between species densities and habitat structure on small scales, and negative effects of patch area due to isolation, or edge effects on larger scales (Ambuel and Temple 1983; Wilcove 1985; Blake and Karr 1987; Villard et al. 1995; Diaz et al. 1998). Yet, as habitats change in structure and resources seasonally, both migratory and resident bird species disperse into different habitats during the non-breeding season. Despite the increase in studies on winter bird communities and their conservation since the early 1990s (e.g. Saab and Petit 1992; Stapanian et al. 1994; Telleria and Santos 1995; Perkins et al. 2000; Telleria et al. 2001), the question of how winter birds respond to environmental factors at different scales has not been fully addressed.

Recently, Thompson et al. (2001) argued about the importance of incorporating non-breeding birds into conservation programmes. Habitat management for breeding birds may also affect populations of endangered winter bird species (e.g. Provencher et al. 2002). Therefore, conservation programmes can be greatly improved by using season-specific habitat management regimes (Morrison et al. 1985). For example, if birds disperse during winter into patches which are larger, or are structurally different than the patches they breed in, then protecting their breeding habitat patches would not be sufficient for their conservation. Hutto (1985b) suggested that while in the breeding season birds respond primarily to habitat structure, winter birds use a different strategy of decision-making when selecting a wintering site by responding to a larger extent to food availability at a local scale. At the larger scale, landscape composition may become a more important factor accounting for the variation in winter bird species richness and diversity (e.g. Pearson 1993). In contrast to breeding season, where habitat fragmentation affects reproductive success, during winter habitat fragmentation may affect flock size, body condition and foraging behaviour (Telleria et al. 2001).

The intrinsic factors that affect bird habitat selection differ between seasons (Hutto 1985b), resulting in habitat shift during winter (Lack 1971). Breeding birds are central-place foragers, constrained by their nest to a relatively small home range. In contrast, during the non-breeding season individual birds are free to spread and forage over larger spatial scales. The question is whether individual birds are indeed more flexible and are able to use a much larger space of the same, or even of different habitat types. Alternatively, once established in wintering grounds, individual's movements may remain restricted within a small area due to evolutionary constraints. If the former is the case, habitat effects on winter bird abundance and distribution may be obscured. Specifically, assessing which environmental variables are associated with bird densities during the non-breeding season may require a larger spatial scale than in the breeding season.

In the northern Negev, Israel, a large scrubland area has been fragmented for almost half a century by forest patches planted by the Jewish National Fund. Shochat et al. (2001) showed that during the breeding season forest and scrubland patches are inhabited by different species assemblages, and that habitat structure in the forest, but patch size in the scrub are the major factors that determine bird abundance and distribution. According to these results, they suggested a management strategy to support rich bird communities, paying particular attention to endangered scrub specialist species such as the Long-billed Pipit. Recommendations for future land management for breeding birds included conservation of scrub patches larger than 50 ha, and enrichment of foliage diversity in forest patches (Shochat et al. 2001). However, the northern Negev also serves as an important wintering ground for many Eurasian bird species. Furthermore, resident species may alter their habitat use in the winter by extending or shifting their niche. Therefore, bird conservation programs in the northern Negev should also consider bird species abundance and distribution during the non-breeding season.

In this project we asked whether the factors that affect winter bird species diversity and population density in the northern Negev are the same factors that affect breeding birds. Specifically, in both forest and scrub patches our four objectives were to test: (1) possible effects of area and habitat structure at the community level (i.e. species richness, diversity, and total density); (2) effects of different environmental variables at the population level (i.e. on each species density); (3) whether gradients in environmental variables predict species abundance better at the habitat or at the landscape scale; and (4) whether resident birds shift their realized niche during the non-breeding season.

Study area and methods

Study area

Thousands of hectares of scrubland in the northern Negev, Israel, have been afforested by the Jewish National Fund since 1956. The plantations formed forest islands embedded within the natural semi-desert scrub. Today, the northern Negev landscape matrix consists of patches of these two major habitats, where each year more scrub area is being transformed into forest. The study area is located on the border between two zoogeographical zones: the Mediterranean in the north and the desert in the south. Average annual precipitation is 350 mm in the northern parts and 250 mm in the southern parts of the study area. Our study area included 14 scrub patches that ranged in area from 2.5 to 2000 ha and 10 forest patches, ranging from 4 to 3000 ha, north and northeast of Beer-Sheva.

Bird and habitat sampling

All bird counts were done during the first 4 h from first light. During two consecutive winter seasons (1996/1997 and 1997/1998) we counted birds along 250 m line transects for 15 min. Within 50 m to each side of the transect, we counted solitary birds that were heard or seen within, or estimated the number of flocking birds (such as Chaffinch and Song Thrush) to the nearest 10 individuals. Birds flying over were not counted. The number of transects varied between 1 and 10, according to patch area, in order to cover different habitat sub-types (e.g. broadleaf versus coniferous, young versus old coniferous). We repeated each transect twice during the winter (December–February), since species composition may change due to temporal changes in weather or food depletion. For the same reason we used, for each species, the mean of each winter's highest count across two winters. The data from winter 1996/1997 and winter 1997/1998 were combined for all statistical analyses. Common and scientific names of bird species are included in Appendix 1.

Environmental gradients used as correlates with bird densities were: habitat patch size, altitude, longitude, latitude, tree height, tree density, basal area (BA), diameter at breast height (DBH), perennial (lower than 50 cm) cover, total number of tree species, bush (taller than 80 cm) density, bush height and bush width. All vegetation measures were done within each bird transect during spring 1997.

