Ornis Fennica 75: 27–37. 1998

Avian community composition and patterns of bird distribution within birch–heath mosaics in north-east Scotland

Simon Gillings, Robert J. Fuller & Andrew C. B. Henderson

Gillings, S. & Fuller, R. J., British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, England
Henderson, A. C. B., Farthings, The Forstal, Preston, Canterbury, Kent, CT3 1DR, England

Received 12 June 1997, accepted 24 November 1997

Territory mapping and transect counts were made in upland birch scrub (46 ha) in north-east Scotland to document the bird community and assess responses of birds to habitat variation. The bird community was species poor, supporting approximately 20 species. Richness and diversity were low compared with other British scrub habitats. The two dominant species were Willow Warbler (52% of territory mapping registrations) and Chaffinch (18% of registrations). Densities derived from territory mapping and transect counts (Distance sampling) were similar. Willow Warbler densities were high and comparable with preferred habitats in lowland England and Fennoscandia. Contour mapping, correlation and canonical correspondence analysis demonstrated that successional stage, represented by birch cover, was the single most important factor determining community composition and individual species' distributions. Meadow Pipits persisted at low densities in sparse birch; Tree Pipits occurred throughout the range of birch densities. Willow Warblers preferred areas of medium height birch at intermediate canopy cover. Wren, Great Tit and Long-tailed Tit occurred in older birch scrub. The relatively simple bird–habitat relationships reported are contrasted with more complex patterns elsewhere. These findings are discussed in the context of scrub and woodland regeneration in upland Britain with particular reference to mosaics and maintenance of avian diversity.

1. Introduction

In lowland Britain, scrub is largely an ephemeral habitat that develops in the vegetational succession following disturbance. In the uplands scrub was once naturally extensive but has been mostly eradicated by grazing and burning. Fuller (1995) reviewed existing knowledge of bird populations of scrub and showed a dearth of information on scrub bird communities generally. Furthermore, he highlighted the potential importance of scrub for the conservation of bird populations stressing that some types of scrub could support distinctive assemblages of species. Though a small number of studies have considered bird communities of mature upland deciduous woodland (e.g. Yapp 1956, 1974, Bibby et al. 1989) few if any have investigated upland scrub. This paper describes the bird community of developing birch *Betula* spp. scrub in Deeside, Scotland.

Scrub regeneration is becoming a significant ornithological issue in the British uplands. Re-

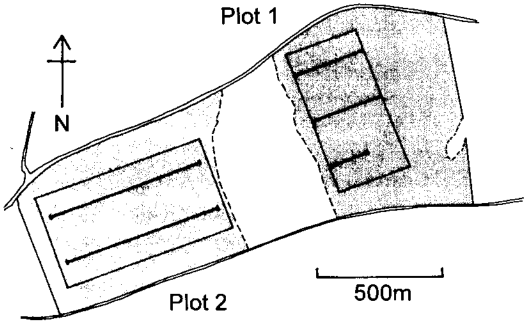

Fig. 1. Map of Westmoor showing the position of scrub patches (shaded) and open moorland (unshaded). The study area was bounded by birch scrub to the north, conifer plantation to the west and south and farmland to the east. Rectangles define the boundaries of the territory mapping plots and the transects are represented by bars within each plot.

ductions in grazing pressure, through lower sheep stocking densities combined with deer control, should favour extensive scrub and woodland regeneration (Hester & Miller 1995). With increasing concern about overgrazing it is likely that some areas of upland Britain will revert to mosaics of open moorland and birch or pine *Pinus* dominated scrub. Usher and Thompson (1993) speculated that such mosaics could provide niches for a wide diversity of bird species including ones associated primarily with scrub and others with open heath. However, there have been few if any studies of bird communities in such mosaics of heath and scrub. We therefore set out to document species composition, richness, diversity and overall density of birds in birch scrub typifying areas where grazing pressure has reduced. We compare these community parameters with those from other scrub habitats in Britain and Fennoscandia. Furthermore, we explore factors influencing the distribution of selected bird species within these mosaics and ask whether species associated with open habitats can persist in scrub–heath mosaics. Additionally, we wanted to compare the densities calculated from territory mapping and from transect counts analysed by various techniques. Recent transect studies have used the distance sampling approach (e.g. Summers & Buckland 1996) but there have been no direct comparisons of the results obtained by this and more ‘traditional methods’.

2. Methods

2.1. Study area

The study was undertaken at Dinnet National Nature Reserve, Deeside, eastern Scotland in 1996. Dinnet NNR (1 415 ha) contains large expanses of birch varying in age from regenerating seedlings through to 125-year-old mature trees and climax Scots Pine. Part of the reserve, a derelict grouse moor called Westmoor, provided a large expanse of birch woodland with a well-documented history. In the 1950s the cessation of burning, vigorous control of the red deer *Cervus elaphus* population, removal of sheep and an outbreak of myxomatosis provided ideal conditions for the regeneration of birch seedlings on Westmoor. Prior to birch invasion Westmoor was predominantly *Calluna vulgaris–Arctostaphylos uva-ursi* heath. A fire in 1974 destroyed most of the trees and in 1996 the scrub consisted of trees 22 years or less in age. Following the fire, birch recolonisation was slow in the drier, sandy areas producing a mosaic of open heath and birch patches at different successional stages from thickets less than 2 m tall to 12 m tall trees. In 1988, ca. 25 ha of birch was clear-felled to preserve the rare *Arctostaphylos* heath community. This effectively created an area of open moorland separating two tracts of birch scrub, ca. 70 ha to the east containing territory mapping plot 1 and ca. 50 ha to the west containing territory mapping plot 2 (Fig. 1).

