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**Habitat selection by breeding Whinchats *Saxicola*
rubetra at territory and landscape scales**

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We determined breeding season habitat preferences for a declining migrant grassland bird, the Whinchat *Saxicola rubetra*, using intensive, territory-scale habitat and invertebrate data, and independently gathered landscape-scale field survey and remotely sensed habitat data to determine whether the same habitat relationships were evident at both spatial scales. At the territory scale, low elevation and a heterogeneous vegetation structure with a high density of perches and tussocks were the dominant features of occupied habitats. The landscape scale model successfully predicted areas where breeding Whinchats were more likely to occur, and similar and consistent relationships with habitat features occurred at both spatial scales. However, plant species richness and topographic slope elicited different responses at different spatial scales, with steeper slopes and high plant species richness favoured at the landscape scale, whereas at the territory scale low plant species richness was preferred and slope did not determine settlement. These differences reflect differences in the way the data were measured and extrapolated. This study identifies important attributes of lowland grassland habitats and landscapes for a stable population of breeding Whinchats, while the analysis shows the good predictive ability of remotely sensed data to model this species' distribution at larger spatial extents. Our findings provide methods for assessing habitat availability for this declining species and for managing habitats and landscapes to provide these essential elements.

Keywords: habitat change, bird conservation management, Maxent, territory occupancy, ground measurements, grassland, large scale distribution modelling

Potential breeding habitats for birds and many other organisms are changing rapidly (Millennium Ecosystem Assessment 2005). One of the main drivers of habitat change is agricultural intensification, which is thought to be at least partly responsible for the recent declines in long distance migrants, farmland and grassland birds (Brennan & Kuvlesky 2005, Wilson *et al.* 2005, Donald *et al.* 2006, Vickery *et al.* 2014). Agricultural intensification often results in homogenisation of the landscape, leading to a loss of the combination of features needed by breeding birds (Vickery *et al.* 2014). The resultant reduction in food availability and increase in predation risk can then lead to reduced productivity and adult survival (Vickery & Arlettaz 2012).

In order to focus conservation action, it is necessary to identify a breeding species' key habitat preferences and requirements (Buchanan *et al.* 2005, Sim *et al.* 2007) and thereby identify strongholds of suitable habitat that still exist (Yost *et al.* 2008, Kassara *et al.* 2014). Detailed, fine-scale habitat sampling and corresponding surveys of the relative abundance of a species can provide accurate information on habitat preferences (e.g. Pearce-Higgins & Grant 2006), but are labour-intensive and therefore often not possible to conduct over large areas, or in more remote locations (Buchanan *et al.* 2005, Brambilla *et al.* 2009). If the habitat cues to which organisms respond at a territory scale can be generalised across whole landscapes, then information on fine-scale habitat preferences (territory scale) can be used to model expected species distributions over a much larger spatial extent (landscape scale). Due to advances in remote sensing technology and large scale environmental monitoring, there is an increasingly wide range of climatic, vegetative, aquatic and topographic data available at different resolutions and covering different geographical areas (Buchanan *et al.* 2005, Elith *et al.* 2011). Landscape scale species occurrence data have also become increasingly available over the last decade due to internet data sharing and the corresponding increase in citizen science (Lepczyk *et al.* 2009). Using these readily available data to create extensive habitat suitability maps for a particular species potentially allows rapid assessment of how much suitable habitat is available and where to target conservation action (Tinoco *et al.* 2009). However, the assumption that the habitat requirements of species determined by intensive studies at the territory scale are transferrable to wider scale landscape suitability models is not always valid. Territory-scale studies may not consider broader scale selection pressures (Chalfoun & Martin 2007, Brambilla *et al.* 2009, Irvin *et al.* 2013). For example, thick vegetation for concealment may be important at a nest-site to reduce predation risk (Martin 1992, 1993, Davis 2005), but the wider vegetation structure and associated food availability may determine predator densities at the landscape scale (Salamolard *et al.* 2000, Chalfoun *et al.* 2002, Chalfoun & Martin 2007). Additionally, it is often not possible to characterise a habitat feature in as detailed a way at the broader landscape scale, and this can then produce misleading conclusions or poor predictive accuracy (Chalfoun & Martin 2007, Brambilla *et al.* 2009, Irvin *et al.* 2013). It is therefore important to investigate response to habitat features with data collected at both territory and

landscape scales to ensure landscape scale habitat suitability models are accurate and to maximise effectiveness of conservation measures (Brambilla *et al.* 2009).

The Whinchat *Saxicola rubetra* is a ground-nesting Afro-Palearctic migrant of grasslands that has recently suffered major and widespread declines in range and abundance. Consequently, Whinchats are increasingly considered a priority species for conservation action (Bastian & Feulner 2015).