Species richness and diversity

We plotted species–area curves for scrub and forest patches on a log–log scale for all species recorded in our transects. To test whether the increase in species richness with area was due to random sampling (e.g. Connor and McCoy 1979), or rather, was a result of a biological process, we calculated Fisher's Alpha diversity index using the total number of species and individuals extracted from the two winter seasons. To test whether changes in species diversity are scale-dependent (i.e. change as patch size increases), we applied linear and higher order polynomial regression analysis to the observed species diversity patterns (i.e. the change in Fisher's Alpha as patch size increases). Additional variables were included in the species–diversity equations when proven significant.

Statistical analysis

We used two methods of multivariate analysis to assess the effects of the environmental variables on bird abundance. At the community level we performed detrended canonical correspondence analysis (DCCA) using the program CANOCO (ter Braak 1986, 1992). For this analysis, densities of each species in each transect were averaged over two winter seasons. Environmental data used in the analysis included both vegetation structure and geographical variables. We used principal component analysis (PCA) to describe gradients in biogeography and vegetation structure among scrub and forest lots based on 13 habitat variables, and calculated component scores for each plot from the first three PCs extracted during the analysis. At the species level we applied stepwise multiple regression models (holding P to enter = 0.05 and P to remove = 0.1) in which species abundances (log abundance averaged across the two winters) were the dependent variable. Species abundances were first regressed against each environmental variable separately, starting with PC1, 2 and 3. When bird abundance was correlated with one or more of these components we did not use the rest of the individual variables in the model, but noted which gave the best fit. The individual variables were used in the regression models only when the PC variables failed to correlate with bird densities. Non-linear functions were applied only in cases where they accounted for a higher variance of bird densities. To compare bird niche breadth between seasons we subtracted the minimum PC (for PC1 and PC2) value from the maximum value for 13 resident species for both summer and winter, and compared the results by rmANOVA.

Results

Habitat structure

Results of PCA are shown in Table 1. The first three PCs accounted for 76% of the variation in habitat structure. The first component (PC1) accounted for 41% of

Table 1. Results of PCA showing the first three axes (PC1, PC2 and PC3) of habitat structure and environmental variables at the northern Negev. The numbers represent correlation of each variable with each axis. Only significant loadings ($P < 0.05$) are shown. DBH = diameter at breast height.[a]

Variable	PC1	PC2	PC3
Area		−0.523	−0.554
Altitude		−0.600	−0.752
Longitude		−0.625	−0.663
Latitude	−0.301		
Tree height	0.942		
Tree density	0.880		
BA	0.961		
DBH	0.942		
Perennial cover	−0.875		
Total tree species	0.856		
Bush density		−0.530	0.562
Bush height		−0.722	0.531
Bush width		−0.743	0.542
Variance (%)	40.5	19.1	17.9
Total (%)	40.5	59.6	77.5

[a] Reprinted with permission from Blackwell Publishing Ltd: Shochat et al. 2001, Breeding bird species diversity in the Negev: effects of scrub fragmentation by planted forests. Journal of Applied Ecology 38: 1135–1147.

the variance and contrasted plots according to vegetation structure. It was positively correlated with tree density, tree height, BA and DBH, and negatively correlated with perennial cover. The second component, which accounted for 19% of the variance, was negatively correlated with patch size, altitude, longitude, and bush density, height and width. The third component accounted for 18% of the variance. It was similar to the second component, but separated bush density, bush height and bush width from PC2.

Addressing objective 1

Bird community composition

Common and scientific names of 42 regular winter bird species (not including birds of prey) in scrub and forests of the northern Negev are given in Appendix 1. Several other irregular species also winter in this area. Of the 42 species, 20 are found in both scrubland and forest, 14 are found only in forest and 6 only in scrubland (Appendix 1). Twenty-three species are permanent residents, 15 are winter visitors and at least two (Greenfinch and Sardinian Warbler) are known to have both resident and wintering populations.

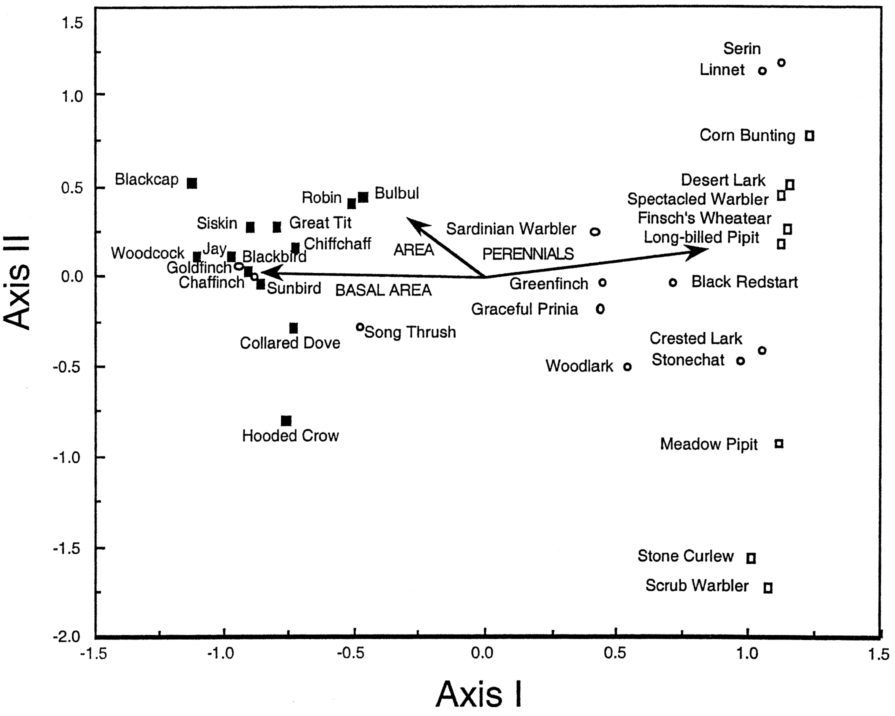

Figure 1. Ordination diagram of the first two axes of DCCA for winter bird species and environmental variables in forests and scrub in the northern Negev, Israel. Axes I and II accounted for 22.8 and 4% of the variance in the species data, respectively. Arrows represent directions of greatest change of environmental variables. The location of a species' score relative to the arrows indicates the environmental preferences of that species. ○ – species wintering in both scrub and forests, ■ – forest wintering species, □ – scrubland wintering species.

