1 **Fine-scale habitat use during the non-breeding season suggests that winter habitat**
2 **does not limit breeding populations of a declining long-distance Palearctic migrant**
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12 ABSTRACT

13 For migrant birds, what habitats are suitable during the non-breeding season
14 influences habitat availability, population resilience to habitat loss, and ultimately
15 survival. Consequently, habitat preferences during winter and whether habitat
16 segregation according to age and sex occurs directly influences migration ecology,
17 survival and breeding success. We tested the fine-scale habitat preferences of a
18 declining Palearctic migrant, the Whinchat *Saxicola rubetra*, on its wintering grounds
19 in West Africa. We explored the influence of habitat at the territory-scale and
20 whether dominance-based habitat occupancy occurs by describing the variation in
21 habitat characteristics across wintering territories, the degree of habitat change
22 within territories held throughout winter, and whether habitat characteristics
23 influenced territory size and space-use within territories or differed with age and
24 sex. Habitat characteristics varied substantially across territories and birds
25 maintained the same territories even though habitat changed significantly
26 throughout winter. We found no evidence of dominance-based habitat occupancy;
27 instead, territories were smaller if they contained more perching shrubs or maize
28 crops, and areas with more perching shrubs were used more often within territories,
29 likely because perches are important for foraging and territory defence. Our findings
30 suggest that Whinchats have non-specialised habitat requirements within their
31 wintering habitat of open savannah and farmland, and respond to habitat variation
32 by adjusting territory size and space-use within territories instead of competing with
33 conspecifics. Whinchats show a tolerance for human-modified habitats and results
34 support previous findings that some crop types may provide high-quality wintering
35 habitat by increasing perch density and foraging opportunities. By having non-

specialised requirements within broad winter habitat types, migrants are likely to be flexible to changing wintering conditions in Africa, both within and across winters, so possibly engendering some resilience to the rapid anthropogenic habitat degradation occurring throughout their wintering range.

INTRODUCTION

For migrant species, conditions in both the breeding and non-breeding season have a strong influence on life history traits (Moore et al. 1995; Newton 2010a). Conditions on the wintering grounds affect body condition (Strong and Sherry 2000; Ottosson et al. 2005), which can influence departure dates (Saino et al. 2004; Studds and Marra 2005), body condition during migration (Bearhop et al. 2004) and migration speed (Tøttrup et al. 2008), and consequently survival and future breeding success (Møller 1994; Aebischer et al. 1996; Potti 1998; Kokko 1999; Norris et al. 2004; Saino et al. 2004; Smith and Moore 2005). Consequently, winter habitat selection has the potential to greatly influence migrant population dynamics. Despite this, we lack even basic knowledge of wintering ecology and winter habitat use for most migrant species (Sillett and Holmes 2002; Sanderson et al. 2006; Vickery et al. 2014), especially details of fine-scale habitat use. Many of these species have declined dramatically in recent decades, especially those which migrant long-distances (Sanderson et al. 2006; Thaxter et al. 2010; Vickery et al. 2014).

Both the range of habitat features migrants use during winter and whether individuals compete for territories based on habitat characteristics have implications for habitat availability, flexibility to changing conditions during winter and

susceptibility to habitat loss and degradation. Broader habitat preferences in the non-breeding season compared to breeding suggests that many migrants are generalists during winter (i.e. use a wide range of habitat features) within their chosen wintering habitats (Rappole 2013); however this is not true for all species (e.g. Lynch 1992; Wunderle and Waide 1994). For some migrants, individuals compete for territories of varying quality, resulting in correlations between territory habitat characteristics and age and sex (Lynch et al. 1985; Parrish and Sherry 1994; Figuerola et al. 2001; Marra and Holmes 2001; Catry et al. 2004). If habitat characteristics do indicate territory quality, then some individuals may hold territories in poorer quality habitats if these characteristics are limited, and could then suffer reduced survival and reproductive success (Rappole et al. 1989; Robbins et al. 1989; Jones et al. 1996; Marra and Holmes 2001; Norris et al. 2004; Reudink et al. 2009). This may lead to skewed population dynamics if dominance varies with age and sex. Establishing the range of habitat characteristics across territories and whether these vary with age and sex can therefore give insights into habitat availability and the implications of habitat loss.