Across Europe, Whinchats declined by 67% between 1980 and 2009 (EBCC 2012). This is thought to be due to agricultural intensification causing losses in both grassland habitat extent and quality on the breeding grounds (Richter & Düttmann 2004, Grübler *et al.* 2008, Broyer 2009, Fischer *et al.* 2013), although in the last 20 years non-breeding season processes may also have contributed (Henderson *et al.* 2014). However, some local breeding populations buck the trend with apparently secure and relatively stable populations. One such population is that on Salisbury Plain in southern England (Taylor 2015), a large expanse of lowland, agriculturally unimproved grassland which supports 400–500 pairs (Stanbury 2005). Salisbury Plain is the only significant lowland population of Whinchats remaining in England and one of few in western Europe (Müller *et al.* 2005, Calladine & Bray 2012, Henderson *et al.* 2014). The persistence of this population suggests that fundamental breeding conditions still exist here. In the UK and in England in particular, it is in lowland landscapes where this species has undergone its greatest long-term population decline (Balmer *et al.* 2013) and there have been similar losses recorded in other lowland habitats across Europe (Müller *et al.* 2005, Broyer *et al.* 2012, Tome & Denac 2012, Fischer *et al.* 2013). Contrary to what is suggested by its current breeding distribution (e.g. Balmer *et al.* 2013, Bastian & Feulner 2015), the Whinchat is therefore not an obligate upland species. It is, however, one of a community of declining UK grassland bird species (Vickery *et al.* 2001, Wilson *et al.* 2005, Donald *et al.* 2006) for which careful determinations of key habitat and landscape characteristics are urgently needed to help understand and reverse population and range loss, especially in lowland agricultural systems. This in turn may allow more effective direction of conservation policy.

This paper quantifies breeding Whinchat habitat associations by comparing and contrasting two different sources of habitat data, the first being habitat and invertebrate prey data collected at the territory scale, and the second (covering a larger spatial extent) being independently sourced vegetation and topographic data derived from remote sensing and interpolation of long-term field surveys conducted as part of the condition assessment of the Salisbury Plain designated area. We aimed to assess which habitat features were most strongly and consistently associated with Whinchat occurrence at the two scales of habitat measurement. Based on a review of grassland bird habitat preferences (Taylor 2015), results of studies on landscape scale habitat use (Osborne *et al.* 2001, Gibson *et al.* 2004, Brambilla *et al.* 2009) and knowledge of Whinchat breeding ecology (Bastian *et al.* 1994, Oppermann 1990, 1992, 1999, Orłowski 2004, Richter & Düttmann 2004, Calladine & Bray 2012, Fischer *et al.* 2013) we predicted that (1) due to the foraging method adopted by Whinchats, territory scale data will indicate a higher abundance of breeding Whinchats in structurally diverse grassland with a high abundance and diversity of invertebrates and a high abundance of perches from which to forage, that (2) relationships with habitat variables will be consistent at territory and landscape scales, and that (3) landscape-scale data will also provide good approximations of habitat suitability and availability for Whinchats.

METHODS

Study area

The study site was an area of 178 km² in the western part of Salisbury Plain, UK (51° 11' 52" N-51° 16' 4" N, 1° 57' 32" W - 2° 9' 32" W), at an elevation of 70–237 m above sea level. Salisbury Plain is a chalk plateau with many shallow valleys. The area has been used for military training since 1897 and consequently has escaped conversion to intensive agricultural land use (Ash *et al.* 2011). It contains the largest area of agriculturally unimproved chalk grassland in north-western Europe and supports many important populations of species of high conservation concern (Ash & Toynton 2000). The site comprises predominantly National Vegetation Classification (NVC, Rodwell 1992) classes CG3d (*Bromus erectus* grassland with *Festuca rubra* - *Festuca arundinacea* sub-community) and MG1

(*Arrhenatherum elatius* grassland with *Festuca rubra* sub-community) (Walker & Pywell 2000).

Low-intensity grazing was reintroduced to parts of the plain around 1995 to control scrub encroachment, but prior to this the area was not grazed for over 50 years (Ash & Toynton 2000).

Grazing is limited to 10–14 days annually on areas of < 8 ha or when the sward height reaches 5 cm.

Mowing is restricted to a few small fields on the edge of the study site and none is allowed until after 1 July to minimise the impact on breeding birds (Ash & Toynton 2000).

Territory scale model

Thirty-two 1-km squares were selected to provide a good coverage of the whole study area (Supplementary Online Appendix S1), 19 of which were surveyed in 2012 and 13 in 2013. For consistency, the 32 squares were the same as those selected for a previous Whinchat survey in 2005 (Stanbury *et al.* 2005). Surveys consisted of two 1-km transects per square, positioned 500 m apart, based on methods used in the British Trust for Ornithology's Breeding Bird Survey (BBS) (Gregory & Bashford 1996). The orientation of transects was randomly assigned. Each square was surveyed once between 20 May and 3 June and again between 3 July and 11 July, with these timings designed to ensure that surveys reflected breeding habitat choices. Most surveys took place between 06:00 and 09:30 (with a small proportion between 16:30 and 19:30) in good visibility. Each transect was then further split into 200-m sections, again following BBS design. Estimated abundance was calculated as the maximum count of territorial Whinchats observed per 200-m section over the two visits. Whinchat territories on Salisbury Plain typically occupy around 30 000 m² (100-m radius, Taylor 2015) so an observer may expect to detect several Whinchat territories in a 200-m transect section depending on how the territories are arranged relative to the transect line. Habitat within a 200-m section was expected to be representative of habitat in Whinchat territories detected in that section. Vegetation structure, invertebrate fauna and topography were sampled for each 200-m section (Table 1). Three sections had to be excluded due to access restrictions. The habitat features measured were selected on the basis of indications provided in the literature (e.g. Bastian *et al.* 1994, Oppermann 1990, 1992, 1999, Orłowski 2004, Richter & Düttmann 2004, Calladine & Bray 2012, Fischer *et al.* 2013) and our own knowledge of Whinchat breeding biology.

