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Relationships between patterns of habitat cover and the historical distribution of the Marsh Tit, Willow Tit and Lesser Spotted Woodpecker in Britain

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Abstract

Spatial analysis of remotely-sensed land cover data in conjunction with species distribution atlases can reveal large-scale relationships between animal taxa and their habitats. We investigated the historical distribution patterns of three declining woodland birds, the Marsh Tit (*Poecile palustris*), Willow Tit (*Poecile montana*) and Lesser Spotted Woodpecker (*Dendrocopos minor*), in relation to a parsimonious landscape metric for describing habitat availability in Britain. Bird distributions were derived from two field-based atlas surveys, conducted in 1968-1972 and 1988-1991, and used to classify areas of the landscape for each species as retained, lost or gained between atlas periods, or unoccupied in both. We used remotely-sensed land cover data from 1990 to compare percentage habitat cover between landscape areas classified by bird occupation, and regional summary data from national woodland inventories to investigate changes in habitat cover and bird distributions. Percentage habitat cover was a sufficient landscape metric to explain the distribution pattern of all three bird species; habitat cover was greatest in areas where each species was retained between atlas surveys, significantly less in areas from which species were lost, and least in areas that remained unoccupied. Reductions in Marsh Tit distribution were less in regions that showed greater increases in habitat cover, but there was no such relationship for other species. Results indicated that spatial studies could be used to infer aspects of the spatial ecology of species where field data is lacking: by comparing distribution patterns with the relatively well-studied Marsh Tit, we found support for the assumption that the Lesser Spotted Woodpecker occupies very large territories in Britain, and provided evidence that the spatial habitat requirements of the Marsh Tit could be used as a proxy for the data-poor Willow Tit. The results showed that the habitat cover required to retain each species in the landscape had increased over time, illustrating how spatial studies can be used to identify priorities for further research and suggest conservation measures for declining species, and these are discussed.

Keywords: bird atlas; habitat cover; Marsh Tit; Willow Tit; Lesser Spotted Woodpecker

1. Introduction

Landscape and habitat information from remote sensing has become a common tool in studies of biodiversity (Nagendra, 2001), with the ability to provide comprehensive coverage of landscape composition and habitat structure at high spatial resolution (e.g. Hill and Broughton, 2009; Morton et al., 2011). However, comparable information on the range, richness and abundance of many animal species are rarely available at a similar resolution. In the UK, birds are an exception due to their popularity as study subjects and the relative ease of detection. Comprehensive atlases of breeding bird distribution have been produced at intervals of approximately 20 years for the whole of Britain since 1968 at a spatial resolution as fine as 2 km tetrads (Gibbons et al., 1993; BTO, 2012). In addition, national land cover maps have been generated from remote sensing and ground-truth information approximately every decade since 1990 at a spatial resolution of 25 m or less, employing a minimum mappable unit of as little as 0.5 ha (Morton et al., 2011). Regional or tetrad-based summary data at varying spatial scales are also available from historical agricultural censuses (Siriwardena et al., 2000) and woodland inventories (Forestry Commission, 2003).

Such data have been employed in exploratory studies aimed at determining broad associations between bird species and habitat types (R.M. Fuller et al., 2005a, 2007), identifying important areas for conservation (Buchanan et al., 2011), and assessing large-scale spatial patterns of change in species distribution (Donald and Greenwood, 2001; Gaston and Blackburn, 2002). Other studies have focussed on individual species to investigate fine-scale habitat-based hypothesis (Donald and Evans, 1995; Gillings and Fuller, 2001), but most attempts to test relationships between land cover classifications and bird distribution or abundance have focussed on farmland birds (e.g. Gates and Donald, 2000; Siriwardena et al., 2000), which have long been a cause of conservation concern in Britain (Newton, 2004). However, the decline of some woodland bird species has also generated significant interest (R.J. Fuller et al., 2005) and site-based investigations have been undertaken for some species of conservation priority (Hinsley et al., 2007; Holt et al., 2010; Stewart, 2010). While some woodland bird studies incorporated a spatial element (Charman et al., 2010), targeted large-scale analyses of the relationships between landscape composition and the distribution of declining woodland species remain rare (Wilson et al., 2005).

