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Are changes in breeding habitat responsible for population declines of the characteristic long-distance migrant birds of upland oakwoods?

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Corresponding Author:	Paul Bellamy Royal Society for the Protection of Birds Sandy, Bedfordshire UNITED KINGDOM
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Royal Society for the Protection of Birds
Corresponding Author's Secondary Institution:	
First Author:	John Mallord
First Author Secondary Information:	
Order of Authors:	John Mallord
	Ken Smith
	Paul Bellamy
	Elisabeth Charman
	Richard Gregory
Order of Authors Secondary Information:	
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Suggested Reviewers:	Catriona Morrison

	British Trust for Ornithology catriona.morrison@bto.org
	Marc-Andre Villard University of Moncton marc-andre.villard@umoncton.ca
	Shelley Hinsley Centre for Ecology and Hydrology sahi@ceh.ac.uk
	Mark Wilson University College Cork mark.wilson@ucc.ie

Are changes in breeding habitat responsible for population declines of the characteristic long-distance migrant birds of upland oakwoods?

John W. Mallord, Ken W. Smith, Paul E. Bellamy, Elisabeth C. Charman and Richard D. Gregory.

Conservation Science, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK

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Corresponding author: john.mallord@rspb.org.uk

Abstract

Recent population declines have highlighted the problems faced by long-distance migrant birds, although the causes of such declines are unknown for most species. One such possible driver is habitat degradation on the breeding grounds and in this paper we have investigated whether change in woodland structure is associated with the UK population declines of four Afro-Palearctic migrants: Wood Warbler *Phylloscopus sibilatrix*, Tree Pipit *Anthus trivialis*, Pied Flycatcher *Ficedula hypoleuca*, and Common Redstart *Phoenicurus phoenicurus*, in one of their core breeding habitats, the upland oakwoods of western and northern Britain. Using data collected during a nationwide survey of woodland bird population and habitat changes, we report that all four species underwent population declines between 1982/84 and 2003/04: Wood Warbler, -37%, Tree Pipit, -56%, Pied Flycatcher, -9%, and Common Redstart, -32%. Over the same time period, there were also small but significant increases in ground cover and a 112%, 181% and 828% increase in understorey cover at 0.5-2m, 2-4m, and 4-10m, respectively, which could impact upon habitat suitability for these birds. However, we demonstrate that such changes in habitat were not adequate to explain the change in the number of birds, nor that the modelled effects of changes in habitat on bird numbers were consistent with overall population trends. Despite there being no evidence that change in habitat is driving population declines, it remains important to maintain habitat suitability of woodland within the core of these species' range, as further degradation may result in the greater loss of birds. Future work on these species, along with other long-distance migrants, should focus across the whole of the migratory flyway, elucidating the needs of these species on their breeding, stopover and wintering sites.

Introduction

Anthropogenic alteration of habitats globally has lead to the beginning of what has been termed the ‘sixth great extinction’ (Wilson 1992), and widespread population declines of many taxa, at various scales, have been reported (Ceballos & Ehrlich 2002; Thomas *et al*. 2004; Conrad *et al*. 2006). In recent decades it has emerged that populations of long-distance migrant land birds may be under particular threat having declined more rapidly than either resident or short-distance migrant species (Robbins *et al*. 1989; Sanderson *et al*. 2006, Vickery *et al.* in press). The causes of decline are unknown for most species, but could involve factors operating in different habitats on a trans-continental scale (Newton 2008; Sheehan & Sanderson 2012, Vickery *et al.* in press). These include phenological mismatch between predator and prey (Both *et al*. 2006; Möller *et al*. 2008), nest predation (Thompson 2007), reduced availability of invertebrate food (Krebs *et al*. 1999) and a reduction in habitat quality at wintering, stopover and breeding sites (Holt *et al*. 2010; Peach *et al*. 1991; Ockendon *et al*. 2012).

Although in UK and elsewhere in Europe there have been significant population declines of bird species associated with farmland (Donald *et al*. 2001; Wilson *et al*. 2009), it has more recently become apparent that in UK in particular similar declines have been occurring in woodland habitats (Hewson *et al*. 2007), especially of long-distance migrants (Gregory *et al*. 2007; Hewson & Noble 2009). Unlike farmland, where many of the declines can be attributed to a single, albeit multi-facetted cause, agricultural intensification (Wilson *et al*. 2009), the causes of woodland bird declines may be diverse and are largely unknown (Fuller *et al*. 2005). As part of a wider investigation into the declines of woodland birds, the Royal Society for the Protection of Birds (RSPB)/British Trust for Ornithology (BTO) Repeat Woodland Bird Survey (RWBS; Amar *et al*. 2006; Hewson *et al*. 2007) measured changes in breeding bird numbers in a large sample of broadleaved woods across Great Britain between 1982/84 and 2003/04. A total of 406 woods were included in the survey and comparable habitat data were collected in both periods from

249 of these in order to relate changes in bird numbers to changes in habitat. From these data, it was clear that there have been major changes in woodland structure since the 1980s (Amar *et al*. 2010), including an increase in sub-canopy cover above 2m across all geographical regions. However, other changes showed regional variation. In the south and east of England there were reductions in both field-layer and understorey cover below 2m, possibly due to browsing by increasing populations of deer (Dolman *et al*. 2010). Meanwhile, in woods in western and northern regions, such cover increased (Amar *et al*. 2010), possibly as a result of a reduction in grazing pressure from sheep (Hopkins & Kirby 2007).

Upland oakwoods, also referred to as Western Atlantic Oakwoods in the UK, are limited in their distribution to the western fringes of Europe, being found in northern Iberia, France, Ireland and the British Isles, and within the latter mainly in the western counties of England, Wales and north-west Scotland (Baarda 2005). They are woods dominated by Oak *Quercus* (mainly *Q. petraea* in the UK), with a temperate, wet maritime climate and an open structure maintained by sheep grazing (Quelch 2005), and are noted for their bryophyte and lichen communities (Rothero 2005). In Britain, they support a specialised breeding bird community including a suite of four long-distance migrants, Wood Warbler *Phylloscopus sibilatrix*, Tree Pipit *Anthus trivialis*, Pied Flycatcher *Ficedula hypoleuca* and Common Redstart *Phoenicurus phoenicurus* (hereafter Redstart), which are less common or absent in other woodland habitats or regions (Fuller 1992). All these species favour an open woodland structure (Cramp & Simmons 1983; Stowe 1987; Smart *et al*. 2007; Mallord *et al*. 2012b), so could be negatively affected by the changes in woodland structure reported since the 1980s (Amar *et al*. 2010). The land-use and land management of the UK uplands is strongly influenced by agricultural and forestry policies, which impact on all upland habitats, and have lead to difficulties in managing upland oak woods for biodiversity (Mitchell and Kirby 1990, Reed *et al.* 2009).