Thirty-two species, including three non-passerines (Woodcock, Stone Curlew and Collared Dove) were detected in our bird counts (underlined in Appendix 1). We recorded 12 species in forest only, 8 species in scrub only, and 12 in both habitats. The ordination analysis included all 32 species (Figure 1). For further analysis we omitted six species with proportions of less than 1% of the total bird counts (Stone Curlew, Woodcock, Blackcap, Orange-tufted Sunbird, Hooded Crow and Siskin).

We used DCCA to describe how individual bird species are distributed with respect to environmental variables. Of the total unconstrained eigenvalue (4.67), the first axis accounted for 23% (0.72) and the second axis for 4% (0.216) of the variance in the species distribution. The arrows for environmental variables in Figure 1, in conjunction with the species points, account for 42% of the variance in the weighted average of the species with respect to each of the environmental variables on the first axis and 54% of the variance on the second axis (ter Braak

1986). The arrows indicate that axis I is a measure of vegetation structure. It is positively correlated with perennial cover, and negatively correlated with basal area. Axis II only correlated with area (patch size). Species–environment correlations for the first two axes are 0.97 and 0.76. These correlations measure how well environmental variables explain the extracted variation in community composition (ter Braak 1986). We applied a Monte Carlo simulation using 99 permutations and found that the overall analysis and the two axes were significant (DCCA, $P < 0.01$; axis I, $P < 0.01$; axis II, $P < 0.01$).

The first axis, describing a vegetation gradient, successfully separated 12 species recorded only in forest (at the left) from eight others recorded only in scrubland (at the right). Between these two groups, 12 species that were recorded in both habitats were distributed along the first axis. Therefore, vegetation profile is the most important factor that the winter bird community responds to. On the second axis, scrub-dwelling species had a longer distribution than forest species. Three resident scrub specialist species (Desert Lark, Spectacled Warbler and Long-billed Pipit) occur at the positive portion of axis II. These species, which were restricted to large patches in the breeding season, remained so during winter.

Species richness and diversity

We tested for an effect of area on species richness (Figure 2A), and diversity (Fisher's Alpha, Figure 2B). We analysed data from each habitat separately, since both species–area and diversity–area curves differed between habitats (ANCOVA, species richness $F_{1,20} = 14.4$, $P = 0.001$, species diversity $F_{1,20} = 9.8$, $P = 0.005$). In forest, species richness increased with patch size (Figure 2A). Species diversity increased with patch size among the small forest patches, but levelled off among the larger ones (Figure 2B). In scrub, species richness steeply increased between the 4–5 small patches, but then levelled off (Figure 2A). Species diversity did not significantly increase with patch size. Though both species richness and diversity in the three smallest scrub patches are much lower than in larger patches, the whole pattern is not significant, since species diversity is more or less constant in larger patches (Figure 2B). Species diversity in both habitats suggests that, at least at small spatial scales, biological factors affect species accumulation in both habitats.

Area and habitat relationships

We tested whether the increase in species diversity could be related to habitat diversity by calculating the coefficient of variation (CV) of vegetation structure, corrected for sample size (Sokal and Rohlf 1981). We applied the analysis separately to each habitat, since the relationship between habitat structure and species diversity differed between habitats (ANCOVA, $F_{1,20} = 8.5$, $P = 0.009$). In the forests we calculated CV for BA, whereas in the scrub CV was calculated for perennial cover. We then used Spearman correlation to test whether Fisher's Alpha increased as vegetation CV increased. In the forests, bird species diversity increased with habitat diversity (Figure 3). In the scrub, correlation between perennial cover CV and Fisher's Alpha was not significant.