2.2. Field methods

The bird community was censused by territory mapping (four visits) and transect counts (four visits) on calm, dry mornings during late May and early June. Two territory mapping plots of approximately 28 ha and 18 ha were marked out and divided into 100 m × 100 m squares. To facilitate position-finding, highly visible numbered markers were placed on trees at the corners and centre of each square. These markers subsequently became recording stations for six primary habitat variables (Table 1). Habitat mapping was undertaken by one observer (RF), and territory mapping was undertaken by another observer (AH) following standard methodology used to differentiate between simultaneous registrations of different birds and multiple registrations of the same bird (see Marchant et al. 1990). The mapping plots encompassed part of a more extensive transect count study area. Plot 1 contained three transect strips (150 m, 300 m and 300 m) and Plot 2 contained two transect strips (both 650 m). Transects were two-banded (0–50 m and 51–100 m) and 200 m apart. Two observers (SG & RF) each made two visits to each transect (four visits in total) and marked field registrations onto pre-prepared 1:2 500 maps using standard notation to differentiate between multiple registrations from the same bird and from different birds. Visits to mapping plots and transects were sequenced so that no one area was censused consistently earlier or later than another.

2.3. Analyses

We described the territory-mapped community using expected species richness ($E(S_{50})$) and Simpson's diversity index (D). $E(S_{50})$ was calculated by rarefaction using 50 registrations drawn randomly without replacement from the pool of detections (see James & Rathbun 1981); D was $1/\Sigma p_i^2$, where p was the proportion of registrations contributed by species i. Density estimates were derived from both mapping and transect counts so that simple comparisons could be drawn between results from the two methods. For territory mapping densities (MAPPING) the total number of territories of each species was compiled by assuming that a territory was defined by registrations from at least two visits; birds holding territory on just one visit were counted as 0.5 territories and the proportion of registrations falling on or within the study boundary was used for peripheral territories. Transect counts were analysed by three different techniques (MEAN, MAX and DISTANCE). MEAN was the mean number of registrations across the four visits. MAX was the maximum number of registrations from any one of the four visits, an adaptation of the 'Blondel method' for point counts (Blondel et al. 1970). In both cases registrations more than 50 m from the transect were excluded and we assumed that each registration related to one 'territory'. Since transect counts were predominantly of territorial individuals (mainly singing birds) density estimates were comparable with MAPPING densities without conversion to 'pairs' or 'territories'. These are not standard methods but we believe that four visits are probably adequate for surveying this simple habitat, particularly since the breeding season is so truncated and involves so few species. Thirdly, densities of the four most common species were calculated from transect counts using the DISTANCE program (version 2.1, Laake et al. 1994). This software fits a detection probability function to model the decline in detectability with distance from the transect line. DISTANCE fits the four basic detection functions (Half-normal, Uniform, Negative exponentials and Hazard-rate) and se-

Table 1. Definition of habitat variables. All variables are recorded within a 25 m radius of the station unless otherwise stated. Percentage estimates are to the nearest 5%. HHGT to nearest 0.1 m.

Primary habitat variables (measured in the field)	
COVB	% cover of all birch
CAN1	% of the birch canopy comprised of trees less than 1 m tall
CAN2	% of the birch canopy comprised of trees between 1 m and 4 m tall
CAN3	% of the birch canopy comprised of trees more than 4 m tall
COVH	% cover of heather within a 5 m radius of the station
HHGT	Estimated modal height (cm) of heather spp. within a 5 m radius of the station
Secondary habitat variables (derived from primary variables)	
COV1	% cover of birch less than 1 m tall (COVB × CAN1)
COV2	% cover of birch between 1 m and 4 m tall (COVB × CAN2)
COV3	% cover of birch more than 4 m tall (COVB × CAN3)
BHGT	Index of birch height (m) calculated using the following formula: BHGT= (0.01 × CAN1 × 0.5) + (0.01 × CAN2 × 2.5) + (0.01 × CAN3 × 6)

lects the model with the smallest Akaike Information Criterion score for density calculations (Buckland et al. 1993). DISTANCE then provides a measure of density by including an estimate of the number of birds not recorded due to their distance from the transect line.

All subsequent analyses used territory mapping data only. The spatial distribution of common passerines was explored by plotting the location of a species' registrations onto contour maps of habitat variables using the SURFER software (Golden Software Inc. 1994). For this analysis and subsequent ones, four 'secondary' habitat variables were calculated (Table 1). Apparent spatial relationships between registrations and contour bands were further explored by Spearman rank correlation in the SAS statistical package (SAS Institute Inc. 1986). Data were the number of registrations of a species per 100 m × 100 m square (the unit of analysis) and weighted means of habitat variables. The latter were calculated because the abundance of a species in a sample square is likely to be influenced by the habitat in that square and, to a lesser extent, by habitat in adjacent squares. Means were weighted more towards observations from the centre of the square than from the corners (ratio 4:1:1:1:1). Contiguous squares therefore cannot be treated independently so two data subsets were created where squares only made contact at corners; an analogy would be the black and white squares of a chequer board. Henceforth, the two subsets will be called datasets A and B.