In this study, we aimed to investigate the relationships between the historical distribution patterns of woodland habitat and the distribution change of the Marsh Tit (*Poecile palustris*), Willow Tit (*Poecile montana*) and Lesser Spotted Woodpecker (*Dendrocopos minor*). These species underwent substantial population declines (> 60%) and contractions in range from the 1970s in Britain (Gibbons et al., 1993; Baillie et al., 2010), the causes of which remain unknown (R.J. Fuller et al., 2005). The species were chosen on the basis of their territorial and non-migratory behaviour within the wider group of declining woodland birds (Cramp, 1985; Cramp and Perrins, 1993). Only the Marsh Tit is well-studied in terms of its spatial habitat requirements in the fragmented woodlands of Britain, occupying relatively large territories of 5-6 ha and dispersing over short distances (Broughton et al., 2010, 2012). In Sweden, the Lesser Spotted Woodpecker occupied breeding territories of 43 ha (Wiktander et al., 2001) and has previously been linked to locally high woodland cover in England (Charman et al., 2010), but there is no detailed information on the spatial habitat requirements of this species in Britain, nor those of the Willow Tit.

For woodland bird distributions, habitat configuration (size, shape and proximity of patches) can be an important factor in moderating the influence of habitat coverage (Dolman et al., 2007), and a wide variety of metrics have been used to assess its effects (Fahrig, 2003). In a comparative analysis using remote sensing data, however, Cunningham and Johnson (2011) found that percentage cover of woodland habitat was the most parsimonious metric for explaining the occurrence of bird species in the landscape. We followed the findings of Cunningham and Johnson (2011) and used percentage habitat cover to attempt to explain the pattern of historical distribution of the selected bird species, testing the response of each to changes in habitat cover using a combination of spatially explicit and regional summary data.

By providing an understanding of the role of habitat cover in earlier patterns of bird distribution, the results may provide insights into the causes of local extinctions (Radford et al., 2005). Furthermore, by comparing the relationship with habitat cover of the relatively well-studied Marsh Tit against the relationships of the two lesser-known species, inferences might be made regarding the spatial ecology of the latter. Finally, the ability to describe habitat using a single landscape metric, and generate ecologically meaningful results, would support the use of percentage habitat cover as an efficient and accessible metric for investigating spatial habitat and bird distribution data (Cunningham and Johnson, 2011).

2. Material and methods

2.1 Bird distribution data

Spatial data describing the historical distributions of Marsh Tit, Willow Tit and Lesser Spotted Woodpecker in Britain were available at 10 km cell resolution from two national bird atlas surveys, conducted in 1968-1972 (Sharrock, 1976) and 1988-1991 (Gibbons et al., 1993). The bird atlases were derived from field surveys during the breeding seasons (April-July) within each 10 km grid square of the British National Grid (BNG). We used the minimum level of breeding evidence to describe bird distribution (presence within a 10 km square) to generate a binary variable of presence or absence for each atlas period. Confirmation of breeding for these species can be difficult to obtain (Cramp, 1985; Cramp and Perrins, 1993) but, due to their territorial and sedentary behaviour, presence during the breeding season is strongly indicative of residence. Comparison between the two bird atlases therefore allowed the mapping of distribution change and persistence for each species by allocating each 10 km square to one of four occupation classifications. These categories contained squares that were retained, lost or gained between the two atlas periods, or remained unoccupied in both. Although the two atlases employed slightly differing field protocols, they are considered to be sufficiently comparable to be used in this way (Greenwood et al., 1997).