Vegetation was sampled between 19 April and 11 May to coincide with Whinchat arrival. In 2012, three 1-m² quadrats were placed at 0, 10 and 20 m from the start of each 200-m section. In 2013 the sampling effort was doubled to six samples, taken every 33 m. These replicates were averaged to give one mean value for each 200-m section for each of seven vegetation variables, summarised in Table 1.

In 2013, invertebrates were sampled using a sweep net (37 cm diameter by 82 cm depth; 10 sweeps per sample). Samples were taken at 0 m, 66 m, and 133 m from the start of each of 130 200-m sections in three separate visits (8 – 21 June, 1 – 7 July, 15 – 20 July). Samples were taken between 09:30 and 17:00 on dry days when the wind speed was less than 16 km per hour. Invertebrate sampling data were summarised in three measures: abundance, richness of invertebrate orders and inferred biomass. Means of each of these measures were calculated from the three samples for each 200-m section. Inferred biomass was calculated following Rogers *et al.* (1976) as: weight (mg) = $0.0305L^{2.62}$, where L = body length (excluding antenna or other protrusions). Invertebrate body lengths were measured in the field to the nearest 2 mm.

The locations of each sampling point in 2012 and 2013 were recorded using a handheld GPS device (Garmin eTrex). These locations were used to determine elevation, aspect and slope from a 5-m x 5-m resolution Digital Elevation Model (NextMap DEM; Intermap Technologies 2007). To account for any difference in detectability of Whinchats in the different 200-m sections, visibility of the surrounding landscape and percentage scrub cover were also included in the analysis. Visibility was calculated individually for each transect using the DEM and a Viewshed tool (ARGIS 10.0, ESRI, 2010). Percentage scrub cover was estimated using analysis of aerial photographs from 2010 (Redhead *et al.* 2012). GIS analyses were then used to determine the percentage area visible and the mean percentage scrub cover for a 250-m radius from the mid-point of each 200-m section along the transects.

Territory scale habitat preferences were modelled in the statistical package R (version 3.1.2 R Development Core Team 2014). All explanatory variables were tested for normality and transformed where necessary (Table S1). Because six of the vegetation variables were highly correlated, a

Principal Components Analysis (PCA) was used to summarise the main variability of these vegetation characteristics (Table S2). The first two principal components summarised 80% of the variation and were then used in the model (Zuur *et al.* 2007). High values of PC1 (60% of the total variation) represented areas with longer, denser, grass-dominated vegetation with higher structural diversity, and more tussocks. High values of PC2 (20% of the total variation) represented species-rich areas, with shorter vegetation, fewer tussocks and less structural variation. PC1 and PC2 were both found to be moderately correlated with the abundance of perches (Pearson's $r = 0.446$ and 0.417 respectively) despite the fact that perch abundance was not highly correlated to the individual vegetation variables which made up PC1 and PC2. Therefore, perch abundance was modelled separately to PC1 and PC2. As the invertebrate data were only collected in 2013 for 130 of the 317 200-m sections, a separate analysis was conducted to model the relationship between Whinchat abundance and occurrence and invertebrate measures.

The counts of Whinchats per 200-m section were highly zero inflated, with excess zero counts causing over-dispersion. Because each square was visited an additional four times to collect data on vegetation and invertebrates, we were able to determine that the main surveys detected approximately 90% of Whinchats seen over all surveys. Most zero counts were therefore deemed to be real absences, and hence a hurdle model was chosen in preference to a zero-inflated model (Mullahy 1986, Zeileis *et al.* 2008). This model consists of two parts: a zero-truncated count component modelled with a Poisson distribution, and a hurdle component which models the zeros versus larger counts using a binomial distribution (Zeileis *et al.* 2008, Zuur *et al.* 2009). This type of model was deemed more appropriate than a simple binomial model because a third of Whinchat counts were greater than one. Initially all variables were included in both components of the model. Interaction terms were not included to avoid overfitting, with one exception; the interaction term between elevation and aspect was modelled because a previous Whinchat study had found this effect to be important (Calladine & Bray 2012). Stepwise deletion was used to simplify the model until only terms significant at $P < 0.05$ remained. Nested models were compared via likelihood ratio tests (lmtest package, Zeileis & Hothorn

2002, Zuur *et al.* 2009). Including 1-km square as a random factor (achieved by creating two separate models, one to model the truncated counts in the response data and one to model the presence versus absences with the glmmADMB package; Skaug *et al.* 2006) did not significantly improve model fit (Table S3). A spline correlogram (ncf package, Bjørnstad & Falck 2001) with 95% bootstrap confidence intervals and a maximum lag distance of 10 km showed no spatial autocorrelation in the Pearson model residuals of the combined hurdle model (Fig. S1).