The UK breeding populations of two of these four species have been in decline in recent years with national declines between 1995-2010 of 65% for Wood Warbler and 50% for Pied Flycatcher. Over the same period, Tree Pipit (-5%) and Redstart (+19%) populations have been relatively stable, although both species were previously more abundant and underwent steep declines in during the 1970's and 1980's (Baillie *et al*. 2012; Eaton *et al* 2012). As these declines have occurred over a similar period to changes in woodland structure, the possibility arises that such changes in habitat may be driving the population declines of these four bird species. Our aims in this paper are to use RWBS data to i) calculate population change of these four migrant species in one of their priority habitats, ii) measure changes in woodland structure, iii) define habitat associations of each species, and iv) assess whether the change in habitat is likely to have driven the observed population changes.

Methods

Study sites

As part of the RWBS (Amar *et al*. 2006; Hewson *et al*. 2007) a total of 406 woodland sites were surveyed in 2003/4, repeating surveys in the same plots first carried out in the 1980s and earlier. Although the RWBS was UK-wide, for the purposes of this study, we have focussed on oakwoods within those regions that fall within the range of Western Atlantic Oakwoods (Figure 1). We have selected woods in these regions dominated by Oak *Quercus* sp. and supporting at least one of the target species. This resulted in a total of 125 woodlands although the number varied between species (Table 1).

Bird abundance

Estimates of bird abundance were obtained using point counts of five minutes' duration, and carried out twice in each period (April / early May and late May / early June). There were usually 10 points per wood, but this varied according to the size of the wood, especially in the first period (mean ± SE, range; 1980s, 10.4 ± 0.2, 5-20; 2000s, 9.7 ± 0.1, 4-10). There was a minimum of 100m between points, and none were within 50m of the edge of a wood. The maximum count across the two visits (and across the two years if a site was surveyed in both) was taken as the abundance estimate for each species (Hewson *et al*. 2007).

Habitat surveys

We used a restricted set of habitat variables which were measured using comparable methods in both the 1980s and 2003/4. Habitat measurements were taken from 25m-radius circular plots centred on each point used for bird counts. Measurements were taken at one of two scales, either at the plot centre or in 5m radius sub-plots centred 12.5m from the main plot centre in each of the four cardinal directions. Estimates were made of the percentage cover of field layer vegetation (and bare ground); percentage cover of canopy at 0.5-2m, 2-4m, 4-10m and above 10m; and the number of standing trees, living and dead, and dead limbs on live trees. Those variables measured in both periods, along with a description of how the data were collected, can be found in Table 2. All habitat surveys were carried out between mid-May and mid-June in both periods, when shrub and canopy foliage was fully developed (Amar *et al*. 2006). In one region, the Forest of Dean, in the first period, field-layer vegetation was measured on a 0-5 scale; to enable a more complete analysis, these values were converted to their corresponding percentages: 0 = absent, 1 = <1%, 2 = 1-10%, 3 = 11-49%, 4 = 50-79%, 5 = 80-100%, taking the mid-point value for each category. Additionally, in the first period, standing dead trees were recorded only as being present or absent, therefore counts from the second period were also converted to either ‘0’ (absent) or ‘1’ (present) at each point when modelling the change in bird numbers as a function of change in habitat. Mean wood-scale values were calculated for all habitat variables.

All variables included in our analyses are ecologically relevant to the species of concern (e.g. Cramp *et al*. 1983; Stowe 1987; Smart *et al*. 2007; Mallord *et al*. 2012b), although one variable, the presence / absence of dead trees has only been included in models for Pied Flycatcher and Redstart as dead trees have the potential to provide nest cavities for these two species. Although many of the habitat variables were interrelated, correlations were not strong (all $r < 0.5$), except for cover at 0.5-2m and 2-4m ($r = 0.56$) and 2-4m and 4-10m ($r = 0.53$). Therefore, as habitat structure and composition at different layers within the woodland are likely to be important for the four bird species, all variables were included in our models.

Statistical analysis

Changes in bird population and woodland structure between survey periods

The change in the number of birds between the two time periods was modelled within a generalised linear mixed model framework (PROC GLIMMIX in SAS 9.2), with bird abundance in each period as the response variable, and ‘period’, ‘region’ and a ‘period x region’ interaction as predictors, the last to test whether there was regional variation in population trends. As counts were made at the same sites in two different periods, ‘site’ was included as a random effect. Models had a Poisson error structure with log link function, the log of the number of points was included as an offset and the degrees of freedom were estimated using the Satterthwaite approximation. Changes in counts between survey periods within each region and their statistical significance from zero change were derived from the ‘lsmeans’ function in SAS. After square root arcsine transforming percentage cover variables, the change in cover of habitat variables between the two periods was modelled as for the change in bird numbers, except with a normal error structure.

Species habitat associations

We investigated habitat associations of each of the four species by modelling bird abundance from 2003/04 against habitat variables in that period. To maintain consistency between the habitat association and population change models, only those variables measured in both periods were included in the analyses. These variables were the field-layer cover of Bramble *Rubus fruticosus*, Bracken *Pteridium aquilinum*, and other herbaceous species, understorey cover at 0.5-2m, 2-4 and 4-10m, the presence / absence of standing dead trees, and tree canopy cover (Table 2). 'Region' (a six-level factor, AR (Argyll), DS (Devon & Somerset), FD (Forest of Dean), GW (Gwynedd), PO (Powys) and WM (the Welsh Marches)) was retained as a fixed effect to allow for regional variation. All habitat variables, along with their quadratic terms, were entered together, before stepwise removal of the least significant until all remaining variables were significant at $P < 0.05$. All non-significant variables were re-entered to check for their lack of effect. Modelling was carried out in PROC GENMOD in SAS 9.2 (SAS Institute Inc 2002-08), with a Poisson error structure and log link function; the natural log of the number of points was included as an offset, so effectively the number of birds per point was being modelled.

Impact of habitat quality and habitat change on bird population changes

To the model of bird population change, measures of habitat in 1982-84, plus their quadratic effects, and the change in habitat (habitat values from 1982-84 subtracted from 2003/04) were entered, before stepwise removal as described above. Given that there is evidence for regional variation in both bird population trends (Amar *et al*. 2005) and changes in habitat (Amar *et al*. 2010), interactions between each habitat variable and 'region' were also included. As canopy cover was not retained in any species' habitat association model, and was not measured on all sites in 1982-84, we did not include it in models of population change.