2.2 Woodland habitat data

National-scale habitat data that were approximately contemporaneous with the second bird atlas (1988-1991), were available from the Land Cover Map of Great Britain 1990 (LCMGB). This is a raster dataset containing 25 land cover classifications at a 25 m cell resolution, produced using supervised maximum likelihood classifications of Landsat

Thematic Mapper data (Fuller et al., 1994). The LCMGB combined summer and winter data to achieve an overall accuracy of 80-85% when referenced to ground-truth data, and had a minimum mappable unit of < 1 ha (Fuller et al., 1994). The Marsh Tit is predominantly associated with deciduous woodland (Hinsley et al., 2007), and this habitat was represented in the LCMGB by the single classification of ‘deciduous broadleaved and mixed woodlands’ (class 15). The Willow Tit and Lesser Spotted Woodpecker also occur in this habitat, but are further associated with more open wooded environments such as scrub, carr or orchards (Cramp, 1985; Cramp and Perrins, 1993). This additional habitat was represented in LCMGB by the classification of ‘deciduous scrub and orchards’ (class 14), which was combined with class 15 to characterise habitat for these two bird species, although class 14 represented only 5% of the combined habitat area. However, for simplification the associated habitat of each species is hereafter referred to as ‘woodland’.

Spatial data for woodland habitat coverage that were contemporaneous with the first bird atlas period (1968-1972) were unavailable, preventing a parallel comparison of changes in bird and habitat distributions over a similar time period. However, summary data for changes in woodland habitat cover that partially overlapped the timeframe between bird atlases were available from two national woodland inventories, from 1979-1982 and 1994-2000 (Forestry Commission, 2003) (hereafter ‘the woodland surveys’). Although the woodland surveys each used different methodologies, comparative figures were available that quantified the change in coverage of broadleaved woodland and scrub habitat between them, including all patches greater than 0.25 ha in extent (Forestry Commission, 2003). It was further possible to exclude woodland from the 1994-2000 survey that was planted after 1990 where this was classified as ‘High Forest Category 1’ (stands that were or had the potential to attain a size and quality suitable for sawlog production). This enabled a partial correction in the temporal mismatch between the period of the second woodland survey and second bird atlas, providing approximate data for assessing relative change in habitat coverage over a coincidental period of 1979-1990. Although further changes in woodland coverage are likely to have occurred in the non-coincidental time periods, these data were unavailable. A single habitat classification (broadleaved woodland and scrub) was therefore used for all three bird species.

2.3 Regionalisation of data

In order to generate a sample for statistical analyses, we divided Britain into the composite geopolitical regions of Wales (Wa), Scotland (Sc) excluding the Western Isles and Northern Isles, and eight administrative English Regions (NE: Northeast England; NW: Northwest

England; YH: Yorkshire and the Humber; EM: East Midlands; WM: West Midlands; EA: Eastern England; SE: Southeast England including London; SW: Southwest England) (ONS, 1998). The classified 10 km squares of bird distributions that fell within each geographical region were extracted in an ArcGIS 9.3.1 environment (ESRI 2009, Redlands, CA, USA) for each of the three bird species. The total landscape area within 10 km squares of the same classification in each region was derived, with areas of sea in coastal squares being excluded. The sampling unit for analyses was therefore the aggregated landscape area of each bird occupation classification within each region, and not individual 10 km squares. Summary data of habitat coverage as classified in the woodland surveys were available for the same regions as the bird atlas data. Regional change in bird distribution was calculated as the net percentage change in occupied 10 km squares in the second bird atlas relative to the number occupied in the first atlas.

2.4 Analysis

For each regional landscape area classified by occupation type for each bird species, we determined the percentage cover of habitat derived from the LCMGB. To limit bias from small sample areas, regions were excluded from analyses if the landscape classified by bird occupation was composed of less than an arbitrary five 10 km squares and if these were less than 5% of the total number of squares present in a region, as relatively minor variation could be related to stochastic effects (Hinsley et al., 1995). Percentage habitat cover for each pair of the four occupation classifications (retained, lost, gained, unoccupied) were compared within each bird species by testing for pair-wise differences in the median values for the regions, where a minimum of six regions in each occupation classification were available for analysis using a two-tailed Wilcoxon signed-rank test. Habitat cover values for the Lesser Spotted Woodpecker and Willow Tit were compared with the Marsh Tit by performing similar tests between the corresponding occupation classifications for each species.