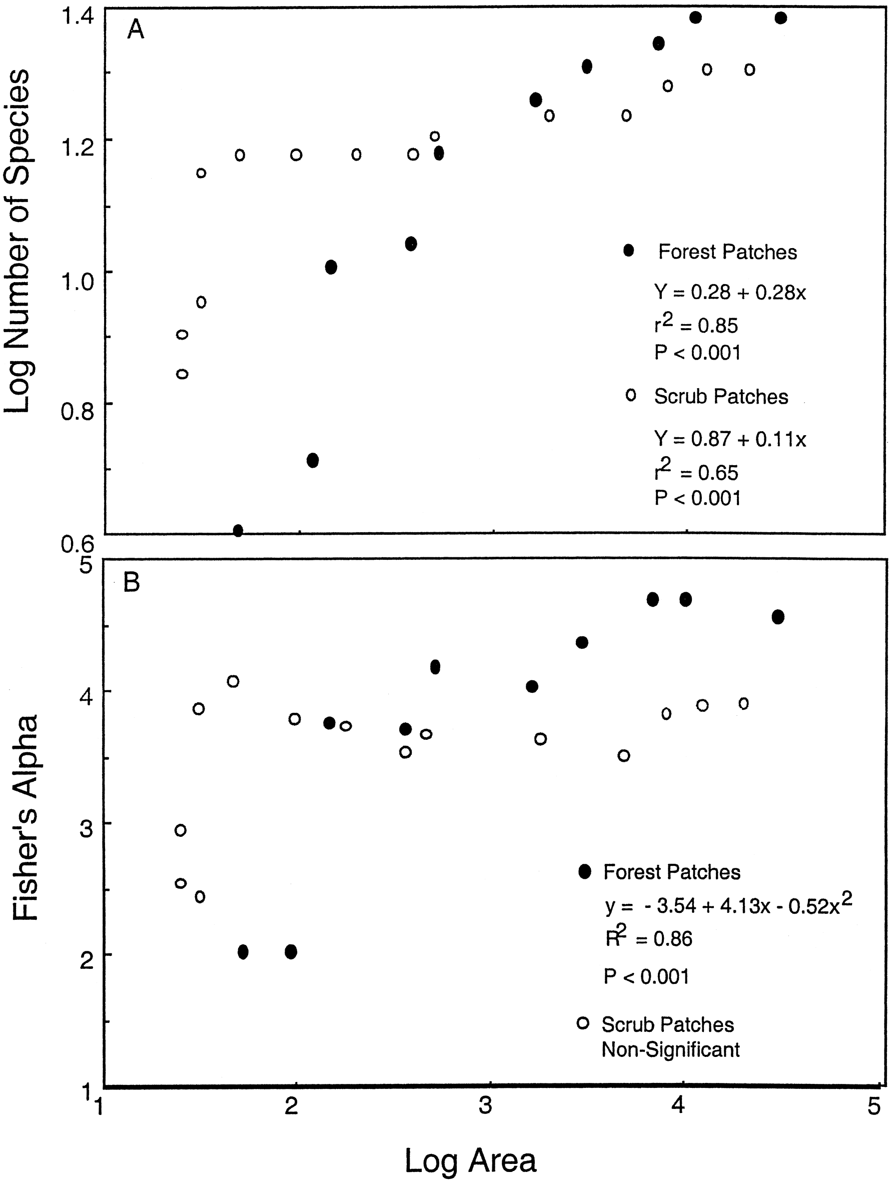

Figure 2. Winter bird species accumulation (A), and Fisher's Alpha species diversity (B) curves for forest and scrub patches in the northern Negev.

We tested whether area or habitat affect total bird densities using MANOVA. A comparison of total bird densities (Table 2) indicated that in both forest and scrub patches densities were not significantly different between years. Therefore, we

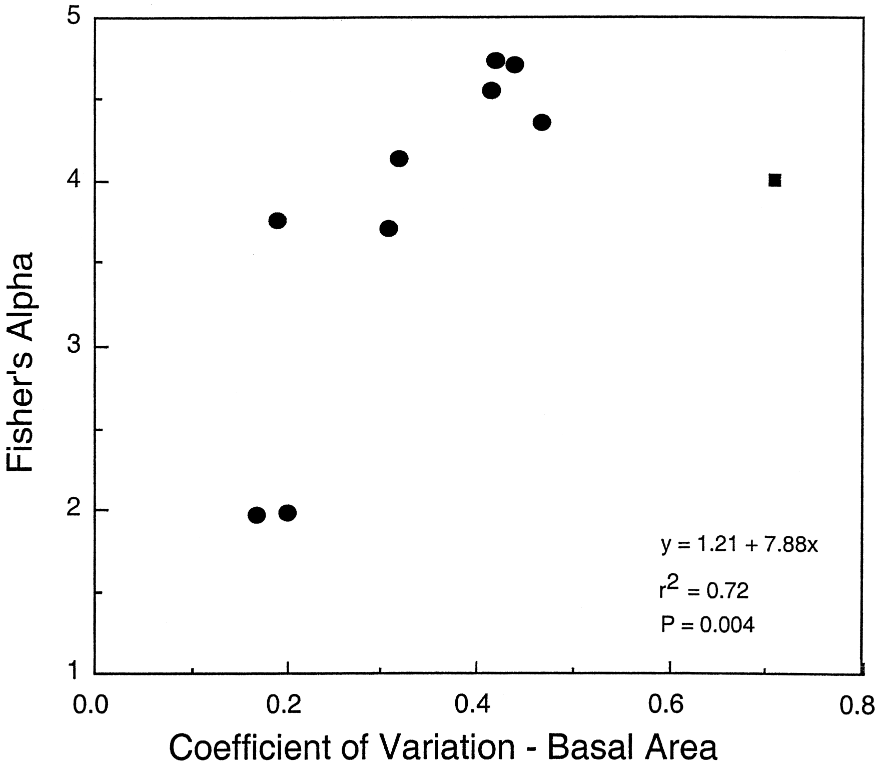

Figure 3. The relationship between habitat diversity and bird species diversity in forest patches. One outlier point is indicated (filled square). Species diversity increased according to habitat sub-type diversity (as measured by coefficient of variance of tree BA). In the scrub, no correlation was found between bird species diversity and habitat diversity (as measured by coefficient of variance of perennial cover).

combined data from the 2 years to analyse the effect of habitat structure and area on bird densities in each habitat. To test for the effect of habitat structure we used stand age in the forests and perennial cover in the scrub.

In the forests, stand age significantly affected bird densities (Table 2), but patch size did not. The interaction between patch size and stand age was significant, indicating that stand age had a different effect on bird densities in different patch sizes. In the scrub there was no significant effect of habitat, or the interaction between habitat and area on total bird densities. In contrast, patch size had a significant effect on bird densities (Table 2). The densities of eight scrubland species varied with patch size. Four species' densities increased with patch size (Desert Lark, Long-billed Pipit, Scrub Warbler and Finsch's Wheatear), while four other species decreased with patch size (Crested Lark, Meadow Pipit, Graceful Prinia, and Stonechat).