Even if broad habitat preferences mean that winter territories are plentiful and there is no need to compete with conspecifics, individuals may respond to heterogeneity in habitat characteristics in different ways, such as by adjusting territory size (Carpenter et al. 1983; Smith and Shugart 1987) or with non-random space-use within territories (Barg et al. 2006). This may also influence habitat suitability and availability. Understanding fine-scale winter habitat use, its influence on population dynamics, and whether dominance-based habitat selection occurs is increasingly

important given the accelerating and widespread anthropogenic habitat modification occurring in Africa (Bourn and Wint 1994; Collier et al. 2008).

In this study we establish the fine-scale winter habitat requirements of a declining long-distance Palearctic migrant, the Whinchat *Saxicola rubetra*. Whinchats hold and defend small territories throughout winter and occupy a range of natural and human-modified habitats typical of open savannah (Barshep et al. 2012; Hulme and Cresswell 2012). This habitat type is predominant throughout their wintering range and can vary considerably depending upon the degree of anthropogenic disturbance. We describe the range of habitat characteristics across territories, how these change throughout winter, whether habitat characteristics differ with the body condition or age and sex of occupants, and how habitat heterogeneity at the territory-level correlates with territory size or space-use within territories. Because perches are an important feature for Whinchats (Fischer et al. 2012; Hulme and Cresswell 2012), we also test interactions between shrub density and maize, both of which provide perches when exploring the influence of habitat characteristics on space-use within territories.

METHODS

Study site

The study took place between February 2011 and March 2014 over three successive wintering seasons (hereby referred to chronologically as winter 1, 2 and 3) during the dry season (early September to late April) on the Jos Plateau in the guinea savannah zone of central Nigeria, West Africa (N09°53', E08°59', approximately 1250

m altitude; Figure 1). Study sites were principally open scrubland with varying degrees of habitat degradation from human habitation, arable farming and livestock grazing, the latter increasing in intensity over the dry season (see Hulme and Cresswell 2012). Sites are typical of wintering habitat for this species in the area (open savannah) and had high densities of Whinchats. Three study sites were used in all winters: site A (open scrub with medium grazing and human activity plus sparse small arable crop fields); site B (open degraded scrub with high grazing and human activity plus small arable crop fields); and site C (scrubland with light grazing and low human activity plus sparse arable crop fields) (Figure 1). Two additional sites were added at the end of the second winter: site D (scrub with light grazing, low human activity and small arable crop fields); and site E (open scrub with heavy grazing and small arable crop fields). Birds were captured at two additional sites in winter 3 (marked 'x' Figure 1) but are only included in analyses exploring age and sex ratios across sites. Note sites represent logistic areas, rather than biologically different distinct areas identified a priori: we therefore consider site effects as potentially confounding nuisance variable (e.g. sampling effort may have varied across sites) rather than representing anything likely to have been correlated with Whinchat biology. Sites in any case were very close together and site boundaries only existed as defined by us during the study.

Study subjects

Birds were captured with spring traps and mist nets using conspecific playback and live bait, and uniquely colour ringed, sexed and aged as either first-winter or adult (Jenni and Winkler 2004), and measured (maximum wing cord, tarsus, mass). Age

and sex proportions were similar across study sites (Chi squared tests on all birds captured across study: age: $\chi^2 = 2.7$, $df = 5$, $p = 0.75$, $n = 409$; sex: $\chi^2 = 5.9$, $p = 0.32$, $n = 407$). In total, 458 birds were captured across three winters, of which 334 were resighted at least once after capture. Of these, 179 were fitted with geolocators for an additional study, of which 116 birds were resighted at least once after capture. Study-specific samples sizes are presented in the following results.