We used the CANOCO package (ter Braak 1990) to perform canonical correspondence analysis (CCA) to relate patterns of community composition to primary and secondary habitat variables. CCA is a multivariate direct gradient analysis approach that produces ordination axes of unimodal species responses which are explained by linear combinations of environmental variables (Jongman et al. 1995). CCA was run separately on subsets A and B of the number of registrations of each species in each 100 m × 100 m square and weighted environmental variables (see above). Loadings of independent variables on canonical axes from each run were ranked and averaged. The ranked mean rank gave an indication of the relative positions of variables along the axis.

3. Results

3.1. Richness, diversity and density

The bird community under investigation was one of very low diversity. Expected species richness by rarefaction was 10.2 and Simpson's diversity index was 4.4. The total species pool from transect counts and territory mapping was only 20 species (Table 2). Willow Warbler and Chaffinch together accounted for 70% of the 336 mapping registrations; Willow Warbler alone accounted for 52% of registrations. Table 2 presents four estimates of species' density based on territory mapping and transect data. Density estimates from transect counts were slightly higher than those derived from territory mapping. Excluding DISTANCE, density estimates which were only calculated for four species, the MEAN method from transect data gave the best approximation to MAPPING density (Spearman rank correlation $r_s = 0.97$, $P = 0.0001$ compared with $r_s = 0.95$, $P = 0.0001$ for the MAX method). Willow Warbler occurred at the highest density followed by Chaffinch and Tree Pipit.

3.2. Contour mapping and density correlates

Contour mapping revealed a strong association between Willow Warbler registrations and birch cover (Fig. 2C and D). This was most apparent on Plot 2 where Willow Warbler registrations were only present in intermediate and high birch cover (Fig. 2D). There was a strong positive relationship between the density of Willow Warbler registrations in birch cover contour bands (both plots combined) and birch cover (Fig. 3B). The distribution of Meadow Pipit and Tree Pipit registrations suggested a preference for low and intermediate birch cover with Meadow Pipit more strongly concentrated into very open areas (< 20% birch cover) than Tree Pipit (Figs. 2A and B and 3A). The distribution of Chaffinch registrations was weakly linked to birch cover (Figs. 2E and F and 3C). There was no clear evidence for any species showing preference for edges, i.e. higher densities of registrations at the edges of glades or birch patches.

Correlation analysis was performed on the number of Willow Warbler registrations (NOWW) in 100 m × 100 m squares and weighted habitat variables (Table 3). Willow Warbler density was positively correlated with overall birch cover (COVB). There was a weak negative correlation between Willow Warbler density and low birch canopy (CAN1) and a positive correlation with medium height canopy (CAN2). There was a high degree of intercorrelation between the habitat variables. In particular, short and medium canopy birch were strong correlates of overall birch cover. The correlation between Willow Warbler density and COV2 was probably a consequence of the strong correlation between COVB and COV2. These results suggest that Willow Warbler distribution was primarily a response to birch cover rather than to more complex elements of scrub or field layer structure. No statistics were performed on Meadow Pipit, Tree Pipit or Chaffinch because sample sizes were small.

3.3. Community analyses

Only the first canonical axis could be interpreted clearly; loadings of variables and species on subsequent axes could not be related to meaningful ecological processes or gradients. Table 4 gives the correlation coefficients of the environmental variables on the first canonical axis. The two largest negative coefficients were consistently COVB and COV2. Axis one explained 35% (mean) of the variance in the species–environment relation and represented a successional continuum from open areas with either very short or scattered tall birches (positive end) to closed canopy birch composed of relatively large amounts of medium height birch (negative end). Table 5 gives species scores for the first canonical axis. Note that three species, Wren, Great Tit and Long-tailed Tit, consistently had large negative weightings, Willow Warbler had an intermediate weighting. Both pipit species had large positive weightings, those for

Table 2. Bird densities (highest first) based on territory mapping and transect census. MAPPING densities are derived from territory estimates (territories/10 ha). Transect densities are birds/10 ha; MEAN uses the mean number of registrations over four visits, MAX uses the maximum number of registrations recorded on any one visit, DISTANCE is the density derived using the detection probability model shown with 95% confidence limits in parentheses. + represents insufficient information for territory definition, – denotes species present but not recorded by this method.

Species	MAPPING	MEAN	MAX	DISTANCE	Model
Willow Warbler (*Phylloscopus trochilus*)	8.2	11.5	12.7	12.8 (10.1–16.2)	Half-normal
Chaffinch (*Fringilla coelebs*)	2.7	2.9	3.4	3.1 (2.4–4.1)	Uniform
Tree Pipit (*Anthus trivialis*)	1.0	1.2	2.4	1.1 (0.7–1.8)	Uniform
Meadow Pipit (*Anthus pratensis*)	0.8	0.6	1.0	0.6 (0.3–1.2)	Uniform
Robin (*Erithacus rubecula*)	0.6	0.9	1.5	–	
Wren (*Troglodytes troglodytes*)	0.6	0.6	1.5	–	
Bullfinch (*Pyrrhula pyrrhula*)	0.2	0.4	1.0	–	
Great Tit (*Parus major*)	0.1	0.1	0.5	–	
Blue Tit (*Parus caeruleus*)	+	0.2	0.5	–	
Coat Tit (*Parus ater*)	0.1	0.1	0.5	–	
Long-tailed Tit (*Aegithalos caudatus*)	0.1	0.1	0.5	–	
Yellowhammer (*Emberiza citrinella*)	+	0.2	0.5	–	
Woodpigeon (*Columba palumbus*)	+	0.2	1.0	–	
Wigeon (*Anas penelope*)	0.2	–	–	–	
Cuckoo (*Cuculus canorus*)	+	–	–	–	
Jay (*Garrulus glandarius*)	+	–	–	–	
Curlew (*Numenius arquata*)	+	–	–	–	
Woodcock (*Scolopax rusticola*)	–	–	–	–	
Black Grouse (*Tetrao tetrix*)	+	–	–	–	
Green Woodpecker (*Picus viridis*)	–	–	–	–	
Skylark (*Alauda arvensis*)	+	–	–	–	
Crossbill spp. (*Loxia*) spp.	+	–	–	–	