While spatial autocorrelation was presumed to be inherent within the data, we attempted to minimise negative effects by the aggregation of dispersed and coarse resolution 10 km squares within the regional samples, and by using the simplified analytical approach that made minimum assumptions regarding the structure of the data. Despite a large number of tests in the analyses, we followed Moran's (2003) recommendations in rejecting use of a Bonferroni-type correction.

We tested for relationships between the change in a species' distribution and the change in percentage habitat cover in a region using a multiple linear regression approach in R version 2.9.1 (The R Foundation for Statistical Computing, 2009). The response variable of change in species distribution was generated by taking the natural logarithm of the product of the number of the 10 km squares in a region that were occupied in the second bird atlas divided by the number that were occupied in the first atlas, i.e. the proportional change in distribution between atlases. The two predictor variables used in the models were percentage change in habitat cover between the two woodland surveys (as a percentage of a region's total area), and the percentage habitat cover for each region from the second woodland survey (partially corrected to 1990). We included both habitat predictor variables (coverage and change), plus an interaction term, in a saturated model and used step-wise backward elimination to reach a minimum adequate model containing only statistically significant parameters. In particular, we wished to examine whether the relationship between change in bird distribution and change in habitat cover was influenced by existing habitat cover of the region.

3. Results

3.1 Comparisons of bird distribution and habitat coverage

The median percentage cover of woodland habitat was greatest in those areas of regions where each species was retained between atlas periods, significantly less in areas where each species was lost, and least of all in areas which remained unoccupied (Tables 1 and 2). Marsh Tit samples were too small to test areas that were gained between atlases, but those areas where Willow Tits were gained had significantly greater habitat cover than areas that were lost or unoccupied, but not significantly different from areas that were retained (Table 2). For the Lesser Spotted Woodpecker, areas which were gained were not distinct from any other occupation category (Table 2). There was no difference between the Marsh Tit and Willow Tit in the percentage habitat cover of corresponding occupation categories (Table 3), but those of the Lesser Spotted Woodpecker were significantly greater than those of the Marsh Tit (Tables 1 and 3).

3.2 Changes in bird distribution and habitat coverage

Percentage habitat cover increased in all regions between the woodland surveys, by 0.4-2.4%, and multiple regression analyses indicated that there was no significant interaction between the change in habitat cover and the remaining cover in a region ($F_{5,6}$ = 2.56, P = 0.17). The minimum adequate model indicated a significant relationship between changes in habitat cover and Marsh Tit distribution: log(proportion distribution change) = 0.17 percentage change in habitat cover + -0.45; this explained 57% of the variance ($F_{1,7}$ = 10.37, P = 0.02). Although all regions analysed experienced a decline in Marsh Tit distribution between the two atlases (Table 1), the model indicated that a greater increase of habitat during this period was associated with lower losses of Marsh Tit distribution. There was no significant effect of regional habitat cover in 1990 on Marsh Tit distribution change, and no significant habitat effects were found in models examining the distribution changes of Lesser Spotted Woodpecker or Willow Tit (results not shown).

4. Discussion

The methodology was successful in identifying significant relationships between percentage habitat cover and the pattern of bird distribution for all three species. In areas of regions were each species was retained between atlas periods, woodland/scrub habitat cover was significantly greater than those areas from which the species were lost or which were never occupied. There was little evidence of a relationship between changes in bird distribution and changes in habitat cover, except for the Marsh Tit where losses in distribution were less in regions that showed the greatest increase in woodland coverage. This suggested a partial buffering effect of increasing habitat on the factors generating the decline in distribution.