Resighting individuals

Colour-ringed birds were resighted in all winters to determine 1) the location and size of their territories; 2) areas within territories used most often; and 3) the degree of residency and site fidelity within and between winters. Resighting efforts in winters 1 and 2 focussed on obtaining accurate locations of undisturbed birds, and focussed on simply relocating returning birds in winter 3. Resightings were carried out from dawn (~06:00) until 11:00 and 16:00 until dusk (~18:30) using binoculars to locate birds (Swarovski SV 8x32), a spotting scope to read colour combinations (Zeiss Diascope 65 mm with 25x eyepiece) and a GPS to record locations (Garmin GPSMAP 64). Resightings were scored for confidence regarding whether the bird was undisturbed before being sighted, and the date and time to the nearest minute of each resighting recorded. A Whinchat could travel across its territory within seconds and the time between observations was found to have no influence on the spatial independence of resightings (Generalised Linear Mixed-effects Model of distance between resightings ~ observation time (controlling for individual): $F_{1,762} = 0.02$, $p = 0.90$; 765 observations of 119 individuals). UTM units (Zone 32N) were used for all analyses to give position on the globe in metres to allow for interpretable distance

calculations, and viewed and edited where necessary in ArcMAP 10.1 (ERSI 2012) and Garmin BaseCamp software (version 4.2.4; Garmin International, Inc., Olathe, KS, USA).

Calculating territory size

The conventional method of using Minimum Convex Polygons (MCP) to estimate territory or range size was inappropriate for this study because it requires a large number of resightings and is subject to several biases (see Hansteen et al. 1997; Börger et al. 2006) which may be more acute at smaller scales. Because we wanted to determine areas of use over winter and the size and location of territories rather than exact territory boundaries, we instead determined an index of territory size, using resightings made in winters 1 and 2. For each individual, the territory centre was determined by averaging the position of all undisturbed resightings. The mean distance between each resighting and the territory centre was then calculated and doubled to give an estimate of territory diameter. This was then used as a measure of territory size. Territory size was calculated for individuals with at least five undisturbed resightings from winters 1 and 2. A minimum of five was chosen to maintain adequate sample sizes whilst reducing the influence that increasing resighting sample size has on territory size estimates (Börger et al. 2006). When we increased the minimum number of resightings required to calculate territory size to 10, the average territory diameter was altered by 4 m (6%) and any results from analyses including territory size were unchanged. This suggests that five resightings were adequate. Of the 35 and 67 birds resighted after capture in winters 1 and 2, 33 and 39 individuals had at least five independent resightings, respectively. When

birds from winter 1 returned in winter 2, we averaged the territory diameter across both years.

Habitat sampling

Territory habitat characteristics were sampled for 84 of the study birds for which territory size had been calculated: 34 of those ringed in winter 1 (of which 21 were resighted in winter 2 also) and 50 of those ringed in winter 2, all of which had at least five resightings. Habitat variables sampled are listed in Table 1. Habitat was surveyed in winter 2 between the end of January and April, the majority before mid-March. For the 21 birds resighted in both winters 1 and 2, we used sightings from winter 2 to locate sampling plots. 13 birds that were ringed in winter 1 were not resighted in winter 2, so in this case, because all individuals return to the same winter territories (Blackburn and Cresswell 2015), we used resighting locations from winter 1 to locate habitat plots and compared photographs of the territory in both years to confirm that the territory habitat characteristics we sampled had not changed substantially.

Three circular plots were sampled within each territory: one 50 m diameter plot (~1950 m²) at the centre of the territory to sample territory habitat characteristics, located by averaging longitude and latitude coordinates for all resightings; and two 10 m diameter plots (~80 m² each) within the territory to sample areas of use and non-use (1) where the bird was seen most often ('present' plot) and (2) in an area that the bird was never seen ('absent' plot). Locations for 'present' and 'absent' plots were found by visually examining resightings in ArcMAP 10.1 (ERSI 2012): we

situated the 'presence' plot at the location of the resighting that was closest to all other resightings, and for the 'absent' plot we used the ruler tool to find coordinates within the territory that were the furthest distance from all resightings. We surveyed both 10 m plots for 73 birds, and only 'absent' plots for seven additional birds because poor weather curtailed the survey period. To explore changes in territory habitat characteristics over the winter, 30 m diameter plots ($\sim 705 \text{ m}^2$) were surveyed twice in winter 3 one at the beginning (October) and one at the end (late February), for 14 individuals that returned to the territory used in winter 2. This was the largest plot size that realistically allowed habitat variables to be surveyed at a fine detail. Because territory locations were the same in both years (Blackburn and Cresswell 2015), 30 m plots were surveyed at the territory centre located in the previous winter (i.e. the location of the 50 m plots). For all plots, we calculated further variables from the raw data (details in Tables 1 and 2).