Whinchat relationships to landscape using remote sensed and modelled data

On Salisbury Plain, habitat data are gathered as part of the statutory habitat condition assessments required by the site's conservation designation. These data include long-term, ground-based vegetation surveys and remote sensed habitat and topographic data using national-scale terrain models (Table 1). These data are available for the whole of the plain and they allow habitat associations of breeding birds to be modelled over a large spatial extent. Presence-only modelling software, Maxent version 3.3.3k (Phillips *et al.* 2007), was used to model habitat suitability for Whinchats over the whole of the western third of Salisbury Plain at the landscape scale (as opposed to the 32 survey squares used in the territory scale model, which formed a subset of this larger area). Maxent was chosen because it performs favourably when compared to other presence-only habitat suitability modelling methods, giving robust and precise estimates (Elith *et al.* 2006, Phillips *et al.* 2006).

In this analysis, Whinchat occurrences were obtained from a variety of sources: the line transect surveys described above, linear valley surveys, during which a valley was walked linearly once and any territorial Whinchats recorded, and mapped data gathered during the intensive daily coverage of six study sites used for monitoring Whinchat breeding success (Taylor 2015, Appendix S1). The environmental variables were selected to be the closest available approximation to the variables used in the territory scale analysis, as a spatial layer at the extent of our study landscape. Whilst some variables were readily represented with landscape coverage datasets derived from remote sensing data (e.g. elevation, scrub cover), others had to be interpolated from broader scale field surveys (e.g. plant

species richness) and some (e.g. number of perches) were unavailable with whole-landscape coverage (Table 1). All landscape variables were transformed to a 100-m x 100-m resolution raster so that each cell corresponded to a Whinchat's approximate territory size on Salisbury Plain (Taylor 2015). To account for any bias arising from variation in survey effort due to the differing sources of occurrence data, a variable was produced which described the varying level of survey effort in the study region (a 'bias layer'). We used AICc to compare the full model against models where lower contributing predictors (with a permuted importance of < 8%) were sequentially removed, and also compared models using simpler transformations of the original covariates (or 'feature types' - Phillips *et al.* 2006) and models with and without a bias layer (Burnham & Anderson 2002, with ENMTools: Warren *et al.* 2010, Warren & Seifert 2011). The model with the lowest AICc was selected as the final model. The Area Under the Receiver Operator Characteristic Curve (AUC) was used to evaluate the final model fit. Values of AUC between 0.7 – 0.9 indicate a moderately useful model, with values above 0.9 indicating excellent performance (Pearce & Ferrier 2000). The importance of each variable in the model was calculated by randomly permuting values of the variable among the data used to fit the model 1000 times, and measuring the resultant decrease in model fit via change in AUC. A large decrease shows the model depends heavily on that variable (Phillips *et al.* 2007). These values were then normalised to give a percentage for each variable.

To validate the final Maxent model predictions, 400 random points, at least 100 m apart, were generated within the study landscape. Such a large number of points were generated to allow for uncertainty in how many it would be possible to survey during the field season, and for any that might prove inaccessible. Tetrads (2-km squares) were randomly selected for survey, and all random points within these tetrads were surveyed, unless a point was inaccessible. A total of 267 of these points were eventually surveyed for Whinchats in 2014, between mid-May and late June. All points were surveyed for five minutes before 11:00 or after 16:00, when Whinchats were observed to be most active (Taylor 2015). Whinchats seen or heard within 100 m of the point were counted as 'presences'. Five minutes was chosen as a compromise to maximise the number of points that could be covered but still ensure a high detection rate. Field observations of the time taken to find a Whinchat within its

territory suggested that five minutes was sufficient time to detect a Whinchat if it was within 100 m of the point. The predicted suitability value for each surveyed random point was extracted from the Maxent habitat suitability raster and square-root transformed to remove the positive skew. These values were then tested in a binomial GLM with detected Whinchats from the ground-truthing survey as the response. The 'lm.moran' test function (Cliff & Ord 1981, Bivand 2014) was used to test for spatial autocorrelation in the model residuals, using an inverse weighted distance matrix, and found no significant autocorrelation (Moran's I = 0.131, $P = 0.060$).

RESULTS

Territory-scale Whinchat habitat preferences

The best-supported model contained PC1 in the count component ($\chi^2 = 7.85$, $P = 0.005$, $n = 317$) and PC1 ($\chi^2 = 8.13$, $P = 0.004$, $n = 317$) and elevation in the hurdle component ($\chi^2 = 10.4$, $P = 0.001$, $n = 317$). Whinchat presence was positively associated with PC1 ($Est = 0.26 \pm 0.09$, $Z = 2.78$, $P = 0.005$; Fig. 1) and in areas of habitat where Whinchats were present, the number of birds increased as the amount of PC1-type vegetation (i.e. long, dense, grassy, structurally diverse vegetation) increased ($Est = 0.31 \pm 0.12$, $Z = 2.61$, $P = 0.009$; Fig. 1). To assist interpretation of the individual effects of the variables that make up the principal components, the means and standard errors from the untransformed variables for 200-m sections where Whinchats were present or absent are presented in Table S4. Whinchats were more likely to be observed at lower elevations regardless of vegetation type ($Est = -0.02 \pm 0.008$, $Z = -3.11$, $P = 0.002$; Fig. 1), indicating a preference for valleys. Visibility and percentage scrub cover, which were included to account for any differences in detectability between sections, did not affect the observed number of Whinchats and were therefore dropped from the model (see Table S5 for chi-square values of other terms as they were dropped from the model). The alternative model using perch abundance instead of PC1 and PC2 found that perch abundance was significantly positively correlated with Whinchat occurrence ($Est = 0.935 \pm 0.316$, $Z = 2.96$, $P =$

0.003) and retained the significant effect of elevation, but overall was less well fitted than the model including PC1 and PC2 ($\Delta\text{AICc} = 5$). The abundance, order richness and inferred biomass of invertebrates showed no relationship to the abundance or the presence of Whinchats per 200-m section when tested individually or in a full model with the vegetation and topography variables (Likelihood ratio test: $P > 0.544$). This suggests that the latter variables influence Whinchat habitat suitability in ways other than simply reflecting the abundance of invertebrate prey.