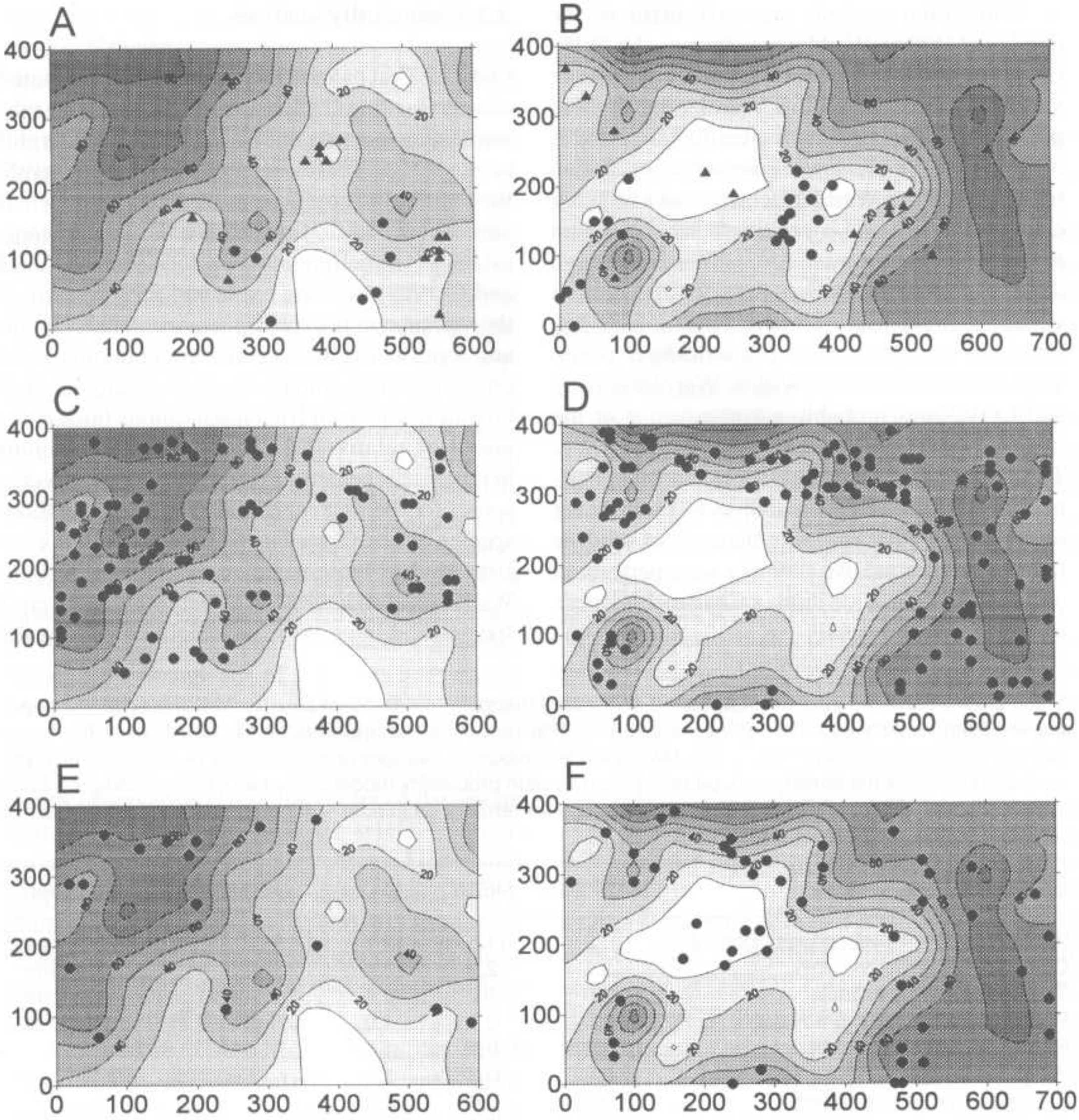

Fig. 2. Contour maps showing the spatial variation in birch cover (%) on Plot 1 (A, C and E) and Plot 2 (B, D and F). Registrations of Meadow/Tree Pipit (A and B), Willow Warbler (C and D) and Chaffinch (E and F) from territory mapping are overlayed. All registrations are filled circles except Tree Pipit registrations (triangles). Axes measure distance (metres). Contour bands are 10% increments of birch cover produced using a kriging algorithm in the SURFER package. Isocline labels are percent cover of birch.

Meadow Pipit being larger than those for Tree Pipit in dataset A but were reversed in dataset B.