Results

Changes in bird populations and woodland structure between survey periods

Populations of all four species declined within the study woods from 1982-84 to 2003-04, all significantly except Pied Flycatcher; however, there was much regional variation in both the direction and extent of the trends for each species (Table 3). The cover of all habitat variables increased between the two time periods, except for a reduction in canopy cover and no change in the cover of herbaceous species or the presence of dead trees (Table 4). All variables showed regional variation in the extent to which they have changed since the 1980s.

Species habitat associations

All habitat variables except canopy cover were included in at least one of the habitat association models (Table 5). The abundance of Wood Warblers in 2003/04 was associated with intermediate levels of understorey cover at 0.5-2m (optimum estimated from model, 17.2% cover) and with lower cover of Bramble and other herbaceous species. Tree Pipit abundance was associated with intermediate understorey cover at 4-10m (optimum, 56%), lower cover of Bramble and understorey cover at 2-4m, and greater cover of Bracken. Pied Flycatcher abundance was positively associated with the presence of dead trees. Redstart abundance was positively associated with the cover of Bracken, understorey at 0.5-2m and the presence of dead trees.

Impact of habitat quality and habitat change on bird population changes

In addition to largely significant effects of survey period, region and their interaction, all seven habitat variables were included in at least one model of population change (Table 6), and the change in abundance of all four species was associated with both habitat in 1982/4, and the change in habitat between 1982/4 and 2003/4. The change in Wood Warbler abundance was negatively associated with the cover of herbaceous species and understorey cover at 0.5-2 m and 4-10m, and with intermediate Bramble cover and understorey cover at 2-4m in 1982/4. Additionally, there were regional interactions with the change in Bramble cover and understorey cover at 0.5-2m (Fig 2a) and a negative association with the change in herbaceous cover (Fig 3a). The change in Tree Pipit abundance was negatively associated with the cover of Bramble, herbaceous species and understorey at 0.5-2m, and with intermediate Bracken cover, in 1982/4, as well as positively with the change in Bracken cover (Fig 3b). The change in Pied Flycatcher abundance was negatively associated with Bramble and understorey cover at 2-4m, and positively with Bracken cover in 1982/4. There were regional interactions with the change in understorey cover at 0.5-2m and the presence of dead trees (Fig 3c). The change in Redstart abundance was positively associated with the cover of Bracken and negatively with understorey cover at 4-10m in 1982/4. There were regional interactions with the change in Bracken cover and understorey cover at 2-4m (Fig 3d).

Discussion

We have shown that all four species have declined since the 1980s, significantly so except for Pied Flycatcher, although the overall trend of this species was strongly influenced by the data from one region (Devon and Somerset) in which there had been a large increase, possibly due to the provision of nest boxes (Marchant *et al*. 1990; Burgess & Barrimore 2012). We have also provided evidence of significant changes in vegetation cover and structure within these oak woods over the same period.

However, there is little evidence that change in habitat has driven the observed bird population declines. Our approach in this study has been, first, to determine which habitat features are favoured by the four migrant species characteristic of upland oak woods in the UK, and secondly to test whether changes in such habitat since the 1980s is related to changes in abundance of each bird species. For each of the species, there was a degree of consistency between the models with at least one habitat variable retained in habitat association models also retained in the change models. Some habitat variables were retained in the latter only, but as they were not associated with abundance were unlikely to be driving population change.

The consistency between the habitat association models and the effects of habitat on the trend in bird numbers suggests that we have identified key habitat features for these species. That the change in bird numbers between the two periods was related to habitat measured in 1982/4 may be due to birds responding to population declines by redistributing to the most suitable habitat (i.e. density-dependent habitat selection; Fretwell & Lucas 1970). Given the long-distance movements that they undertake, migrants may be especially able to track habitat suitability, and respond to reduced interspecific competition by settling in more favourable areas (Fuller *et al*. 2007). All four species have shown a contraction of their ranges, with populations most stable in western Britain (Balmer *et al*. 2013), although Pied Flycatcher has always had a predominantly western distribution (Holloway 1996)). However, our results indicate that there have also been significant declines within this core range, although this does not preclude redistribution based on fine-scale variation in habitat quality (Chamberlain & Fuller 1999).

Based on existing knowledge of the habitat preferences of the four bird species (Cramp & Simmons 1983; Stowe 1987; Smart *et al*. 2007; Martinez *et al*. 2010; Mallord *et al*. 2012b), the change in habitat observed in this study, i.e. increases in the cover of all but one variable (canopy cover) between 1982/4 and 2003/4, could be predicted to have a negative impact on these species' population trends. Indeed, there were significant relationships between the changes in abundance of all species with the change in at least one habitat variable (Table 6). However, this does not prove there is a causative link between the two, and additional questions can be asked to assess the likelihood that habitat change has driven the population declines of these species. Firstly, by comparing the magnitude of change in habitat to predicted optimal habitat from our habitat association models (Table 5), we can assess whether the change is sufficient to explain the observed bird population trends. Although statistically significant, the mean increase in Bramble and herbaceous cover (9.5-12.8% and 14-16.6% respectively) is unlikely to be large enough to explain the decline of Wood Warblers, the only species to show a negative association with these habitat types. The negative relationship with herbaceous cover is due to particularly large increases in cover on a relatively small number of sites (Fig. 3a). Larger increases were observed for the cover of Bracken (11.1-22.1%), but this should have been beneficial for Tree Pipit and Redstart, both of which showed positive relationships with cover, and may reflect selection of preferred nest-sites (Burton 2007, 2009) or foraging areas (Martinez *et al*. 2010), respectively. However, the direction of population change for Tree Pipit was still largely negative for sites with increasing habitat suitability (Fig 3b). From the parameter estimates in Table 5, the optimum value of understorey cover at 0.5-2m for Wood Warblers was predicted to be ca.17%, while cover at 4-10m for Tree Pipits was 56%. Table 4 shows that mean understorey cover at 0.5-2m has increased from 9.3% in the 1982/3 to 19.7% in 2003/4 and cover at 4-10m from 4.6% to 38.1%. Therefore, although there were very large increases in understorey cover, the current mean values are similar to optimal levels for each species. In fact, larger values for optimal habitat have been previously estimated for Wood Warbler (Mallord *et al*. 2012b), supporting our contention that such changes in habitat are unlikely to have a negative impact. It is likely that habitats are recovering from overgrazing, which in the past lead to impoverished understorey and reduced tree regeneration (Mitchell and Kirby 1990).