Landscape-scale model

The Maxent model with the lowest AICc included all variables and no bias layer (Table S6). The final, cross-validated model had an average AUC of 0.773 (+/- SD 0.058). All tested models performed significantly better than a random model (Binomial test of omission: $P < 0.0001$).

Validation surveys (Appendix S2) confirmed the model's predictive capacity; observing a Whinchat was significantly more likely at sampling points with a higher suitability (GLM: $Est = 4.25 \pm 1.35$, $P = 0.002$, $n = 267$). Table 2 displays the permuted relative importance for each environmental variable (for response curves see Fig. S2). Elevation contributed most to predicting suitability (47.9%; Table 2) followed by slope (11.5%), leading to a strong trend for higher habitat suitability in cells with lower elevations and steeper slopes. There were weaker trends for higher habitat suitability at lower scrub densities, more westerly aspects, higher grassland plant species richness and less bare ground (though a small amount of bare ground is favoured). A higher percentage cover of MG1 and CG3d was also preferred, indicating a preference for unimproved, tussock-rich, structurally diverse grassland.

DISCUSSION

We identified important qualities of lowland grassland habitat and landscape that are associated with a higher probability of presence of territorial Whinchats in a stable breeding population, and determined the success of using field survey and remote sensed data to model this species distribution at larger

spatial extents. In general, though the landscape model could not incorporate the detailed information on vegetation structure, Whinchats showed similar relationships with habitat variables at both spatial scales and the landscape model exhibited good ability to predict where Whinchats were more likely to occur. This suggests that it is possible to use landscape scale data to make reliable inferences about the availability of suitable habitat, saving time and expense and allowing a much broader coverage. Our findings provide information for assessing habitat availability or for managing habitats and landscapes to provide these essential elements.

Whinchat habitat preferences on Salisbury Plain

Across the Salisbury Plain landscape, breeding Whinchats were not randomly distributed but rather aggregated along valley contours (as also found by Stanbury *et al.* 2005). Lower valley elevations in particular represented an important co-occurrence of habitat characteristics that the birds associated with, comprising tussock-rich grassland, low scrub cover and high sward structural diversity and perch density to suit the species' visual foraging behaviour (Bastian & Bastian 1994, Richter & Düttmann 2004). Due to the high correlations between the structural vegetation variables it was not possible to determine the relative importance of each to Whinchat occupancy. However, these features are consistent with habitat structural characteristics identified in other studies from quite different locations and contexts across Europe (Oppermann 1990, 1992, Pearce-Higgins & Grant 2006, Broyer *et al.* 2012, Fischer *et al.* 2013).

Unexpectedly, higher elevations on Salisbury Plain were less likely to be occupied by Whinchats even when controlling for the key structural vegetation attributes identified above. This relationship suggests that the 'preferred' valley lower slopes must also provide other, more subtle, advantages, perhaps in terms of microclimate. For example, shelter or drier ground conditions on the valley sides may benefit foraging efficiency or nestling thermoregulation (Visser 1998). In upland studies in the UK a similar association has been found between breeding Whinchats and elevation and slope, which are assumed to provide thermal advantages (Calladine & Bray 2012). The elevation of Salisbury

Plain, however, is well within the thermal limits that breeding Whinchats encounter across Europe (Hagemeijer & Blair 1997) and therefore the difference is more likely to be attributable to microclimatic differences and possibly related influences on food availability, accessibility or predictability. Invertebrate mean abundance, diversity and inferred mean biomass did not appear to determine variation in Whinchat settlement on Salisbury Plain, unlike in other studies (e.g. Bastian *et al.* 1994, Oppermann 1999). However, those studies compared Whinchat settlement between habitats with very different invertebrate populations due to different intensities of agricultural management, whereas Salisbury Plain is comprised almost wholly of agriculturally unimproved grassland (Ash & Toynton 2000, Ash *et al.* 2011) and invertebrate populations for Whinchats may be, by comparison, universally high. This assumption is supported by our parallel studies on the population which revealed little evidence of variation in nestling condition or incidents of nestling starvation and indicated that by far the largest cause of breeding failure was nocturnal predation (Taylor 2015, Taylor *et al.* 2015). On Salisbury Plain, there are variations in grazing frequency that may contribute to the difference in microclimate between valley ridges and floors, and may cause differences in prey availability rather than prey abundance which lead to a preference for lower elevations.