Table 2. MANOVA table for tests of time, habitat and area effects on total bird abundances. Wilk's λ values are given. Bird densities in both scrub and forest did not vary significantly between years. Therefore, habitat and area effects were tested for the whole 2 year data set in each habitat. In the forest, habitat affected bird densities but area did not. In the scrub there was no effect of habitat, while area significantly affected bird densities. Num. = numerator, Den. = denominator, DF = degrees of freedom.

Factor	Wilk's λ	*F*-value	Num. DF	Den. DF	*P*-value
A. Forest					
Year	0.732	1.415	14	54	0.178
Log area	0.640	1.684	14	42	0.096
Habitat (age of forest)	0.524	2.728	14	42	0.006
Log area × habitat	0.501	2.982	14	42	0.003
B. Scrubland					
Year	0.551	1.587	18	35	0.119
Log area	0.606	2.794	10	43	0.009
Habitat (perennial cover)	0.809	0.992	10	42	0.466
Log area × habitat	0.921	0.350	10	41	0.961

Addressing objective 2

Habitat function

We tested which environmental variables were correlated with the densities of individual species using stepwise multiple regressions. The variables entered each species equation according to their relative importance. In the forest, nine species densities could be related to environmental variables. Eight of these species equations included a single variable, whereas one equation (Graceful Prinia) included two variables (Table 3). Eight out of the 10 variables that entered forest species equations were variables that describe a gradient in vegetation structure (e.g. PC1, BA, DBH, and bush height). Area was correlated with the density of only one species (collared Dove; a negative correlation). In the scrub 14 variables entered the equations of 11 species. In contrast to forest species, scrub-dwelling species tended to correlate more with PC2 and PC3 than with PC1 (Table 3). The equations of scrubland species suggest that both vegetation and patch size are important variables affecting individual species density. Meadow Pipit and Linnet densities were directly correlated with shrub and bush density, and the densities of Spectacled Warbler and Stonechat were correlated with PC1. In contrast, the densities of Long-billed Pipit, Graceful Prinia and Finsch's Wheatear correlated with area (Table 3).

Addressing objective 3

Community dynamics between seasons

In winter, environmental variables are more likely to account for species abundance at the landscape scale, rather than at the habitat scale, if species are not restricted to

Table 3. Stepwise multiple regression equations for species abundances versus log total area and habitat variables at the habitat level (scrubland and forest data are separated). Variables in each equation are listed from most to least important. PC = principal component, DBH = diameter at breast height, Bush = bush density, ht = height.

Species	Equation	R^2	*P*
Forest species			
Collared Dove	$0.298 - 0.074 \log(\text{area})$	0.117	=0.031
Yellow-vented Bulbul	$0.571 - 0.012 (\text{PC1:Basal})$	0.107	=0.039
Graceful Prinia	$0.582 - 0.011 (\text{PC1:Basal}) + 0.087 \log(\text{longitude})$	0.452	<0.001
Sardinian Warbler	$0.026 + 0.21 \log(\text{Bush}^2)$	0.218	=0.002
European Robin	$0.869 - 0.034 \log(\text{Basal})$	0.112	=0.037
Blackbird	$-0.082 + 0.005 (\text{PC1:Basal}^2)$	0.100	=0.047
Chaffinch	$-0.569 + 0.028 (\text{PC1:Basal}^2)$	0.323	<0.001
Goldfinch	$-0.255 + 0.01 (\text{PC1:DBH}^2)$	0.306	<0.001
Eurasian Jay	$-0.478 + 0.009 (\text{PC1:DBH}^2)$	0.105	=0.041
Scrubland species			
Crested Lark	$0.321 + 0.178 (\text{PC2}) + 0.867 \log(\text{latitude})$	0.391	=0.003
Desert Lark	$1.006 - 0.925 \log(\text{latitude})$	0.287	=0.004
Meadow Pipit	$1.078 - 0.285 \log(\text{perennial}^2)$	0.156	=0.041
Long-billed Pipit	$-0.285 + 0.117 (\text{PC2:area})$	0.182	=0.026
Graceful Prinia	$0.514 - 0.121 (\text{PC3:area})$	0.253	=0.008
Scrub Warbler	$-0.102 - 0.089 (\text{PC3:altitude})$	0.223	=0.013
Spectacled Warbler	$-1.045 - 0.843 (\text{PC1})$	0.338	<0.001
Stonechat	$1.765 + 0.689 (\text{PC1}) + 0.157 (\text{PC3})$	0.342	=0.007
Finsch's Wheatear	$-0.435 - 0.122 (\text{PC2}) - 0.083 (\text{PC3:area})$	0.325	=0.009
Greenfinch	$1.111 + 0.213 (\text{PC2:longitude})$	0.205	=0.018
Linnet	$0.151 + 0.401 \log(\text{Bush})$	0.216	=0.015

one habitat, but rather spread into both scrubland and forest. To test whether bird species disperse in winter we compared the winter bird community with the summer bird community from the same study area (Shochat et al. 2001) (Table 4A). The total number of species recorded in the area in five seasons (three summers and two winters) is 41, of which only 13 were found in both summer and winter. We used the Jaccard index to calculate similarities between seasons, and between habitats within each season. The between season Jaccard index values were similar for scrubland and forest. These values were similar to the between habitat value of the winter season, but higher than the same value calculated for summer communities (Table 4A). The higher similarity between scrubland and forest assemblages in winter (Table 4A) was well illustrated by the continuous species gradient along axis I of the ordination diagram (Figure 1). In contrast, forest and scrubland breeding bird assemblages were completely separated on the first ordination axis (Shochat et al. 2001).