Secondly, is the regional variation in the predicted effects of change in several of the habitat variables consistent with the regional population trends reported in Table 3? If habitat change were driving the declines of bird populations, we would expect a positive correlation between the estimated effects from our change models and the observed change in bird abundance (Table 3). However, this was only the case for the effect of understorey cover at 0.5-2m on Wood Warbler abundance, whereas the relationships of the other species/habitat combinations were either non-existent or negative (Fig 2). Although the one positive correlation is suggestive, we have already discussed (see previous paragraph) that the increase in understorey cover since the 1980s is unlikely to have been sufficient to have a negative impact on Wood Warbler abundance. What these figures suggest is that, within declining populations, on sites where habitat quality improved, trends in the number of birds were more positive / less negative. Along with the significant effect of habitat measured in the 1980s, this could be explained by birds redistributing into the best quality habitat in response to population declines, rather than there being a causative role for habitat change (Fuller *et al*. 2007).

We should also bear in mind that in these analysis we have only been able to use a limited set of habitat variables measured in a consistent way in the two survey periods. Not only were these measured in a relatively crude way but they are also very limited in their scope focussing mainly on simple structural variables. Woodland habitats are notoriously difficult to measure in a quantitative and ecologically meaningful way. Our variables are ones that are likely to be important for these birds as shown by other studies and, although we think it unlikely, we cannot rule out the possibility that there are subtle changes to the habitat that are important for the birds that we have not detected.

In the UK where these species are at the edge of their range, upland oak woods and the regions in which they are found, constitute the core breeding range of each of these species, with the exception of Tree Pipit (Gibbons *et al*. 1993), and their densities are substantially higher here than found in other habitats and regions (Bibby 1989; Bibby *et al*. 1989; Fuller 1992; Fuller & Crick 1992). Despite the lack of evidence linking habitat and population change, further habitat changes could result in the loss of birds from woods. Concern has been expressed over the increase in the number of sheep in upland regions of the UK (Fuller & Gough 1999), including upland oak woods (Palmer *et al*. 2004). However, in recent decades sheep grazing in many of these woods has declined as a result of conservation efforts to ensure adequate natural regeneration, and this has lead to an increase in cover of palatable species such as Bramble, and greater sapling regeneration, resulting in increased sub-canopy cover (Hopkins & Kirby 2007). Thus, the reduction in overgrazing by sheep has potentially improved breeding habitat for some of these species, but populations have continued to decline. Further reductions in sheep grazing are likely to be detrimental to this specialised bird community (Bibby *et al*. 1989; Mallord *et al*. 2012b), as well as to other taxa for which this habitat is renowned (Rothero 2005), and the regeneration of the oak woodland itself (Mitchell & Kirby 1990). Therefore, there is a need from a conservation standpoint, as well as a legal obligation (Maddock 2008; JNCC 2012), to maintain the suitability of upland oak woods for these four species and prevent further degradation of the habitat.

We have shown that the magnitude of the changes in habitat may not have been sufficient to drive the observed population declines, and may even have been beneficial, and that the modelled effects on bird numbers were not consistent with the overall population trends. So what else could account for the decline of all four species? On the breeding grounds, predation is the main cause of failure of nests (Ricklefs 1969), but there was no evidence that predation rates had changed in a Wood Warbler population in the UK between the 1980s and 2000s (Mallord *et al*. 2012a). Resource asynchrony due to differential shifts in phenology of predator and prey has been related to the decline of Pied Flycatcher populations in the Netherlands (Both *et al*. 2006), but the effects have been shown to vary according to habitat (Burger *et al*. 2012). Greater flexibility in the diet of Wood Warblers (Maziarz & Wesołowski 2010; Mallord *et al*. in press) suggests this species may be at less risk of such phenological mismatch. Of course, all four species are long-distance migrants wintering in sub-Saharan Africa; all, except Redstart, winter in the humid zone, and all utilise wooded habitats, which have both been correlated with negative population trends (Ockendon *et al*. 2012). This may implicate land-use change in West Africa in the declines (Morel & Morel 1992) but more data on their ecology there is urgently needed. Future work on this suite of species, as with other long-distance migrants, must incorporate information from all periods of the annual cycle, at breeding, stopover and wintering sites (Sheehan & Sanderson 2012).

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Table 1 The number of woods in each region used in the study.

Region	Number of woods in sample	Number with Wood Warbler	Number with Tree Pipit	Number with Pied Flycatcher	Number with Redstart
Argyll	13	13	13	0	13
Devon & Somerset	18	18	8	15	16
Forest of Dean	15	14	9	4	5
Gwynedd	25	25	24	25	25
Powys	25	25	25	25	25
Welsh Marches	29	27	23	25	25
Total	125	122	102	94	109

Table 2 A list of habitat variables measured.

Variable	Level / Units	Description
Field-layer vegetation	Sub-plot / % cover	% cover below 0.5m: Bramble *Rubus fruticosus*, Bracken *Pteridium aquilinum* and other herbaceous species
Understorey	Plot centre / % cover	% cover as if viewed from above of canopy at height: 0.5-2m, 2-4, 4-10m
Canopy cover	Sub-plot / no.	No. of 2cm squares in 4x4 grid in which at least 50% occupied by canopy >10m height. The grid was held horizontally 60cm above observer's head using a marked stick and plumb line
Dead trees	Plot centre / no.	Number of standing dead trees within 25m-radius plot

Table 3 Estimates of the change in the number of birds of four species in upland oakwoods between 1982/4 and 2003/4 in six UK regions: Argyll (AR), Devon & Somerset (DS), Forest of Dean (FD), Gwynedd (GW), Powys (PO) and the Welsh Marches (WM). Estimates are derived from a generalised linear mixed model containing 'period', 'region' and 'period*region' interaction, with 'site' declared as a random factor, and a Poisson error structure with log link function. Estimates are taken from back-transformed values from the 'lsmeans' function in SAS (SAS Institute 2002-2008). $P <$ $^{+}$, 0.1; *, 0.05; **, 0.01; ***, 0.001; ****, 0.0001. Pied Flycatchers were not present within the Argyl (AR) region.

	Region						
Species	**AR**	**DS**	**FD**	**GW**	**PO**	**WM**	**All**
Wood Warbler	-11	**-64******	**-61******	**-28****	**-19***	-12	**-37******
Tree Pipit	-6	+52	**-76*****	**-46******	**-64******	**-89******	**-56******
Pied Flycatcher	-	**+49****	-26	-9	**-15***	**-27**$^{+}$	-9
Redstart	-10	-1	**-76*****	+9	**-37******	**-28***	**-32******

Table 4 Changes in the cover of habitat variables between 1983/4 and 2003/4 in upland oakwoods. N = 125 woods, except for canopy cover which was only recorded in 82 sites in Period 1. Percentage cover values of field layer vegetation, understorey and canopy cover were first square root arcsine transformed before testing for effects of period and region. Counts of dead trees were converted to a presence / absence score (0/1). + denotes an increase in cover between the two periods, - a decline; $P <$ *0.05, **0.01, ****0.0001.