We used satellite photographs of territories to measure larger-scale habitat features that could not be accurately sampled on the ground. Images taken within three months of habitat sampling were obtained from Google Earth (Google 2012). Photographs of territories, field notes, and comparison of satellite images taken more than three months before and after the period of habitat sampling confirmed that larger features remained unchanged at the scale at which we were measuring. A circular plot divided into a 1 x 1 m grid was digitally placed over images where each 50 m plot had been sampled, and each patch of vegetation covering > 50% of one 1 x 1 m square (henceforth 'vegetation patch') was counted. Each vegetation patch was scored for the number of contiguous 1 x 1 squares it covered and the minimum

distance (in metres) to the next nearest vegetation patch that also covered > 50% of any 1 x 1 m square. From these data, the number of vegetation patches, the average patch size (m²), the average distance between patches (m), and the cover of dense vegetation (proportion of all squares covered in %) were calculated (Table 1).

Principle component analyses

We conducted principle components analyses (PCA) For both 50 m and 10 m sample plots to reduce the number of habitat variables and to account for correlated variables (Table 2). In both cases, an orthogonal Varimax rotation (Kaiser 1958) was applied to aide interpretation. We chose a suite of habitat variables based on whether their inclusion produced interpretable PCA results: excluded variables were modelled separately in later analyses providing that no collinearity resulted. Extracted axes ('components') were retained if their Eigenvalue was at least 1.0 (i.e. the component contributed to at least 10% of the total variation) (Abdi and Williams 2010). A variable was considered to contribute to a component if the loading was at least ± 0.4 after rotation.

For 50 m plots, the analysis yielded three axes with eigenvalues >1, accounting for 86% of the total variation from 10 original variables (Table 2). High scores for PC1 (58% of the total variation) implied a lower number of shrubs, particularly perching shrubs, and fewer individual plants: PC1 was therefore named 'shrub density'. The scores for PC1 were then inverted for all further analyses so that a higher score related to higher shrub density. High scores for PC2 (18% of the total variation) implied that any patches of vegetation were small and the total amount of

vegetation in the territory was low: PC2 was therefore named 'vegetation cover'. High scores for PC3 (10% of the total variation) implied that number of green plants was low and that patches of vegetation were sparse and far apart: PC3 was therefore named 'vegetation clumping'. For the 10 m plots, the analyses also yielded three axes with eigenvalues >1 accounting for 83% of the total variation from eight original variables (Table 2). High scores for PC1 (51% of the total variation) implied a lower number of perching shrubs and fewer individual plants: PC1 was therefore also named 'shrub density', and was again inverted so that a higher score related to higher shrub density. High scores for PC2 (18% of the total variation) implied low litter cover and high grass cover: PC2 was therefore named 'amount of grass'. High scores for PC3 (13% of the total variation) implied high plant diversity and a large number of green plants: PC3 was therefore named 'plant diversity score'.

Statistical analyses

Birds which could not be confidently aged or sexed were excluded from models including age and sex as predictors. One individual was excluded from all analyses as its territory was in an unrepresentative habitat (dense coffee farm), which grossly inflated any vegetation counts within that territory. Nonetheless, removing this individual did not change the main findings from any analyses.