The grassland on Salisbury Plain is not mown, but managed through moderate ground disturbance from military vehicles, some scrub removal and a carefully regulated, rotational grazing regime by cattle and sometimes sheep (Ash & Toynton 2002). Low frequency grazing can control scrub encroachment, create open areas suitable for foraging (Murray *et al.* 2016) and maintain the grassland structure in the long term. However, intensive grazing during the breeding season has a negative effect on Whinchat occupancy and breeding success, even though the sward generally recovers to a more suitable structure within a year (Taylor 2015). The pressure, frequency and timing of grazing are therefore all critical to the structural suitability of the habitat. In practice, grazing tends to occur more frequently on the drier upper hillsides and plateaux than on the lower valley floors that can be wet in winter, or the steep valley sides. These differences in grazing frequency and/or the wet winter conditions may modify not just structure but possibly also the microclimate and its suitability for

Whinchats. High moisture and humidity are features common to the habitats of many breeding populations of Whinchats (e.g. Fischer *et al.* 2013, Besnard *et al.* 2015) and may suit this cool-temperate breeding species that avoids the hotter, drier habitats of southern Europe. These subtleties of sward condition deserve closer research as it is a characteristic that could affect the long term suitability of habitats following global climate change.

Comparing landscape features to territory level habitat associations

In general, there was high congruence in the direction of relationships between habitat associations at territory and landscape scales. This suggests that it is possible to predict Whinchat occurrence from the creation of habitat suitability maps using features such as topography and vegetation characteristics from large scale monitoring (such as with the NVC survey on Salisbury Plain - Pywell *et al.* 2006). However, Whinchats did not simply select habitat based on easily measured vegetation characteristics but instead responded to a complex combination of local topography and vegetation, and some responses differed between territory and landscape scales. Plant species richness and slope were both positive influences (albeit minor in the latter case) at the scale of the whole site, but neither were important to the specific location of Whinchat territories, where instead a heterogeneous vegetation structure was the most influential habitat feature. This may be due to the fact that even though the survey unit for field surveys and the cell size chosen for landscape modelling are both selected to be 'territory scale', the datasets were necessarily constructed in different ways. The average value of slope per cell is more likely to indicate the general topography of the cell and its location in the valley than average of point measures which are more likely to be influenced by minor topographic variations. Landscape-scale plant species richness was also interpolated, so will be much more indicative of the general richness of the surrounding grassland rather than sward within the territory. Therefore, plant species richness may be positively correlated with invertebrate abundance when using landscape scale data (Oppermann 1990, Woodcock *et al.* 2005) but not at the territory scale, where differences between plant communities are likely to be finer. Therefore, despite overall

similarity in the relationships between landscape and territory scales, there were some notable differences which reflect differences in the way the data was collected and extrapolated to the landscape scale, and the coarser vegetation data available for the landscape approach. These factors are important to consider when collating datasets to perform a landscape scale analysis, especially in terms of ensuring appropriate conservation management (Chalfoun & Martin 2007, Brambilla *et al.* 2009).

Behavioural influences, such as conspecific attraction (Ward & Schlossberg 2004), site fidelity (Lane *et al.* 2001) and individual assessments of conspecifics' breeding success (Doligez *et al.* 2002), may all influence settlement decisions, and so contribute to residual variation in territory distribution that is not immediately attributable to habitat quality. In the case of the Salisbury Plain Whinchat population, a high proportion of apparently suitable habitat appears currently unoccupied. The population exhibits low breeding success due to high nest predation and is currently maintained by immigration (Taylor *et al.* 2015, Taylor *et al.* in prep). This poses interesting questions for further research on whether Whinchats choose to inhabit particular valleys due to historic site fidelity or whether the current distribution is in some way determined by variation in predator abundance. The general conclusion that can be drawn from this study is that landscape scale data can provide a useful role in indicating areas likely to be suitable for a species but fine scale measurements will still be needed to form reliable detailed management plans.

Conclusions and implications for Whinchat conservation

Identifying a declining species' key habitat preferences is important for effective conservation initiatives. The grassland landscape of Salisbury Plain, whilst unique in its extent the UK, is not so unusual in the wider context of European breeding sites for Whinchats. It is extensive, predominantly treeless, unenclosed and agriculturally unimproved, all of which are features common to most of the larger Whinchat breeding populations in Europe (e.g. alpine meadows; Gruebler *et al.* 2008; lowland grasslands; Denac & Tome 2012, Fischer *et al.* 2013) or moorland margins and hillsides (Pearce-

Higgins *et al.* 2012)). None of the structural or topographical habitat characteristics identified as influencing Whinchat occupancy here are intrinsically unobtainable elsewhere, either regionally or nationally within the UK. Therefore, there are opportunities to manage existing grasslands to create habitat conditions more suitable for breeding Whinchats (i.e. dense grass, higher structural diversity, and plentiful tall woody plants for use as perches such as the Apiaceae family) as well as potential for targeting efforts to restore grassland to areas with the topography preferred by Whinchats on Salisbury Plain.

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SUPPORTING INFORMATION

Additional Supporting information may be found in the online version of this article:

Appendix S1. Figures showing the locations of Whinchat surveys.

Table S1. Transformations of variables for the territory scale model.

Table S2. Results of a Principal Component Analysis for vegetation data from the territory scale analysis.

Figure S1. Spline correlogram showing no autocorrelation in the territory scale hurdle model residuals.