	Period 1 (1983/4)		Period 2 (2003/4)				
Habitat variable	Mean	Range	Mean	Range	Period	Region	Period x Region
Bramble	9.5	0-67.5	12.8	0-66.0	+****	****	****
Bracken	11.1	0-45.5	22.1	0-72.5	+****	****	****
Herb	14.0	0-65.5	16.6	0-82.5	ns	**	****
Cover 0.5-2m	9.3	0-55.0	19.7	0-57.6	+****	****	****
Cover 2-4m	8.5	0-62.0	23.9	2.1-65.8	+****	ns	**
Cover 4-10m	4.6	0-44.0	38.1	2.0-86.5	+****	****	****
Dead trees	0.6	0-1	0.6	0-1	ns	****	**
Canopy cover	71.4	27.8-94.0	65.2	19.5-89.0	-****	****	*

Table 5 Final models of habitat associations of Wood Warblers, Tree Pipits, Pied Flycatchers and Redstarts in upland oakwoods. Maximum counts of birds in the second period (2003/4) modelled against habitat variables measured in the same period.

	Wood Warbler				Tree Pipit			
Variable	**df**	**est.**	**χ^2**	***P***	**df**	**est.**	**χ^2**	***P***
Region	5,112		15.3	0.009	5,91		47.5	<0.0001
Bramble	1,112	-0.0174	6.2	0.013	1,91	-0.038	5.0	0.025
Bracken					1,91	0.013	4.9	0.027
Herb	1,112	-0.0295	18.6	<0.0001				
cov_2	1,112	0.0930	13.1	0.0003				
cov_2^2	1,112	-0.0027	16.3	<0.0001				
cov_4					1,91	-0.023	5.4	0.02
cov_10					1,91	0.056	6.9	0.009
cov_10^2					1,91	-0.0005	5.3	0.021
Deadtree								

	Pied Flycatcher				Redstart			
Variable	**df**	**est.**	**χ^2**	***P***	**df**	**est.**	**χ^2**	***P***
Region	4,88		76.6	<0.0001	5,100		69.8	<0.0001
Bramble								
Bracken					5,100	0.017	10.3	0.001
Herb								
cov_2					5,100	0.019	6.8	0.009
cov_2^2								
cov_4								
cov_10								
cov_10^2								
Deadtree	1,88	0.092	4.7	0.03	5,100	0.13	8.8	0.003

Table 6 The effects of habitat quality and habitat change on the change in numbers of Wood Warblers, Tree Pipits, Pied Flycatchers and Redstarts in upland oakwoods between the 1980s and 2003/4. The table shows final GLMM models with ‘Period’ (1980s / 2000s), ‘Region’ (AR, DS, FD, GW, PO, WM) and ‘Period*Region’ interaction retained in all models to allow for regional variation in initial population size and population trends, and ‘site’ declared as random as individual woods are being compared between time periods. Prefix ‘i’ refers to habitat in 1982-84, ‘c’ to change in habitat, and superscript suffix ‘^{2}’ to quadratic relationships. The effect of dead trees was tested in relation to those species for which they are relevant, i.e. as potential nest sites for Pied Flycatcher and Redstart.

	Wood Warbler			**Tree Pipit**			**Pied Flycatcher**			**Redstart**		
Variable	**Estimate**	***F***	***P***	**Estimate**	***F***	***P***	**Estimate**	***F***	***P***	**Estimate**	***F***	***P***
Period	1 > 2	67.3	<0.0001	1 > 2	42.0	<0.0001		0.8	0.37	1 > 2	10.9	0.001
Region		2.0	0.08		16.6	<0.0001		10.6	<0.0001		11.0	<0.0001
Period*Region		10.1	<0.0001		11.9	<0.0001		3.7	0.007		3.2	0.01
i_bramble	0.023	1.9	0.17	-0.015	6.8	0.01	-0.01	4.7	0.032			
i_bramble^2	-0.0004	4.3	0.04									
c_bramble		4.2	0.04									
“ x region		4.1	0.002									
i_bracken				0.053	10.8	0.002	0.012	6.6	0.014	0.012	7.4	0.01
i_bracken^2				-0.0009	6.1	0.016						
c_bracken				0.008	4.2	0.046					8.9	0.003
“ x region											2.6	0.03
i_herb	-0.019	14.2	0.0003	-0.013	7.5	0.008						
c_herb	-0.013	8.4	0.005									
i_cov_2	-0.064	8.0	0.006	-0.033	12.3	0.0006						
i_cov_2^2	0.002	7.2	0.008									
c_cov_2		2.8	0.1					1.1	0.29			
“ x region		3.3	0.009					4.6	0.002			
i_cov_4	0.082	12.8	0.0005				-0.02	7.1	0.01			
i_cov_4^2	-0.004	24.0	<0.0001									
c_cov_4											1.2	0.28
“ x region											2.8	0.02
i_cov_10	-0.041	3.5	0.065							-0.027	9.0	0.003
i_cov_10^2	0.003	12.4	0.0006									
c_deadtree								0.01	0.94			
“ x region								4.6	0.002			

Figure legends

Fig. 1 The distribution of upland oakwood study sites and the regions in which they are found

Fig. 2 Relationship between the predicted effect of change in habitat, derived from significant interactions between habitat and region (Table 6; 1 = no change), and the change in numbers of Wood Warbler (a-b), Pied Flycatcher (c-d) and Redstart (e-f) derived from model parameter estimates (Table 6). Region abbreviations are: Argyll (AR), Devon & Somerset (DS), Forest of Dean (FD), Gwynedd (GW), Powys (PO) and the Welsh Marches (WM)

Fig. 3 Relationship between change in (a) herb and (b) bracken cover and log population change (log (n_2+0.1/n_1+0.1)) of Wood Warbler and Tree Pipit respectively. The log ratio is used to provide a simple graphical representation of the results of the Poisson models