Niche shifts and niche breadth during winter

To assess whether winter birds responded to habitat and landscape structure similarly to breeding birds, we compared the numbers and proportions of birds that

Table 4. (A) Similarity between summer and winter bird communities, as calculated by Jaccard's coefficient. (B) A summary of the total occurrences of all species in scrub and forest patches, which represent the number of possible habitat function equations. The numbers in parentheses are of the obligatory species. A much higher proportion of the variance in species abundance has been accounted for in the breeding season. H.F. = habitat function.

A

	Summer	Winter	Total
Species richness	22	32	41
Species occurring in both habitats	6	9	

	Similarity
Between season	
Scrub	0.27
Forest	0.29
Between habitat	
Winter	0.27
Summer	0.13

B

	Summer		Winter	
	Scrub	Forest	Scrub	Forest
Species	9 (6)	14 (11)	19 (7)	19 (12)
Total occurrences	23		38	
H.F. equations obtained	20		20	
Percentage of variance explained	87		52	

correlated with environmental variables between the two seasons. In both seasons, habitat function equations were calculated at the habitat level by separating scrubland and forest guilds, in order to produce 'fine grained' equations. Since in each season several species occurred in both habitats, the total species occurrence in both habitats during a season was 23 in summer and 38 in winter (Table 4B). These numbers therefore represent all possible habitat function equations in each season. Obviously, for several species it may not be possible to obtain habitat function equations since (a) they were too rare, (b) the variable that they are associated with has not been sampled, or (c) sample errors may have been made. Yet, if the spatial scale is appropriate, environmental variables are likely to explain the variance in species abundance. In summer, stepwise regression models accounted for the abundance of 87% of the species (Table 4B), while only for 52% in the winter.

Of the 19 species detected in forest transects during winter, the densities of six were not accounted for by any variable, whereas in the scrub, 8 of the 19 species did not correlate with any variable. These included seven common and widespread species (Table 5) that were expected to correlate with the environmental variables we measured.

Table 5. Stepwise multiple regression equations for species abundances versus log total area and habitat variables at the landscape level (scrub and forest data are combined). Only species whose densities did not correlate with environmental variables at the habitat scale (six in scrub, and two in forest patches, marked with *) are shown. Variables in each equation are listed from most to least important. PC = principal component, DBH = diameter at breast height.

Species	Equation	R^2	P
Wood Lark	$0.238 - 0.005$ (PC1:DBH)	0.187	=0.016
Sardinian Warbler	$0.036 - 0.005$ (PC1) $- 0.046$ (PC2)	0.245	<0.001
Chiffchaff*	$0.056 + 0.008$ (PC1)	0.376	<0.001
Black Redstart	$0.156 - 0.004$ (PC1)	0.203	<0.001
Song Thrush	–	–	–
Great Tit*	$0.012 + 0.005$ (PC1)	0.308	<0.001
Corn Bunting	$0.195 - 0.005$ (PC1)	0.110	=0.006
Chaffinch	$0.102 + 0.002$ (DBH^2)	0.367	<0.001
European Serin	$0.171 - 0.004$ ($PC1{:}Perennial^2$)	0.157	=0.001

We therefore tested whether the habitat scale was too small to account for species abundance in winter. To assess how these species densities change along environmental gradients we calculated their habitat function equations at the landscape scale (Table 5). To do this, we combined data of species densities and environmental values from scrub and forest transects and applied stepwise multiple regressions for the species that did not respond to environmental variables at the habitat scale. The landscape level habitat function equations in Table 5 reveal that six of these species are associated with PC1, which describes gradients in vegetation along the whole landscape. Yet, the abundance of one species, the Song Thrush, did not correlate with any variable even at the landscape level (Table 5).

Addressing objective 4

Changes in resident species' niche breadth

To test whether the differences in bird abundance gradients between seasons are indeed the result of a larger scale dispersal during winter, we compared the distribution of all 12 permanent resident species that were detected in both summer and breeding surveys along the two main environmental gradients extracted by the principal component analysis – PC1 and PC2. We assumed that for each species throughout its range, the minimum and maximum values of each PC define the niche breadth for the species along an environmental gradient. We calculated the niche breadth by subtracting the minimum from the maximum PC value (for PC1 and PC2), and then compared the summer and winter niche breadth by using repeated measures ANOVA. The total gradient length of PC1 ranged between -1.92 in the most extreme scrub transect and 61.06 in the most extreme forest transect. The gradient length on the PC2 axis was much shorter and ranged between -7.03 and -1.75. Average niche breadths of resident bird species during summer and winter were 25.55 and 31.90, respectively. The extension in species distribution

Table 6. A comparison between the summer and winter niche breadth of resident birds along PC1 and PC2, using a repeated measures ANOVA. Resident bird species significantly extended their distribution along PC1 in winter. No change in niche breadth was detected along PC2. SS = sum of squares, DF = degrees of freedom, P = probability.

Source	SS	DF	F ratio	P
PC1				
Time	241.36	1	7.37	0.020
Error	360.13	12		
PC2				
Time	0.427	1	0.562	0.469
Error	8.349	12		

in winter along this axis is significant (Table 6). Along PC2 we did not find a significant difference in niche breadth between seasons (Table 6), with average niche breadth in summer and winter of 3.13 and 2.86, respectively.

Discussion

Winter bird species diversity patterns in the northern Negev were similar to those described for the breeding bird community (Shochat et al. 2001). Densities of winter bird species mostly correlated with vegetation structure as indicated by ordination (Figure 1). The first ordination axis, a measure of vegetation cover, separated scrub-dwelling from forest-dwelling species. However, despite the similarities in species diversity between seasons, the ordination suggests that unlike among breeding birds, more species do not discriminate between scrubland and forest during the winter (25% of the species are found in both habitats in the winter, while only 13% in summer). Though this may be the result of winter dispersal into food-rich patches, as suggested by Hutto (1985b), individual bird species were still distributed along a vegetation structure gradient as the major axis (Figure 1).