Analyses were performed in R version 3.0.1 (R Development Core Team 2013) and RStudio Version 0.98.507. Data were checked for normality when necessary and for multicollinearity using variance inflation factors (CARS package; Fox and Weisberg, 2010). The Shannon-Wiener Species Diversity Index was calculated from the number

and proportion of each plant species recorded in each plot. We subsequently refer to this as 'plant diversity', where a higher number indicates higher species diversity (Shannon 2001). Paired *t*-tests and paired Wilcoxon tests were used to assess changes in habitat characteristics over the winter. Standard *t*-tests and Wilcoxon tests were used to explore differences in habitat characteristics between territories of males and females, and first-winter and adult birds. The sequential Bonferroni procedure (Rice 1989) was used to correct for Type 1 error rate. Predictors of territory size were explored with General Linear Models. We used a Generalised Linear Mixed-effects Model (GLMM) to explore predictors of space-use within territories, controlling for individual territory. Here we reassigned land type 'old farm' to 'pasture' due to an inadequate sample size for 'old farm' ($n = 1$ territory).

Multiple regression model simplification was based on Akaike Information Criterion (AIC) (Bozdogan 1987). Variables failing to improve AIC or add a significant contribution to the model (as determined by a non-significant ANOVA performed between models) were removed. For models where all variables had the same or similar sample sizes, dredge analyses were used to identify minimal models (Bartoń 2012): cases with missing values were removed from the dataset as required for dredge analyses, and resulting minimal adequate models were produced using complete datasets. We chose $\Delta AIC = 3$ as a threshold for which models to present from dredge analyses because this value contained what we felt were a representative number of models ($\Delta AIC = 2$ too few and $\Delta AIC = 4$ too many). Model fits were evaluated from diagnostic model plots and models presented if assumptions were reasonably met (Crawley 2007). Mean values are presented as

means $\pm$ one standard error in all cases. Test-specific samples sizes are presented as accordingly within tables and results. A statistical significance level of $p < 0.05$ was chosen to reject null hypotheses.

RESULTS

1. Variation in habitat characteristics

Habitat characteristics varied substantially across individual territories (Table 3; $n = 83$). Most territories were situated in pasture (72 of 83 territories), with territories also situated amongst active crop fields ($n = 8$) and on old farmland ($n = 3$). The average Whinchat territory had low levels of grazing, low levels of human disturbance and some chopping. The average territory sample plot contained active farmland (11%). Maize made up 57% ($\pm 11.9\%$) of a typical territory plot if this crop was present ($n = 10/82$ territories).

Habitat characteristics changed significantly between the start and the end of the winter (Table 4, Figure 2). Specifically, the amount of long grass decreased, the amount of bare ground increased, and shrubs had sparser leaf coverage at the end of the winter. Grazing intensity increased as the winter progressed.

2. Evidence for dominance-based territory occupancy

There were no significant differences in shrub density, vegetation cover or clumping, plant diversity, percentage of farmland or maize, grazing intensity or the amount of herbaceous vegetation between the territories of males and females, or first-winter and adult birds (Table 5, Figure 3).

324

325 *3. Predictors of territory size and space-use within territories*

326 Average territory diameter across winters 1 and 2 was 65 m (± 1.9 m), range 30-106
327 m, $n = 83$). Individuals had smaller territories if shrubs were at a higher density and
328 maize was present within the territory (Figure 4; Table 6). None of the other territory
329 habitat characteristics explored correlated to territory size (Table 6).

330

331 Within winters, Whinchats used areas of their territories that had significantly more
332 perching shrubs (Figure 5; Table 7). No other habitat characteristics influenced
333 space-use within territories.

334

335 DISCUSSION

336 *Winter habitat requirements*

337 Our findings suggest that Whinchats have non-specialised habitat requirements
338 within their wintering habitat of open savannah and farmland. This is because we
339 found reasonably large variation in territory-scale habitat characteristics, variation in
340 the land-types in which territories were established, significant temporal changes
341 within territories of resident birds, and a preference for non-specific, generic habitat
342 characteristics (e.g. perching structures). The percentage of farmland, maize and
343 other crops, levels of grazing and human disturbance found in territories ranged
344 across all recorded levels, with similar frequencies of territories with high or low
345 values for these variables. Plant diversity index varied from 0 to 2.39 (equivalent to 1
346 – 17 plant species within territory plots), and along with shrub density, and again
347 there was wide variation across the complete range of values recorded across

territories. Territories thus varied from fairly typical degraded open Guinea savannah through to completely anthropogenic-modified monoculture.