Fig. 1

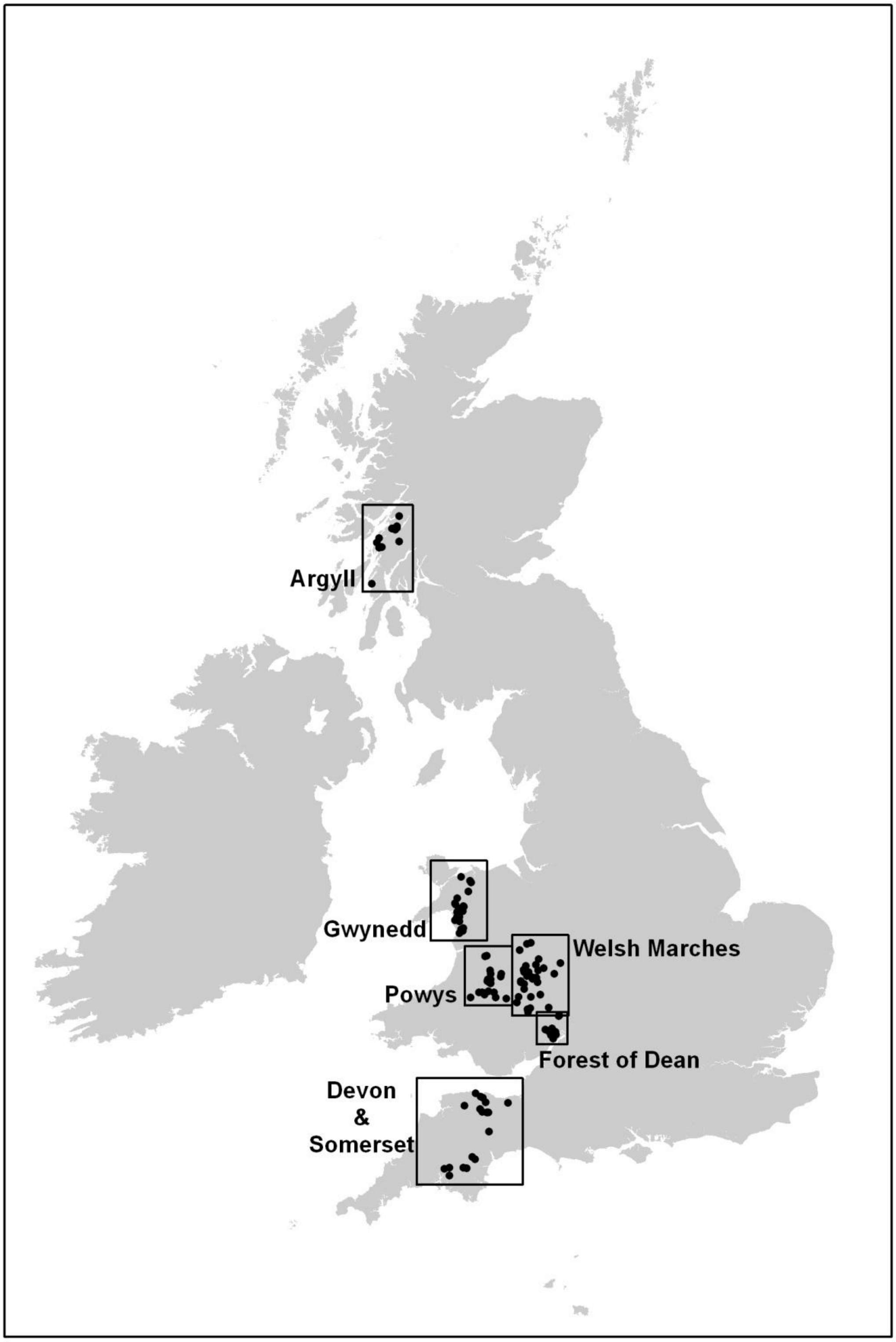

Argyll
Gwynedd
Welsh Marches
Powys
Forest of Dean
Devon
&
Somerset

Fig. 2

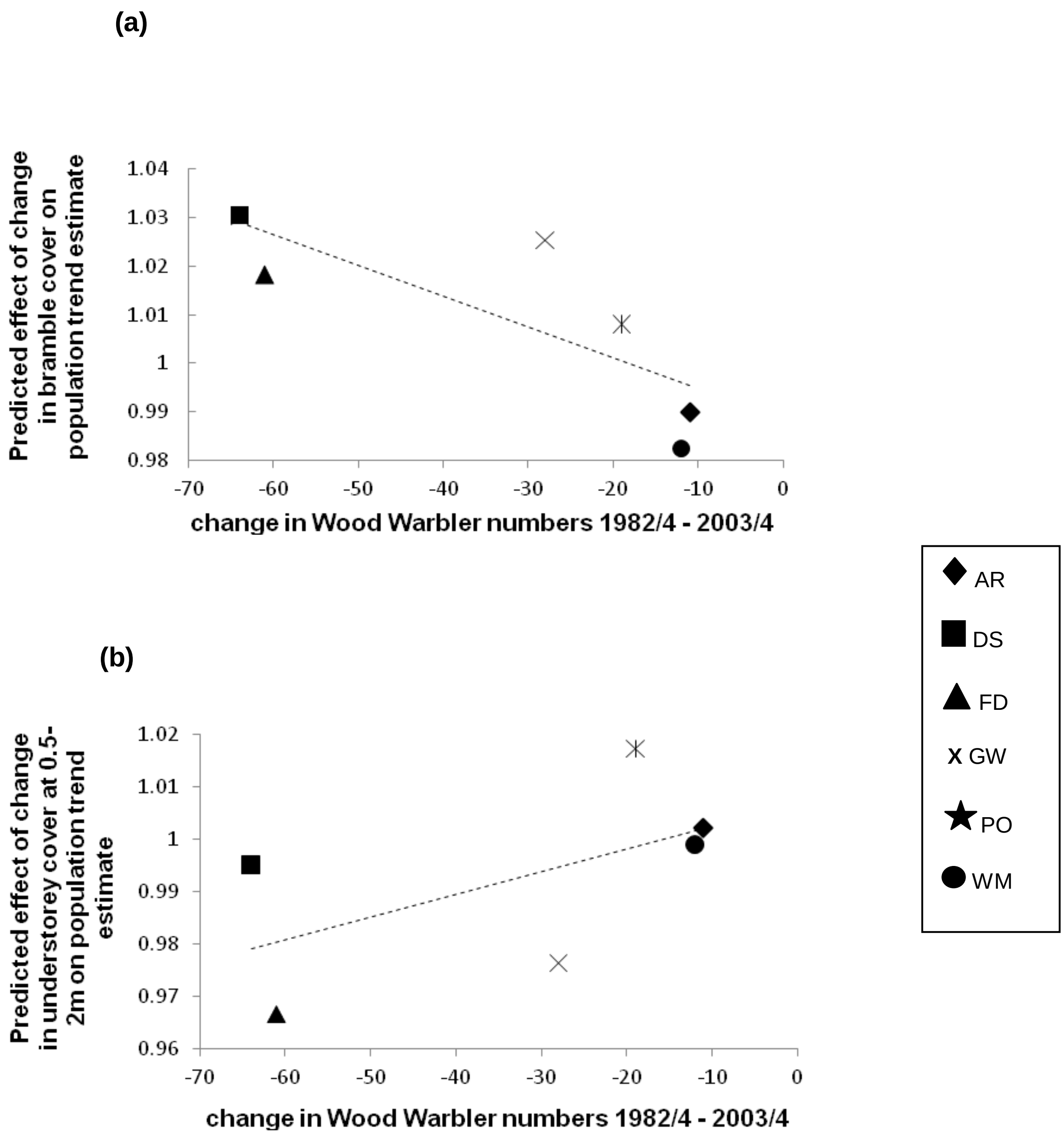

(a)
Predicted effect of change in bramble cover on population trend estimate
1.04
1.03
1.02
1.01
1
0.99
0.98
-70
-60
-50
-40
-30
-20
-10
0
change in Wood Warbler numbers 1982/4 - 2003/4
(b)
Predicted effect of change in understorey cover at 0.5-2m on population trend estimate
1.02
1.01
1
0.99
0.98
0.97
0.96
-70
-60
-50
-40
-30
-20
-10
0