Table S3. The best random effect models selected by stepwise deletion examining territory scale effects on Whinchat abundance and occurrence.

Table S4. The mean and standard error for each predictor variable for 200 m sections where Whinchats were present and 200 m sections where Whinchats were absent.

Table S5. Model selection for the territory scale model.

Table S6. AICc scores for the candidate landscape scale models.

Appendix S2. Maps showing the projected predictions for Whinchat occurrence from the landscape scale model.

Figure S2. Response curves for variables in the landscape scale model.

Tables and Figures

Table 1. Descriptions and sources for the predictor variables used in the territory and landscape scale models.

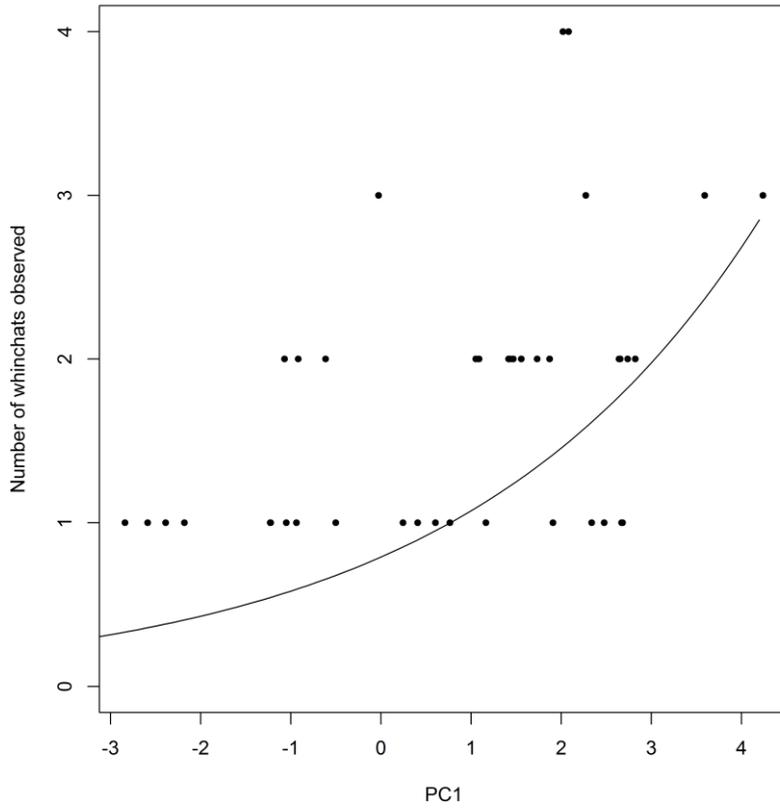
All territory scale variables are measured in 1-m quadrats. All landscape scale variables are per 100-m cell.

	Variable	Definition and source
Territory scale	Plant species richness	Number of plant species
	% Cover ground level	Percentage of ground covered with vegetation
	% Cover > 20 cm	Percentage of vegetation cover 20 cm above ground
	% Grass to herb ratio	Percentage of grass relative to herb
	Mean vegetation height	Mean of 5 drop disk (135 g, 20 cm diameter) measurements (cm)
	SD vegetation height	Standard deviation of above measurements
	Perch abundance	Number of projections above the height of the general vegetation that can support a Whinchat
	Maximum perch height	The height of the tallest perch in the quadrat (cm)
	% Tussock cover	Percentage of quadrat area covered by clumps of grass suitable for Whinchat nest-sites
	Invertebrate abundance	Total abundance of invertebrates
	Invertebrate richness	Number of invertebrate orders
	Invertebrate biomass	Estimated biomass following Rogers <i>et al.</i> (1976)
	Altitude	Height in meters above sea level. NextMap Digital Elevation Model (DEM, Intermap Technologies 2007)
	Aspect	Aspect in degrees. Calculated from DEM
Slope	Steepness of the slope in degrees. Calculated from DEM	
Landscape scale	% Scrub cover	Percentage of cell covered in scrub. Image analysis of aerial photography (Redhead <i>et al.</i> 2012)
	% Bare ground	Percentage of cell that is bare ground. Image analysis of aerial photography (Redhead <i>et al.</i> 2012)
	% CG3d	Percentage cover of CG3d type vegetation. Vegetation survey (Walker & Pywell 2000)
	% MG1	Percentage cover of MG1 type vegetation (Walker & Pywell 2000)
	Perimeter of CG3d	Edge length of CG3d in meters. (Walker & Pywell 2000)
	Perimeter of MG1	Edge length of MG1 in meters (Walker & Pywell 2000)
	Plant species richness	Interpolated richness from plot-based vegetation surveys (Redhead <i>et al.</i> 2014)
	Altitude	Mean height in meters above sea level. Calculated from DEM
	Slope	Mean steepness of the slope in degrees. Calculated from DEM
	Northing	$\cos((\text{aspect in degrees} * \pi) / 180)$. Calculated from DEM
Easting	$\sin((\text{aspect in degrees} * \pi) / 180)$. Calculated from DEM	