We only found one territory characteristic that substantially influenced Whinchats. Habitat characteristics associated with perch density influenced both territory size and space-use within territories. For Whinchats, perching shrubs and structural vegetation diversity are important features both within breeding territories (Horch and Birrer 2011; Fischer et al. 2012), and during winter (Barshep et al. 2012; Hulme and Cresswell 2012), and are the feature most important for habitat selection at stopovers sites (Koce and Denac 2010). An absence of perches significantly influences habitat selection during breeding (Labhardt 1988; Oppermann 1990; Bastian and Bastian 1996). During winter, perches are likely essential for effective foraging and territory defence (Fischer et al. 2012 and references therein), and the influence of perching shrubs and maize crops on territory size suggests that a minimum perch density is required. Despite significant habitat changes during winter, shrub density remained unchanged. Though our findings clearly demonstrate that perches are key requirement during winter, we observed no preference for any particular perch type, with Whinchats using a large variety of both natural and artificial structures for perches. Although clearly perch ‘specialists’, any structure or vegetation type likely provides a suitable perch. These structures are plentiful within open savannah, meaning that Whinchats still have broad habitat preferences. Conservation measures directed on the wintering grounds should consider the importance of perching structures for winter habitat suitability.

Non-specialised requirements within broad winter habitat types likely increases wintering habitat availability, resilience to habitat loss or change both within and between winters, lessens the implications of overwintering in degraded habitats, and consequently increases survival and future fitness, especially for site-faithful species. Site selection for juvenile birds undertaking their first migration is likely to be stochastic to some degree within their wintering range because migratory routes and wintering conditions are unknown for first-time migrants (the serial residency hypothesis; Cresswell, 2014). Broad winter habitat requirements therefore increase the likelihood of arriving in suitable wintering habitat, which both directly increases survival and reduces the amount of time actively migrating or in unfamiliar surroundings where mortality risk is higher (Cuadrado 1997; Yoder et al. 2004; Lind and Cresswell 2006; Hedenström 2008; Newton 2010b; Piper 2011; Cresswell 2014). Broad habitat requirements would allow Whinchats to maintain their wintering strategy of extremely high winter site fidelity (Blackburn and Cresswell 2015), even if habitat changes between winters, again removing the costs associated with relocating and allowing the defence of familiar, predictable resources. Having a more generalist strategy may also reduce competition with African resident species (Salewski et al. 2007 and references therein).

Evidence suggests that a generalist wintering strategy is relatively common amongst long-distance migrants (Stiles 1980; Hutto 1992; Rappole and McDonald 1994; Marra and Holmes 2001; Cresswell 2014). Much accessible and suitable habitat remains unoccupied during winter (Wilson and Cresswell 2006; Cresswell et al. 2007; Hulme and Cresswell 2012), individuals are not restricted to what are described as optimal

sites (Karr 1976; Waide 1980; Hutto 1988; Greenberg 1992; Lynch 1992), and winter territories often span many habitat types of varying quality (Karr 1976; Rabøl 1987; Leisler 1990; Jones et al. 1996; Petit et al. 1999; Marra and Holmes 2001; Salewski and Jones 2006). For example, migrating Eurasian Blackcaps *Sylvia atricapilla* occupy more diverse habitats than resident species, suggesting a more generalist strategy in the non-breeding season (Pérez-Tris and Tellería 2002).