4. Discussion

The most striking feature of the bird community of Scottish birch scrub is its low species richness and diversity, being strongly dominated by a small number of species. To put this study into context Fig. 4 compares species richness by rarefaction and Simpson's diversity index for Westmoor with the 39 British scrub mosaic sites examined by R. J. Fuller, S. Gillings and S. J. Gough (unpubl.). The 39 sites were all censused by territory mapping between 1966 and 1982 as part of the British Trust for Ornithology's Common Birds Census (see Marchant et al. 1990). Despite differences in study methods, the three sets of data are probably comparable because of the simple nature of the communities involved. Of these sites, Westmoor is one of the most northerly and its scrub bird community rates as the most species poor (by rarefaction) and the third lowest in terms of diversity. This relationship parallels the pattern shown by Fuller (1982) who mapped species richness in woodland throughout Britain noting that woods in south-east England supported between 1.8 and 2.8 times more species than woods in northern and western Scotland. Total bird density in scrub and woodland also is relatively low in northern Scottish birchwoods and can be as little as 25% of total density in English and Welsh birchwoods (Yapp 1956). Latitude explains some of the observed differences in Table 2 but additionally the immature and structurally simple nature of birch scrub probably reduces the number of niches. For example, there are few large trees, little dead wood to accommodate hole-nesters, and typically the scrub is overwhelmingly composed of just one tree species.

Bird communities in Scottish scrub and woodland closely resemble those in similar Fennoscandian habitats which are also dominated by just two species, Willow Warbler and Chaffinch (or Brambling *Fringilla montifringilla*). In published studies of birch, Willow Warbler and one or other of the *Fringilla* finches account for between 36% and 59% of the bird community (Yapp 1956, 1974, Enemar et al. 1984, Bibby et al. 1989, Järvinen & Rajasärkkä 1992, Solonen 1996). A varied list of species, each occurring at low frequency, make up the remainder of the community.

Density estimates derived from the four different methods were in broad agreement though those from transect data tended to be slightly higher. This anomaly may arise because transect methods make use of all registrations (including those of females and non-territorial birds) whereas densities derived from territory mapped data focus on actively-territorial birds. To our knowledge, the similarity between estimates derived by mapping and DISTANCE sampling has not been demonstrated previously.

Despite small inconsistencies, the presented densities compare well with those from published

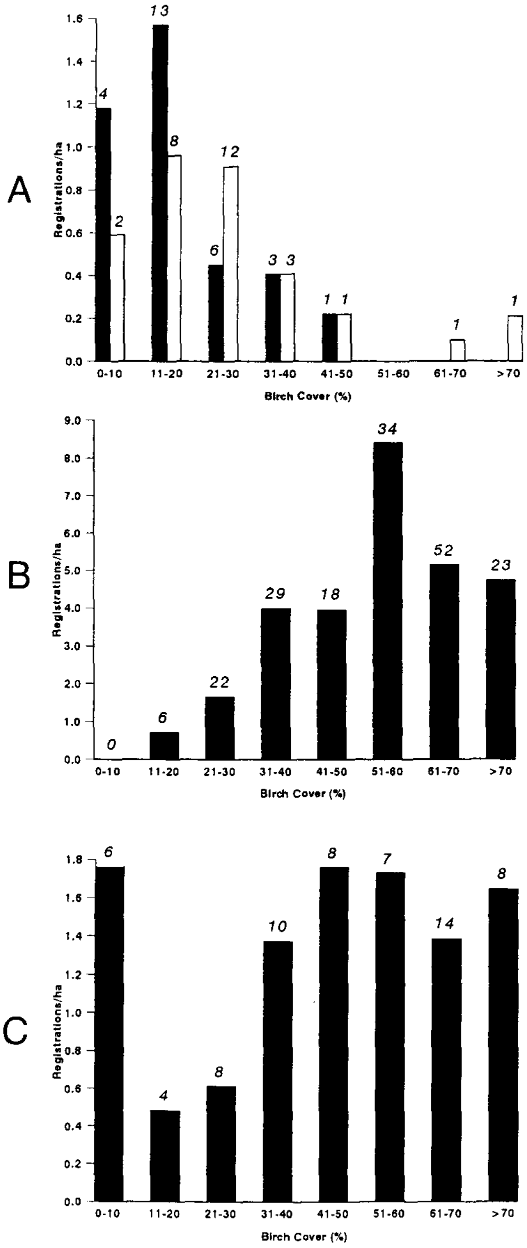

Fig. 3. Histograms of Meadow/Tree Pipit (A), Willow Warbler (B) and Chaffinch (C) density at different levels of birch canopy cover for both plots combined. Density is the number of registrations per hectare of mapping plot contained within each contour band shown in Fig. 1. Numbers are the frequency of registrations in each contour band across both plots. For comparative purposes Meadow Pipit density (solid bars) and Tree Pipit density (shaded bars) are shown on the same histogram.

studies in a range of habitats. For instance, birch scrub, even where sparse, appears to be a poor habitat for Meadow Pipits which occur at 18–24 birds/10 ha on moorland in southern Scotland (Thirgood et al. 1995). Published Willow Warbler densities in northern birch habitats are quite varied, ranging from 2.2 pairs/10 ha in Finnish mountain birch wood, 5.0 pairs/10 ha in lush Finnish birch woodland, and 10–12 territories/10 ha in Finnish deciduous woodland (a density similar to the present paper), to a mean of 19.9 territories/10 ha in Swedish subalpine birch forest (Tiainen 1983, Enemar et al. 1984, Virkkala 1988, Järvinen & Rajasärkkä 1992). In southern England Willow Warblers reach their highest density in scrub, coppice and young plantations (Fuller 1995). For example, a 62 ha wood containing compartments at different stages of coppice growth supported an overall density of 10.3 territories/10 ha. Here Willow Warblers favoured six-year-old stands in which densities reached 26 territories/10 ha (Fuller & Henderson 1992). R. J. Fuller, S. Gillings and S. J. Gough (unpubl.) calculated a mean Willow Warbler density of 11.5 territories/10 ha from 15 sites containing mature scrub mosaics dominated by hawthorn *Crataegus* spp., Elder *Sambucus nigra* and oak *Quercus* spp. Willow Warbler densities, therefore, appear to be high in upland birch scrub and comparable with preferred habitats in lowland England and Fennoscandian subalpine birch forest. Birch-dominated scrub and woodland may be one of the preferred habitats of the Willow Warbler. In support of this, Virkkala (1988) found that Willow Warblers for-