change in Wood Warbler numbers 1982/4 - 2003/4
AR
DS
FD
X GW
PO
WM

Fig. 2 (cont'd)

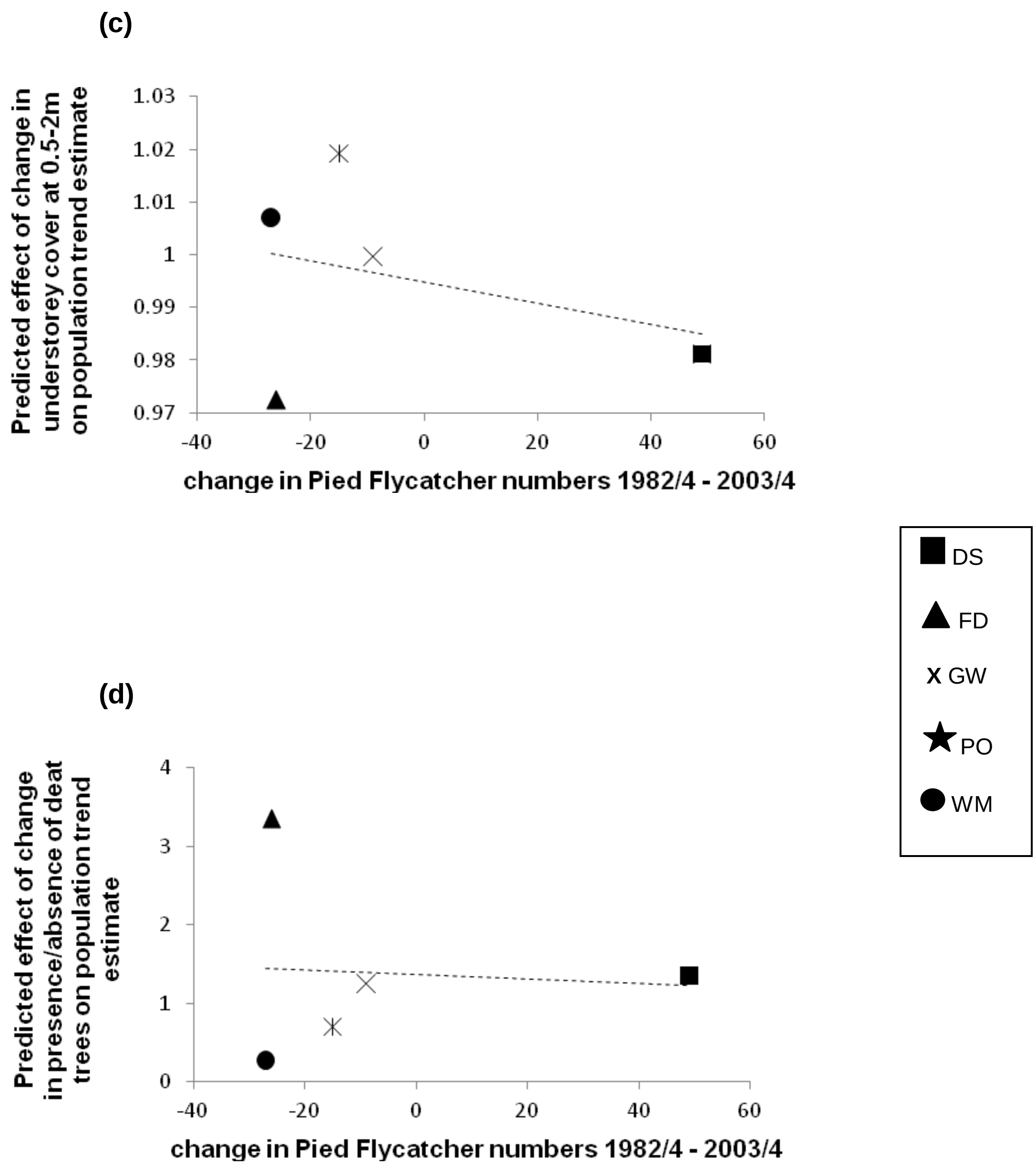

(c)
Predicted effect of change in understorey cover at 0.5-2m on population trend estimate
1.03
1.02
1.01
1
0.99
0.98
0.97
-40
-20
0
20
40
60
change in Pied Flycatcher numbers 1982/4 - 2003/4
DS
FD
X GW
PO
WM
(d)
Predicted effect of change in presence/absence of deat trees on population trend estimate
4
3
2
1
0
-40
-20
0
20
40
60
change in Pied Flycatcher numbers 1982/4 - 2003/4

Fig. 2 (cont'd)