Lack of dominance-based habitat occupancy

Neither habitat characteristics within territories or territory size differed according to age, sex or condition, indicating an absence of dominance-based winter habitat occupancy. We propose that this is due to broad wintering requirements, which mean that sufficient winter territories are available and the need to compete with conspecifics is removed. The reasons for holding and defending a distinct, non-overlapping winter territory (Barshep et al. 2012; Blackburn and Cresswell 2015) are therefore most likely for the defence of familiar resources and to increase predictability within and between winters. Whether this lack of dominance-based habitat occupancy is typical of Palearctic migrants is unclear, although high site fidelity between years (another indicator of a lack of competition for territories of varying quality) appears to be common (e.g. Kricher and Davis 1986; Holmes and Sherry 1992; Salewski et al. 2000). Although data are sparse for Palearctic migrants (Catry et al. 2004; Vickery et al. 2014), winter habitat segregation between the sexes occurs in Red-backed Shrikes *Lanius collurio* (Herremans 1997) and Eastern Great Reed Warblers *Acrocephalus orientalis* (Nisbet and Medway 1972). Wintering Eurasian Blackcaps show no habitat segregation between sexes, but juvenile birds

are more likely to winter in poorer quality habitats (Pérez-Tris and Tellería 2002).
Wintering European Robins *Erithacus rubetra* exhibit habitat segregation according
to age, sex and body size, in which subordinate juveniles and females are found in
poorer quality habitats and have lower body condition as a result (Catry et al. 2004).
Many Neotropical migrants also exhibit dominance-based habitat segregation during
winter (e.g Lynch et al. 1985; Ornat and Greenberg 1990; Parrish and Sherry 1994;
Wunderle Jr 1995; Marra 2000; Latta and Faaborg 2001), and these differences often
lead to differential survival and reproductive success (Marra and Holmes 2001;
Reudink et al. 2009). Yet this habitat segregation is absent for some of these species
in other wintering areas (Holmes et al. 1989), suggesting that the degree of
segregation may be population or habitat-specific. It may be that species exhibiting
dominance-based habitat occupancy have more specialist requirements.

Resilience to winter habitat degradation

Our findings suggest that Whinchats may have some population resilience to or may
even benefit from anthropogenic habitat degradation such as grazing and
agriculture. A lack of dominance-based habitat occupancy, along with broad habitat
requirements, indicates that winter habitat is plentiful, and also that the effects of
habitat degradation should be similar across age and sex groups. If winter habitat
availability were limited – as is suggested to be the case for Neotropical migrants
(Rappole and McDonald 1994; Sherry and Holmes 1996; Rappole et al. 2003) – we
would expect greater competition for limited territories. Consequently, higher
quality individuals should occupy both poor and high quality habitats and would still
survive even under disproportional loss of one habitat type. Additionally, most

territories had some level of human disturbance (e.g. chopping, some active farmland, and grazing), and Whinchats did not relocate when grazing intensity increased over winter (Blackburn and Cresswell 2015). Wood harvesting and structural crops provide more suitable perches, and grazing may create foraging opportunities by increasing prey accessibility (Schaub et al. 2010) and appears to have little impact on perching structures. Maize may be a particularly high-quality wintering habitat because it combines dense perches with bare ground. Overall, these findings indicate that population declines in Whinchats are unlikely to be due to winter habitat availability or carry-over effects due to variation in habitat quality between individuals.

In summary, by documenting winter habitat use at the territory-scale, we demonstrate that Whinchats have broad winter habitat preferences at the small-scale and show no dominance-based winter habitat occupancy. Broad habitat requirements within the savannah biome of Africa and a preference for few key but plentiful and non-specific habitat characteristics likely promote flexibility both within and between winters, and so may engender population resilience to habitat change and degradation. Whinchats may thus show resilience to anthropogenic habitat modification and may even benefit from an increase in farming in the region, and therefore some resilience to the rapid anthropogenic habitat degradation occurring in Africa.

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Table 1. Description of habitat variables measured during habitat surveys and the plot(s) for which the variable was measured: A = 50 m, B = 30 m (start/end), C = 10 m (present/absent), plus variables calculated for inclusion in PCA analyses