The temporal mismatch between the bird atlas and woodland survey data may partly explain the lack of significant results for Willow Tit and Lesser Spotted Woodpecker in the habitat change analyses. Differing methodologies used to produce the two bird atlases also led to variation in the intensity of survey coverage (Greenwood et al., 1997), an effect that could be more acute for species that can be difficult to detect (such as the Lesser Spotted Woodpecker). There is, however, strong support for apparent shifts in bird distribution being treated as genuine, as the reduction of distribution in most regions for each species is corroborated by substantial and widespread declines in populations recorded from other surveys (Baillie et al., 2010). The significant relationship between bird abundance and spatial distribution (Lawton, 1993) reinforces the conclusion that observed losses in distribution were not an artefact of the survey methods. Furthermore, while some differences in median habitat cover between occupation classifications may have been within the uncertainty terms of the data, the differences between the retained, lost and unoccupied classes were statistically significant for all species. In addition, the pattern of habitat cover and occupation was the same for all species, with median cover in those areas from which a species was lost being intermediate between those from which the species was retained and which remained unoccupied. This indicated a genuine ecological signal in the observed patterns, and not artefacts resulting from inaccurate categorisation or poor data precision.

The results also support previous work on these bird species. The large territories and short dispersal distances Marsh Tits (Broughton et al., 2010, 2012) are consistent with a requirement for well-wooded landscapes and the strong connection between habitat cover and occupation present in the results. Charman et al. (2010) found that Lesser Spotted Woodpeckers were more likely to occupy English woods where woodland cover in the local area was greater, and our results support this by quantifying the habitat coverage associated with occupation in the wider landscape. Lesser Spotted Woodpeckers required significantly greater habitat cover than Marsh Tits to maintain occupation, and the spatial study therefore provides support for the assumption that the large territories recorded in Sweden (Wiktander et al., 2001) can be used to contextualise British studies of Lesser Spotted Woodpeckers (Charman et al., 2010).

Our study is also the first to analyse the distribution patterns of the British Willow Tit and its habitat (see Stewart, 2010). Values of habitat cover in the Willow Tit occupation categories were similar to those of the Marsh Tit, indicating that spatial habitat requirements are also similar for both species. In the absence of specific data for the Willow Tit, this result suggests that information on the territory size and dispersal behaviour of the closely-related Marsh Tit may be used as a valid interim proxy. The Willow Tit is one of the most rapidly declining bird species in Britain (Baillie et al., 2010), and such information is crucial for the effective conservation of remaining populations by indicating the need to maintain or create sufficient habitat networks (cf. Broughton et al., 2010). This is an example of where spatial analyses can suggest beneficial conservation measures for a data-poor species based upon evidence of a similar landscape response for a relatively well-studied species.

Spatial studies of the large-scale interaction between species distribution and habitat may also suggest fundamental underlying causes of changes in range or population, where conservation measures or future study could be directed. The relationship between bird distribution and habitat cover for all three species in the current study described a contraction in range to areas of greatest habitat cover. This indicates an increase in the habitat threshold required to maintain these species in the landscape during the 1970s and 1980s, leading to local extinctions in areas with only moderate habitat cover. This is consistent with a metapopulation hypothesis of increasing landscape resistance to dispersal and recruitment due to declining connectivity between relatively sparse habitat cover (Opdam, 1991), and one possible mechanism for such an effect is the widespread loss of hedgerows throughout Britain during the period of study (Hunting Surveys and Consultants, 1986). Field studies support this theory, with Marsh Tit dispersal being less successful between smaller woods (Broughton et al., 2010), and occupation by this species and Lesser Spotted Woodpecker becoming less likely as woodland isolation increases (Opdam et al., 1985). Further spatial analyses would be required to confirm the hypothesis of declining habitat connectivity, using a greater range of landscape metrics than percentage habitat cover, although spatially explicit data for historical changes in national hedgerow distribution are currently unavailable. As such, spatial studies may offer a source of indirect evidence of the effect of historical landscape processes on later species distributions where contemporary data with which to directly test the hypotheses may be lacking.

5. Conclusions

The use of percentage habitat cover as a single metric to describe habitat availability in the landscape (Cunningham and Johnson, 2011) was successful in explaining broad patterns of Marsh Tit, Willow Tit and Lesser Spotted Woodpecker distribution. The results identified a unifying trend of all three species being sensitive to differences in percentage habitat cover, with this being most acute for the Lesser Spotted Woodpecker, but only the Marsh Tit showed a relationship with the regional change in habitat cover. This suggested an effect of confounding variables on the decline of these species, such as decreased connectivity between habitat patches and increased landscape resistance to successful dispersal, but the current analyses were insensitive to these factors. In addition to the need for spatial ecology and demographic studies in order to fully understand the declines of these species, further detailed analyses of habitat configuration and connectivity would be valuable.