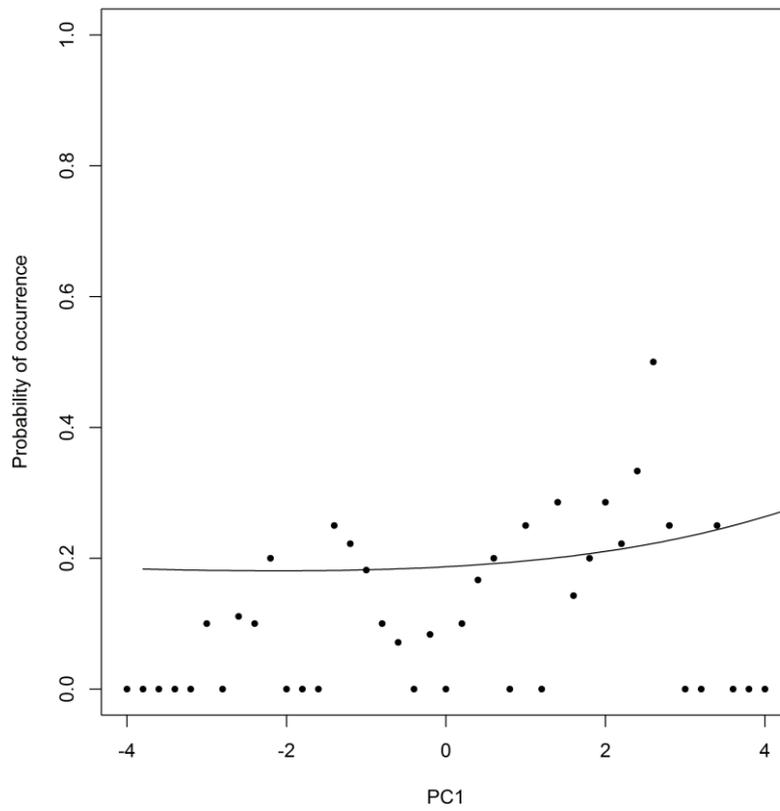
Table 2. Output from the landscape scale analysis showing how much each variable contributes to predicting the habitat suitability for Whinchats (permutated importance %) and the direction of response for each variable. Positive values indicate a variable is positively correlated with habitat suitability, negative values indicate a variable is negatively correlated with habitat suitability.

Variable	Permutated importance %	Response
Altitude	47.9	–
Slope	11.5	+
Percentage scrub cover	8.7	–
Easting	8.7	–
Plant species richness	5.8	+
Area of CG3d vegetation	4.4	+
Percentage bare ground	4.1	–
Perimeter of MG1 vegetation	2.8	-
Northing	2.6	-
Area of MG1 vegetation	2.3	+
Perimeter of CG3d vegetation	1.2	+

a)



b)



c)

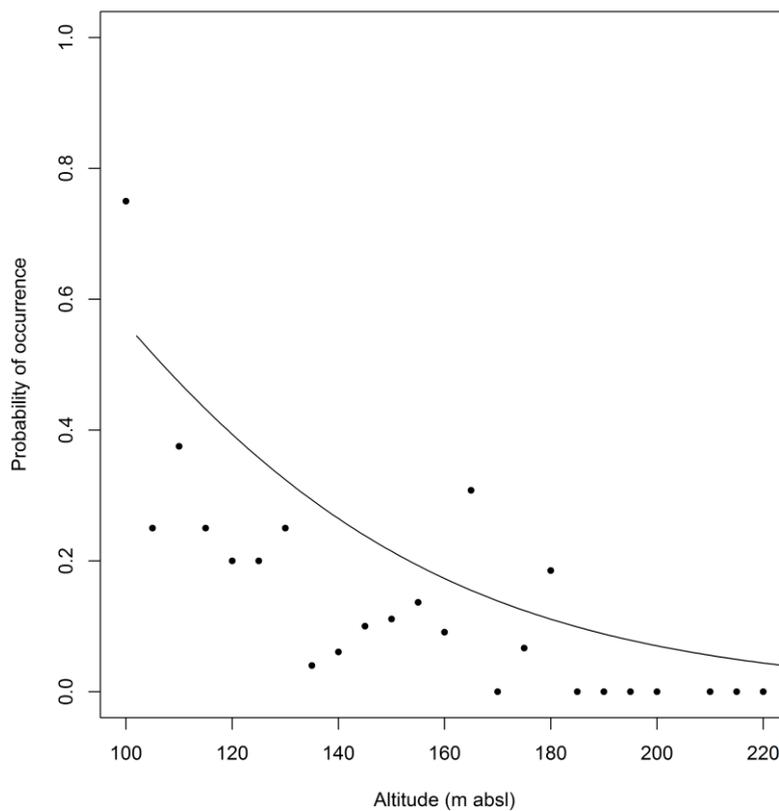


Figure 1. The predicted effect of PC1 (positively correlated with % ground cover 20 cm above ground, mean vegetation height, standard deviation in vegetation height, tussock cover, negatively correlated with plant species richness and herb to grass ratio) on (a) the number of Whinchats observed, and of (b) PC1 and (c) altitude on the occurrence of Whinchats from the best hurdle model from the territory scale analysis. The lines are the predicted affect; the dots show the raw data. For the binomial plots this is categorised in bins (5 m for altitude, 0.2 for PC1) and the presences and absences for each bin are averaged to give the probability of occurrence.