Table 3. Spearman rank correlation matrix of independent variables and NOWW (number of Willow Warbler registrations). For definitions of the habitat variables see Table 1. For each pair two correlation coefficients are presented representing datasets A and B (n = 23 each). Significance levels are * P < 0.05, ** P < 0.01, *** P < 0.001.

		NOWW	COVB	CAN1	CAN2	CAN3	COVH	HEHT	BHGT	COV1	COV2
COV3	A	0.26	0.43*	– 0.45*	– 0.12	0.86***	– 0.09	0.07	0.87***	– 0.35	0.09
	B	0.11	0.53**	– 0.53**	0.33	0.69***	0.05	0.04	0.80***	– 0.33	0.43*
COV2	A	0.57**	0.82***	– 0.77***	0.90***	– 0.37	0.45*	0.52*	0.14	– 0.60**	
	B	0.66***	0.94***	– 0.75***	0.88***	– 0.22	0.52*	0.36	0.47*	– 0.42*	
COV1	A	– 0.23	– 0.44*	0.92***	– 0.63**	– 0.14	– 0.32	– 0.24	– 0.59**		
	B	0.03	– 0.24	0.89***	– 0.68***	– 0.22	– 0.25	– 0.26	– 0.73***		
BHGT	A	0.26	0.35	– 0.60**	0.06	0.80***	– 0.00	0.00			
	B	– 0.02	0.39	– 0.79***	0.59**	0.59**	0.19	0.12			
HHGT	A	0.12	0.43*	– 0.38	0.44*	– 0.20	0.60**				
	B	0.22	0.32	– 0.29	0.35	– 0.29	0.47*				
COVH	A	– 0.00	0.38	– 0.41	0.42*	– 0.25					
	B	0.39	0.42*	– 0.34	0.47*	– 0.26					
CAN3	A	0.00	– 0.03	– 0.12	– 0.47*						
	B	– 0.35	– 0.16	– 0.13	– 0.17						
CAN2	A	0.44*	0.56**	– 0.69***							
	B	0.44*	0.73***	– 0.88***							
CAN1	A	– 0.39	– 0.70***								
	B	– 0.28	– 0.63**								
COVB	A	0.52*									
	B	0.71***									

aged more often in birch (58%) than pine (25%) and spruce (13%). Furthermore, Mason (1997) found that Willow Warblers in south-east England preferred to locate their territories in patches of woodland habitat that contained birch trees.

The densities as presented above conceal the high degree of spatial variation which exists within plots. Meadow Pipits persist from open moorland into scrub–moorland mosaic up to 50% birch cover though they were far more abundant at < 20% cover. Willow Warbler densities were highest in medium height, medium canopy cover birch similar to in southern English coppice (Fuller & Henderson 1992). The single strongest predictor of Willow Warbler distribution in coppice was an index of shrub layer density and, when canopy closure occurred, Willow Warbler density rapidly

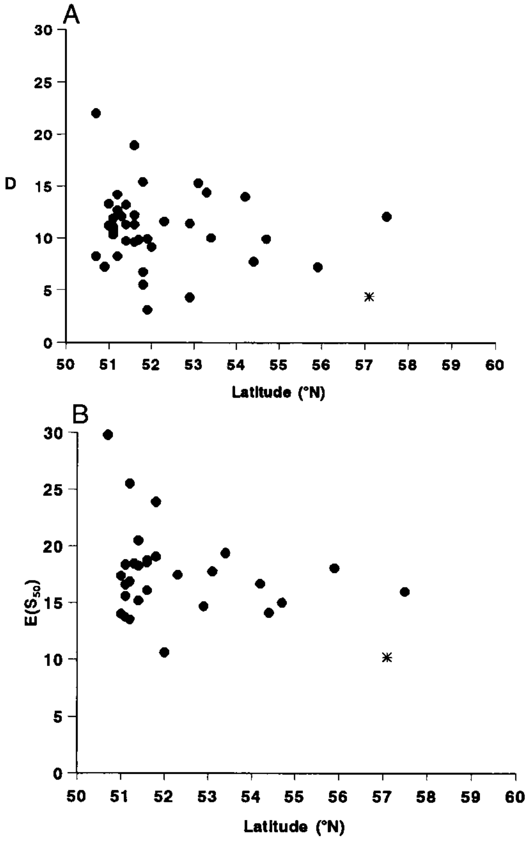

Fig. 4 (Right). Scatter plots of latitude against, A, Simpson's diversity index and, B, expected species richness by rarefaction. Filled circles denote scrub sites studied by R. J. Fuller, S. Gillings and S. J. Gough (unpubl.), the cross symbol represents the Westmoor community. Note that there are fewer points on B because rarefaction was not possible on some sites because there were insufficient individuals.

Table 4. Correlation coefficients (r × 100) of environmental variables with the first canonical axis defined by CCA. Rank is the rank of averaged rank from runs A and B. Variance explained is the percentage of the variance in the species–environment relation explained by axis one. CCA was undertaken separately on dataset A and B (n = 23 each). See Table 1 for definitions of variables.