Species diversity patterns, especially in the scrub, may suggest a ‘passive sampling’ of species by habitat patches (Figure 2B). However, biological factors such as area and habitat structure do affect bird densities in scrubland and forest, respectively (Table 2). Furthermore, vegetation structure that was correlated with bird species diversity in the forest, had no effect on scrub species diversity (Figure 3). These results are similar to those from the breeding bird community (Shochat et al. 2001), suggesting that the structure of the scrub–forest matrix determines the abundance and distribution of species in the landscape in the same way for relatively different temporal communities. These results are important for conservation and future management programs, since they indicate that recommendations for habitat management for breeding birds (Shochat et al. 2001) may also be appropriate for winter birds. Most importantly, scrub patches larger than 50 ha should be conserved. This is a crucial step for the conservation of the endangered scrub specialist Long-billed Pipit, which suffers from the continuous fragmentation of the scrub habitat. This species density was negatively correlated with PC2 (Table 3), which in turn was negatively correlated with area (Shochat et al. 2001).

The question of whether area or habitat are the primary factors that affect species diversity has been addressed in the past with respect to breeding bird communities (Ambuel and Temple 1983; Blake and Karr 1987). During the breeding season nest predation and brood parasitism are associated with edge effects in small habitat patches (Brittingham and Temple 1983; Wilcove 1985; Robbinson et al. 1995). In winter, patch size may determine bird flocking behaviour and vigilance (Telleria et al. 2001). In our study, area was negatively correlated with the density of Long-billed Pipit. While large scrub patches seem to passively sample bird species, there is a steep increase in both species richness and diversity in small patches (Figure 2). Species density (Table 2) also correlated with area and not with habitat structure in the scrub, though area effects were somewhat more confounded than in summer at the species level (Table 3). Resident scrub-dwelling species are probably associated with area year round, since whether they are restricted to large patches (e.g. Long-billed Pipit) or small patches (e.g. Graceful Prinia) they remain within the same home range.

In the forest, winter species abundance and distribution were very similar to those found for breeding birds. Forest birds were associated with habitat structure variables, rather than with area (e.g. Figures 1 and 3, Tables 2 and 3). Altogether, the results may suggest that relatively different communities respond to landscape structure in a similar way. The patterns of species abundance and distribution in the northern Negev are determined by the same factors in each habitat, even after 'replacing' a high proportion of the species in the species pool. Therefore, future management strategies as suggested for breeding birds (Shochat et al. 2001) will also be appropriate for maintaining or even increasing winter bird species diversity.

Winter niche shifts and the niche breadth dimensions

A crucial step for conservation of winter bird population is to assess the scale at which species abundance and habitat variables are correlated. Our results suggest that assessing habitat structure and bird abundance correlations may require larger spatial scales than those used to study breeding birds.

There are three ways to assess the differences between summer and winter bird communities: (a) compare species–habitat relationships within the same species between its summer and winter ranges (see e.g. Hutto (1981, 1985b) for the new world warblers); (b) at the community level, compare habitat use by different species guilds (winter versus summer) within the same region; (c) compare the niche breadth of the same species, in the same area, between summer and winter (i.e. dispersal of resident species), as done by Root (1967) and also in this study.

Specifically, we tested whether the evidence of our study concurs with a previous study on summer birds, on both the community and the population level (Shochat et al. 2001).

The higher similarity between forest and scrubland species assemblages during winter (Table 4B) supports the idea that many species 'view' the landscape as an 'undivided heterogeneous' matrix (Addicott et al. 1987). If so, the question of whether patch area affects species diversity may not be relevant for many species during winter. Our hypothesis that bird species extend their niche, including dispersal from large into small habitat patches, did not hold for resident scrub-dwelling species. On one hand, the Long-billed Pipit, Desert Lark and Scrub Warbler remained restricted to large patches. On the other hand, Graceful Prinia density decreased with area as in the breeding season. The Crested Lark, showing no correlation with area in summer, negatively correlated with area in winter. Altogether, these results suggest that the summer distribution of resident scrub-dwelling species remains similar in the non-breeding season.

At the population level, it seems that different dispersal patterns of species in winter grounds change the relationship between species and habitat and therefore should be evaluated at a much larger scale. That is, out of the breeding season, species that breed in one habitat sub-type may move across several distinct habitat sub-types while foraging. The same phenomenon may occur at a larger scale, where birds that breed in one habitat move across several foraging habitat types during winter. Lack (1971) and Hutto (1981, 1985a,b) defined this phenomenon as a habitat or niche 'shift'. Our results suggest that *extension* of the niche breadth would be a more accurate term than a *shift* in niche. A comparison between the niche breadth of resident species revealed that this is indeed the case in the northern Negev (Table 6). This niche extension may occur on the basis of habitat structure or area constraints. For instance, birds that only breed on forest trees may use both forest and savannah habitats for foraging during winter. Another possibility is that species disperse from larger, source habitat patches to smaller patches, where breeding populations cannot persist.

In the northern Negev, a good example for the latter case is the Great Tit, that spreads into small forest patches in winter (Shochat 1999). At the habitat scale, regression models can no longer account for the variation in tit abundance. An extension in the spatial scale to also include scrub patches is required to reveal a pattern in its abundance (Table 5). The apparently random distribution of three other species across forest patches can be interpreted at three different scales. At the habitat scale, the Chiffchaff is a widespread wintering species, restricted to forest. Chiffchaffs are found across a large variety of forest sub-types (in terms of tree type and age of stand). Within the forests, no gradient in their abundance has been identified. At the inter-habitat scale, the Greenfinch, like other granivorous species that breed in the forests, flocks in winter and forages mainly in scrub. Greenfinch density showed no correlation with any variables within the forests. Across the forest–scrubland landscape Greenfinch abundance correlated with PC2 (data not shown). Therefore, to understand the gradients in Chiffchaff and Greenfinch abundances one should measure these gradients across the whole landscape. The PC2 gradient within forest transects is not sufficient for assessing Greenfinch abundance, whereas in the case of the Chiffchaff, its absence from the scrub gives a better resolution, revealing a pattern in its abundance. At the entire landscape scale, the Song Thrush did not yield any pattern, neither at the habitat nor at the landscape scale. It may require a biogeographical scale to reveal any pattern in the distribution of this species.