The study demonstrated how simple spatial analyses of bird and habitat distribution data could provide valuable insights into the spatial ecology of conservation-priority species where detailed field studies are lacking. By comparing the spatial patterns shown by such species to those of a relatively well-studied species utilising similar habitat, investigations can suggest priority areas of future research or practical conservation measures (such as planting/protecting hedgerows). The availability of a growing time series of British land cover maps (R.M. Fuller et al., 2005b; Morton et al., 2011), and bird atlas data (BTO, 2012) offers comprehensive repeat surveys with which to conduct more powerful spatial analyses of the relationships between bird species and their habitat over time. Such studies may be used to predict responses to climate change (Donald and Fuller, 1998), and also test theories of biogeography using the increasingly robust datasets. These opportunities, however, would be enhanced by detailed information on the spatial ecology and habitat associations of target species in order to populate models with realistic variables, determine the parameters of spatial analyses, and provide an appropriate ecological context in which to interpret the results.

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Table 1. Percentage change in bird distribution by region between the 1968-1972 and 1988-1991 bird atlases, and median values of percentage habitat cover in areas classified by occupation as retained, lost or gained between atlases, or remaining unoccupied in both. Superscript values refer to the number of 10 km bird atlas squares in each classification. Median values exclude regions with small sample areas (highlighted in italics). See section 2.3 in text for description of regions.

Species, region	Retained	Lost	Gained	Un-occupied	Region total	Distribution change (%)
Marsh Tit						
EA	3.6^{160}	1.8^{32}	3.9^{3}	0.7^{19}	1.6^{214}	-15.1
EM	5.8^{74}	3.8^{43}	2.6^{6}	2.7^{35}	2.5^{158}	-31.6
NE	2.9^{41}	2.0^{26}	2.4^{4}	0.9^{25}	1.2^{96}	-32.8
NW	5.8^{45}	3.5^{30}	3.7^{14}	3.1^{73}	2.5^{162}	-21.3
SE	11.7^{180}	5.5^{30}	7.9^{3}	2.6^{12}	5.3^{225}	-12.9
SW	8.1^{236}	6.2^{31}	4.2^{2}	2.1^{16}	3.9^{285}	-10.9
Wa	12.7^{130}	11.8^{43}	15.4^{20}	9.4^{61}	6.4^{254}	-13.3
WM	5.7^{116}	4.3^{11}	5.6^{3}	$\mathit{1.0}^{2}$	2.8^{132}	-6.3
YH	4.5^{67}	4.8^{55}	4.2^{12}	3.8^{34}	2.4^{168}	-35.3
Sc	$\mathit{2.3}^{7}$	$\mathit{2.4}^{9}$	2.4^{10}	$\mathit{2.4}^{871}$	2.6^{897}	6.3
Median	5.8	4.3	4.1	2.7	2.6	-14.2
Willow Tit						
EA	4.5^{126}	2.6^{51}	3.4^{13}	1.2^{24}	1.6^{214}	-21.5
EM	5.6^{114}	2.8^{22}	3.5^{11}	0.1^{11}	2.5^{158}	-8.1
NE	3.1^{33}	2.8^{18}	2.0^{15}	1.2^{30}	1.2^{96}	-5.9
NW	5.0^{46}	4.7^{29}	5.7^{8}	3.7^{79}	2.5^{162}	-28.0
SE	12.6^{164}	10.1^{24}	13.2^{13}	4.3^{24}	5.3^{225}	-5.9
SW	10.2^{85}	9.1^{50}	11.1^{46}	6.7^{104}	3.9^{285}	-3.0
Wa	13.7^{119}	12.6^{33}	13.9^{40}	10.7^{62}	6.4^{254}	4.6
WM	6.1^{110}	6.8^{7}	7.2^{13}	$\mathit{9.5}^{2}$	2.8^{132}	5.1
YH	5.0^{85}	4.5^{31}	6.5^{15}	4.0^{37}	2.4^{168}	-13.8
Sc	3.8^{29}	2.8^{40}	3.7^{16}	2.6^{812}	2.6^{897}	-34.8
Median	5.3	4.6	6.1	3.7	2.6	-21.5
Lesser Spotted Woodpecker						
EA	4.2^{135}	3.5^{36}	2.6^{19}	1.6^{24}	1.6^{214}	-9.9
EM	6.9^{36}	5.6^{25}	5.4^{27}	3.6^{70}	2.5^{158}	3.3
NE	$\mathit{0.0}^{0}$	$\mathit{6.2}^{2}$	$\mathit{3.2}^{8}$	$\mathit{2.0}^{86}$	1.2^{96}	300.0
NW	5.4^{38}	6.1^{21}	5.8^{8}	3.3^{95}	2.5^{162}	-22.0
SE	13.0^{150}	8.8^{28}	9.1^{22}	6.8^{25}	5.3^{225}	-3.4
SW	10.4^{83}	8.7^{97}	13.7^{16}	7.8^{89}	3.9^{285}	-45.0
Wa	15.0^{57}	13.6^{43}	14.9^{37}	11.4^{117}	6.4^{254}	-6.0
WM	6.1^{76}	6.6^{20}	6.3^{25}	8.4^{11}	2.8^{132}	5.2
YH	6.2^{24}	5.2^{16}	5.3^{28}	4.3^{100}	2.4^{168}	30.0
Sc	$\mathit{0.0}^{0}$	$\mathit{0.0}^{0}$	$\mathit{0.0}^{0}$	$\mathit{0.0}^{0}$	2.6^{897}	0.0
Median	6.6	6.4	6.1	5.5	2.6	-1.7