Variable	A	B	Rank
BHGT	– 344	516	3
COVB	– 728	– 670	10
COVH	– 82	38	3
HHGT	– 99	– 428	7
CAN1	676	– 74	2
CAN2	– 496	– 235	8
CAN3	2	785	1
COV1	256	– 312	5
COV2	– 601	– 545	9
COV3	– 363	108	6
Eigenvalue	0.434	0.512	
Variance explained	42.0	28.4	

Table 5. Species scores for the first canonical axis from CCA run on datasets A and B. Species not represented in a subset are denoted by *.

Species	A	B
Wigeon	*	0.47
Curlew	2.41	*
Woodpigeon	1.17	– 0.65
Cuckoo	0.51	*
Skylark	*	– 0.01
Tree Pipit	0.29	1.93
Meadow Pipit	1.76	0.60
Wren	– 0.65	– 0.94
Long-tailed Tit	– 0.82	– 0.81
Willow Warbler	– 0.29	– 0.33
Coal Tit	*	– 0.91
Blue Tit	*	– 1.12
Great Tit	– 0.81	– 0.91
Jay	*	– 0.54
Chaffinch	– 0.10	0.20
Crossbill spp.	– 0.35	*
Bullfinch	0.75	– 0.03

decreased to zero (Fuller & Henderson 1992). In contrast, in birch scrub Willow Warblers are present at moderate densities through all stages of canopy cover, even though the shrub layer is generally sparse, and they persist in mature stands. Here habitat selection appears simpler than in southern habitats and Willow Warblers are tolerant of a wider range of conditions, indeed Tiainen (1983) described the Willow Warbler as a habitat generalist. Chaffinches seem to prefer areas of birch exceeding 30% cover while their use of 0–10% cover is probably restricted to males using isolated tall birches in clearings as song posts.

CCA of the community data for the two plots revealed that the main determinant of community composition was successional stage. Axis one was primarily a birch cover gradient though there were subtle shifts in canopy height. The gradient was a gradual switch from relatively dense thickets of medium height to open canopy birch (either as short bushes or isolated standards). Both pipit species received positive species weightings indicating a preference for early successional stages characterised by open areas with scattered birches. At the other extreme the large negative weightings of Wren, Long-tailed Tit and Great Tit indicated preference for tall birch nearing canopy closure. Birch at this stage lacks cavities for hole nesting species such as the Great Tit which might simply be feeding in this stage. Willow Warbler had a low negative weighting which, in agreement with earlier results, suggested a preference for medium height birch at intermediate canopy cover.

In the context of continued birch regeneration we can make some predictions about the bird communities likely to develop. Scrub regeneration is likely to be spatially variable as a result of local factors such as soil condition, grazing pressure and exposure. Therefore mosaics of birch thickets and open moorland are likely to be evident for protracted periods following initial scrub colonisation. Fine-grained mosaics may allow the persistence of Meadow Pipit and Curlew up to medium canopy cover but species such as Skylark, Golden Plover and Red Grouse probably require more coarse-grained mosaics or even large expanses of open moorland. Skylarks were present on a block of open moorland of approximately 0.75 km^2 but we did not record them using the open glades within our study areas. The present study suggests that Willow Warblers will colonise early successional stages and that they are largely unaffected by mosaic grain at this scale. Willow Warblers and Chaffinch will be the dominant species throughout most of the birch succession in eastern Scotland though as tree height increases and the canopy closes species such as Wren, Long-tailed Tit and Great Tit will colonise. Ultimately hole-nesting species such as Redstart *Phoenicurus phoenicurus*, Tawny Owl *Strix aluco* and woodpeckers will colonise as has happened in areas of more mature birch adjacent to our study plot. Our survey may have overlooked rare or clustered birch scrub inhabitants such as Black Grouse. Conservation of such species might require maintenance of early stages of birch scrub but the majority of moorland and woodland species can probably be accommodated in a coarse-grained mosaic of old birch scrub and large moorland patches. It would be valuable to undertake further work to determine minimum open-area requirements for moorland birds.

Acknowledgements. We thank the Dinnet Estate and Scottish Natural Heritage for allowing us to carry out this work on their reserve and particular thanks go to Jim Parkin for his advice, help and hospitality throughout our stay. This work was funded by the Joint Nature Conservation Committee (on behalf of Scottish Natural Heritage, English Nature and the Countryside Council for Wales and the Environment and Heritage Service in Northern Ireland). We also thank Su Gough for producing the graphs, and Mick Marquiss, Kathy Martin, an anonymous referee and the editor for comments on an earlier draft.