In the scrub, the density of 8 out of 19 species (Wood Lark, Black Redstart, Song Thrush, Sardinian Warbler, Chaffinch, Goldfinch, European Serin and Corn Bunting) could not be accounted for by habitat scale. All are widespread across the entire landscape. Five of them are granivorous species that forage in flocks and move across large areas and habitat types. Flocking granivorous species that move across very large foraging patches during winter may not be related to environmental variables at any scale (habitat or landscape) as found by Pearson (1993). Yet, this may also support the idea that food abundance may become as important as habitat structure in affecting habitat use by non-breeding birds (e.g. Hutto 1981, 1985a, b; Meents et al. 1982; Robinson and Sutherland 1999; Donald et al. 2001; Johnson and Sherry 2001; Moorcroft et al. 2002). This does not exclude association between bird density and vegetation structure. However, since birds extend their ‘habitat concept’, these relations may be obvious only across a larger spatial scale. Indeed, 6 of the 8 species responded to vegetation (PC1 or DBH) at the landscape level (Table 5). The fact that at the landscape level, all species that did not show a pattern at the habitat level correlated with PC1 (Table 5) concurs with the results shown in Table 6, with niche breadth extension during winter along the PC1 gradient. This indicates that birds disperse in winter along a vegetation gradient to patches that may provide food and shelter for individual birds, but cannot serve as breeding territories.

To conclude, the results of this study suggest that at the population level the niche breadth of winter birds is wider than that of summer birds. Despite this, the same factors that were found to shape the breeding bird community (habitat structure in the forest and area in the scrubland) seem to affect the winter bird community. The fact that area remains a major factor that affects scrub-dwelling birds in winter may suggest that, in principle, the extension of niche is a unidirectional process, common to a majority of the forest birds. Altogether, the accumulated data on the dispersal of winter bird habitat use strongly suggest that differences in decision-making by individuals in different seasons may lead to niche extension, and should be incorporated into future bird habitat conservation programmes.

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Appendix 1. Common and Latin names of regular winter bird species in scrubland and forest in the northern Negev. Species wintering in other habitats in the area are not shown. Underlined species are those that were detected in our line transects. Status: R = resident, W = winter visitor, (N) = nomadic, (D) = local dispersal. Habitat: S = scrubland, F = forest (in cases where birds occupy both habitats, the major habitat is mentioned first).

Species	Status	Habitat
Chukar (*Alectoris chukar*)	R	S F
Stone Curlew (*Burhinus oedicnemus*)	R	F S
Woodcock (*Scolopax rusticola*)	W	F
Rock Pigeon (*Columba livia*)	R	S F
Collared Dove (*Streptopelia decaocto*)	R	F
Little Owl (*Athene noctua*)	R	S F
Hoopoe (*Upupa epops*)	R	F S
Syrian Woodpecker (*Dendrocopus syriacus*)	R	F
Crested Lark (*Galerida cristata*)	R	S F
Wood Lark (*Lullula arborea*)	W	F S
Desert Lark* (*Ammomanes deserti*)	R	S
Long-billed Pipit (*Anthus similis*)	R	S
Meadow Pipit (*Anthus pratensis*)	W	S F
Yellow-vented Bulbul (*Pycnonotus xanthopygos*)	R	F
Hedge Accentor (*Prunella modularis*)	W	F
Stonechat (*Saxicola torquata*)	W	S F
Black Redstart (*Phoenicurus ochruros*)	W	S F
Finsch's Wheatear (*Oenanthe finschii*)	W	S
Robin (*Erithacus rubecula*)	W	F
Blackbird (*Turdus merula*)	R	F
Song Thrush (*Turdus philomelos*)	W	F S
Graceful Prinia (*Prinia gracilis*)	R	S F
Scrub Warbler** (*Scotocerca inquieta*)	R	S
Sardinian Warbler (*Sylvia melanocephala*)	RW	F S
Spectacled Warbler (*Sylvia conspicilata*)	R	S
Blackcap (*Sylvia atricapilla*)	W	F
Chiffchaff (*Phylloscopus collybita*)	W	F
Great Tit (*Parus major*)	R	F
Orange-tufted Sunbird (*Nectarinia osea*)	W (D)	F
Jay (*Garrulus glandarius*)	R	F
Hooded Crow (*Corvus corone cornix*)	R	F
Rock Sparrow (*Petronia petronia*)	R	S
House Sparrow (*Passer domesticus*)	R	F S
Spanish Sparrow (*Passer hispaniolensis*)	R (N)	S F
Chaffinch (*Fringilla coelebs*)	W	F S
Brambling (*Fringilla montifringilla*)	W	F
Siskin (*Carduelis spinus*)	W	F
Goldfinch (*Carduelis carduelis*)	R	S F
Greenfinch (*Carduelis chloris*)	RW	S F
Linnet (*Acanthis cannabina*)	W	S F
European Serin (*Serinus serinus*)	W	S F
Corn Bunting (*Miliaria calandra*)	R (N)	S F

*Restricted to southern and eastern scrubs.

**Restricted to eastern scrubs.

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