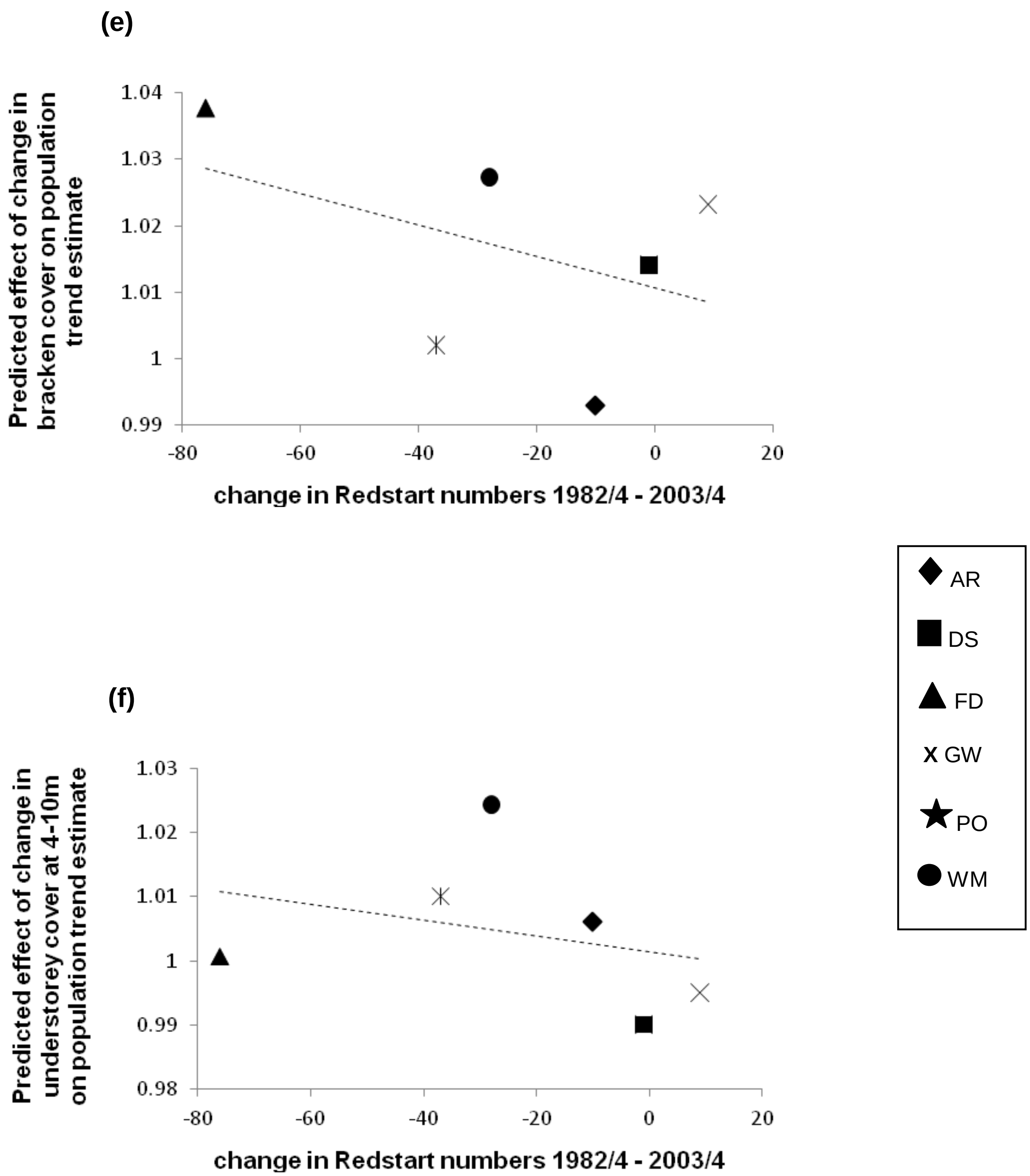
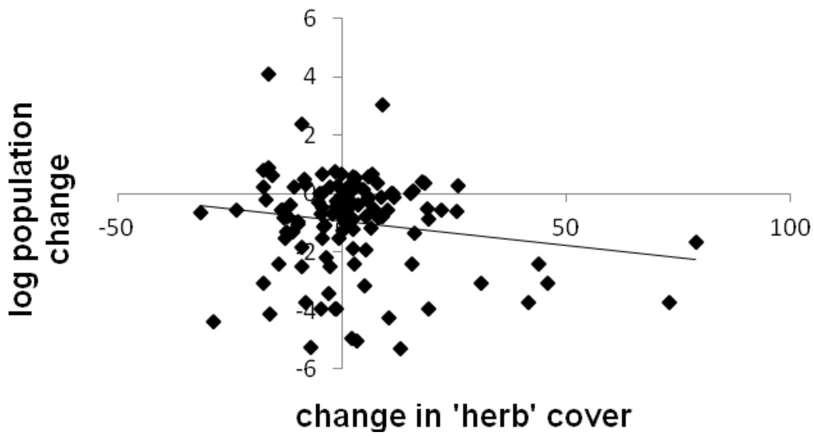
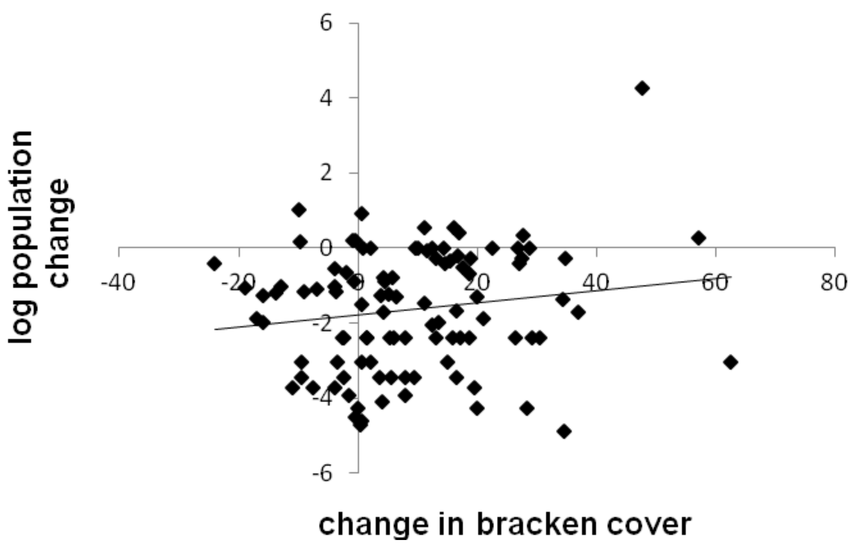

(e)
Predicted effect of change in bracken cover on population trend estimate
1.04
1.03
1.02
1.01
1
0.99
-80
-60
-40
-20
0
20
change in Redstart numbers 1982/4 - 2003/4
(f)
Predicted effect of change in understorey cover at 4-10m on population trend estimate
1.03
1.02
1.01
1
0.99
0.98
-80
-60
-40
-20
0
20
change in Redstart numbers 1982/4 - 2003/4
AR
DS
FD
X GW
PO
WM

Fig. 3

(a)


6
4
2
0
-2
-4
-6
-50
50
100
log population change
change in 'herb' cover

(b)


6
4
2
0
-2
-4
-6
-40
-20
20
40
60
80
log population change
change in bracken cover