Selostus: **Lintuyhteisöjen rakenne ja lintujen levittäytyminen koivua kasvavilla nummilla Koillis-Skotlannissa**

Kirjoittajat tutkivat reviirikartoitus- ja linjalaskentamenetelmän avulla lintuyhteisöjen rakennetta ja yksittäisten reviirien sijoittumista suhteessa kasvillisuuden rakenteeseen 46 hehtaarin koivua kasvavalla nummialueella Koillis-Skotlannissa. Laskennoissa havaittiin 20 lajia. Tässä työssä kuvattu lintuyhteisö oli suhteellisen vähälajinen ja sen lajidiversiteetti oli alhainen verrattuna muihin Britannian pensaikkohabitaateissa tehtyihin tutkimuksiin (Kuva 4). Käytetyt kaksi menetelmää antoivat hyvin samansuuntaisen tuloksen lajien runsaudesta alueella. Yhteisössä oli kaksi selkeää valtalajia: pajulintu (52% havaituista reviireistä) ja peippo (18%; Taulukko 2). Tässä suhteessa tutkittu lintuyhteisö muistuttaa eniten Fennoskandian vastaavissa habitaateissa todettuja yhteisörakenteita. Pajulinnun tiheydet olivat jotakuinkin samansuuruisia kuin muualla Englannissa ja Fennoskandiassa havaitut tiheydet. Kasvillisuuden rakennetta kuvaavista muuttujista koivun kokonaispeittävyys, joka kuvaa koivikon sukkessiovaihetta, oli lintuyhteisön rakenteeseen ja reviirien sijoittumiseen voimakkaimmin vaikuttava tekijä (Taulukot 4 ja 5). Niittykirvinen esiintyi vain harvaa koivua kasvavissa osissa aluetta, kun taas metsäkirvinen ei näyttänyt reagoivan koivun peittävyyteen (Kuvat 2 ja 3A). Pajulintujen tiheys oli korkeimmillaan sellaisissa osissa aluetta, missä koivut olivat keskimääräisen kokoisia ja esiintyvät keskimääräisillä tiheydellä (Kuvat 2 ja 3B). Peukaloinen, talitiainen ja pyrstötiainen suosivat vanhempia koivikoita (Taulukko 5). Meneillään oleva laidunnuksen väheneminen tulee aiheuttamaan muutoksia koivikon rakenteessa pitkällä aikavälillä ja tämä todennäköisesti johtaa alueen linnuston rakenteen muutoksiin laajemminkin.

References

Bibby, C. J., Bain, C. G. & Burges, D. J. 1989: Bird communities of highland birchwoods. — Bird Study 36: 123–133.

Blondel, J., Ferry, C. & Frochot, B. 1970: La méthode des indices ponctuels d'abondance (I.P.A.) ou des relevés d'avifaune par "stations d'ecoute". — Alauda 38: 55–71.

Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L. 1993: Distance sampling: estimating abundance of biological populations. — Chapman & Hall, London.

Enemar, A., Nilsson, L. & Sjöstrand, B. 1984: The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study. — Annales Zoologici Fennici 21: 321–338.

Fuller, R. J. 1982: Bird habitats in Britain. — Poyser, Calton.

Fuller, R. J. 1995: Birdlife of woodland and forest. — Cambridge University Press, Cambridge.

Fuller, R. J. & Henderson, A. C. B. 1992: Distribution of breeding songbirds in Bradfield Woods, Suffolk in relation to vegetation and coppice management. — Bird Study 39: 73–88.

Golden Software Inc. 1994: SURFER for Windows. Version 6. Golden Software Inc. — Colorado, USA.

Hester, A. J. & Miller, G. R. 1995: Scrub and woodland regeneration: prospects for the future. — In: Thompson, D. B. A., Hester, A. J. & Usher, M. B. (eds.), Heaths and moorland: cultural landscapes: 140–153. — HMSO, Edinburgh.

James, F. C. & Rathbun, S. 1981: Rarefaction, relative abundance, and diversity of avian communities. — Auk 98: 785–800.

Järvinen, A. & Rajasärkkä. 1992: Population fluctuations in two northern land bird communities: effects of habitat, migration strategy and nest-site. — Ornis Fennica 69: 173–183.

Jongman, R. H. G., ter Braak. C. J. F. & van Tongeren, O. F. R. 1995: Data analysis in community and landscape ecology. — Cambridge University Press, Cambridge.

Laake, J. L., Buckland, S. T., Anderson, D. R. & Burnham, K. P. 1994: DISTANCE user's guide V2.1. — Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University, Fort Collins.

Marchant, J. H., Hudson, R., Carter, S. P. & Whittington, P. 1990: Population trends in British breeding birds. — BTO/NCC, Tring.

Mason, C. J. 1997: Association between Willow Warbler Phylloscopus trochilus territories and birch in woodlands in southeastern England. — Ibis 139: 411–412.

SAS Institute Inc. 1986: SAS User's guide. Version 6. — SAS Institute Inc., Carey.

Solonen, T. 1996: Patterns and variations in the structure of forest bird communities in southern Finland. — Ornis Fennica 73: 12–26.

Summers, R. & Buckland, S. 1996: Numbers of wintering Woodcock Scolopax rusticola in woodlands in the Highlands of Scotland. — Wader Study Group Bulletin 80: 50–52.

ter Braak, C. J. F. 1990: CANOCO – a FORTRAN program for CANOnical Community Ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis, version 3.10. — Microcomputer Power, Ithaca, NY.

Thirgood, S. J., Leckie, F. M. & Redpath, S. M. 1995: Diurnal and seasonal variation in line transect counts of moorland passerines. — Bird Study 42: 257–259.

Tiainen, J., Vickholm, M., Pakkala, T., Piiroinen, J. & Virolainen, E. 1983: The habitat and spatial relations of breeding Phylloscopus warblers and the goldcrest Regulus regulus in southern Finland. — Annales Zoologici Fennici 20: 1–12.

Usher, M. B. & Thompson, D. B. A. 1993: Variation in the upland heathlands of Great Britain: conservation importance. — Biological Conservation 66: 69–81.

Virkkala, R. 1988: Foraging niches of foliage-gleaning birds in the northernmost taiga in Finland. — Ornis Fennica 65: 104–113.