Table 2. Results of pair-wise Wilcoxon signed rank (*W*) tests of median percentage habitat cover between areas of each region classified by bird occupation as retained, lost or gained between two bird atlases surveys, or remaining unoccupied in both. Sample size was insufficient to perform tests using gained occupation for the Marsh Tit.

	Retained	Lost	Gained
	W (*P*)	*W* (*P*)	*W* (*P*)
Marsh Tit			
Lost (n = 9)	44.0 (0.01)	-	-
Gained	-	-	-
Unoccupied (n = 8)	36.0 (0.01)	36.0 (0.01)	-
Willow Tit			
Lost (n = 10)	51.0 (0.02)	-	-
Gained (n = 10)	24.0 (0.76)	3.0 (0.01)	-
Unoccupied (n = 9)	45.0 (0.01)	45.0 (0.01)	45.0 (0.01)
Lesser Spotted Woodpecker			
Lost (n = 8)	38.0 (0.04)	-	-
Gained (n = 8)	24.0 (0.44)	15.0 (0.73)	-
Unoccupied (n = 8)	33.0 (0.04)	33.0 (0.04)	32.0 (0.06)

Table 3. Comparisons of Willow Tit and Lesser Spotted Woodpecker with Marsh Tit, using pair-wise Wilcoxon signed rank (*W*) tests of median percentage habitat cover in areas of regions classified by bird occupation as retained or lost between two bird atlases surveys, or remaining unoccupied in both.

	Retained	Lost	Unoccupied
	$W\ (P)^n$	$W\ (P)^n$	$W\ (P)^n$
Willow Tit	$7.0\ (0.08)^9$	$6.0\ (0.06)^9$	$7.0\ (0.14)^8$
LS Woodpecker	$35.0\ (0.02)^8$	$36.0\ (0.01)^8$	$36.0\ (0.01)^8$

Figure 1. Regions of Great Britain used in the summary and analyses of habitat and bird atlas data: Sc = Scotland (excluding the Western Isles and Northern Isles); NE = Northeast England; NW = Northwest England; YH = Yorkshire and the Humber; EM = East Midlands; WM = West Midlands; Wa = Wales; EA = Eastern England; SE = Southeast England (incorporating Greater London); SW = Southwest England.