Variable	Description
Plant, shrub and tree count (A,C)	Each identified to species level and counted in size categories: 1) 30-60 cm; 2) 60-200 cm; 3) 2-4 m; 4) 4-8 m; 5) >8 m. Plants of the same species sharing >50% of their canopy were counted as one plant.
Shrub leaf cover (C)	Leaf cover of each shrub scored on a scale of 0-4, representing 25% cover categories (4 = 100% cover)
Land type (A,B,C)	% cover of: pasture, old farmland (>2 years old), active farmland
Herb cover (A)	% cover of herbaceous vegetation (including shrubs <30 cm): 0-25% / 26-50% / 51-75% / 76-100%
Ground cover (B,C)	% cover of: bare ground, litter and short grass, long grass, herbaceous vegetation, shrubs
Grazing (A,B,C)	Level of grazing pressure: none / low / high
Human activity (A,B,C)	Evidence of people using the immediate area: none / low / high
Plant diversity*	Shannon-Wiener index of plant species diversity
Green plant score*	The number of plants in each height category multiplied by the height category
Perching shrub score*	The number of perching shrubs in each height category multiplied by the size category (1-5)
Shrub score*	The score of green plants x 1 and score of perching shrubs x 2
Vegetation score*	The number of plants in each category multiplied by the size category (1-5), summed
Total plants*	Total of tree and shrub count across all species

* variables calculated from plant, shrub and tree counts

733 **Table 2.** Results of the three top ‘components’ (i.e. variables) derived from principle
734 component analyses on a range of habitat variables for both 50 m ($n = 83$) and 10 m ($n =$
735 159) sample plots, plus the variables contributing to each component (those with loadings of
736 at least ± 0.4 following a Varimax rotation). For 50 m plots, six further extracted axes (not
737 shown) cumulatively explained less than 15% of the total variation in habitat variables. For
738 10 m plots, five further extracted axes (not shown) cumulatively explained less than 17% of
739 the total variation in habitat variables. Habitat variables only included in analyses for one
740 plot type are shown in italics

	<i>Principle component</i>					
	50 m			10 m		
	PC1 ‘Shrub density’	PC2 ‘Vegetation cover’	PC3 ‘Vegetation clumping’	PC1 ‘Shrub density’	PC2 ‘Amount of grass’	PC3 ‘Plant diversity score’
<i>Standard deviation</i>	2.28	1.26	0.85	2.03	1.22	1.02
<i>Explained variance</i>	58%	18%	10%	51%	18%	13%
<i>Cumulative variance</i>	58%	75%	86%	51%	70%	83%
<i>Variable loadings following Varimax Rotation</i>						
	50 m plots			10 m plots (present/absent)		
Total shrub score	-0.51			-0.52		
Perching shrub score	-0.54			-0.59		
Total plants	-0.46			-0.44		
% <i>Shrub cover</i>				-0.42		
<i>Vegetation score</i>	-0.47					
<i>Average patch size</i>		-0.70				
% <i>Vegetation cover</i>		-0.59				
<i>Number of patches</i>			-0.56			
<i>Average distance between patches</i>			0.54			
Green plant score			-0.49			0.64
<i>Plant diversity</i>						0.69
% <i>Litter cover</i>				-0.70		
% <i>Grass cover</i>				0.69		

Table 3. The range of habitat characteristics observed within 50 m habitat plots across all territories ($n = 83$) and not later included in PCA scores, as either mean values ($\pm$ SE), or number of territories. Where a characteristic was present, the number of territories where this characteristic occurred in high or low values is also presented (see *Methods* and Table 1 for detailed descriptions of how habitat characteristics were categorised)

Habitat characteristic	Average ($\pm$ SE)	Range
% Farmland	11.3% (± 2.9)	0 – 100%
% Maize	6.9% (± 2.5)	0 – 100%
% Other crop type	4.4% (± 1.8)	0 – 100%
Plant diversity	1.37 (± 0.05)	0 – 2.39
<i>Number of territories ($n = 82$)</i>		
	<i>Absent</i>	<i>Present (low/high)</i>
Maize	72	10
Human disturbance	2	80 (52/30)
Degree of chopping	29	52 (48/6)
Level of grazing	2	80 (44/47)

748 **Table 4.** Results of paired *t*-tests (#) and paired Wilcoxon tests (*) to assess changes in
749 habitat characteristics within territories between the start and the end of the winter. Sample
750 size for average leaf cover is lower due to the absence of shrubs in some plots. Significant *p*
751 values are shown in bold

752

Habitat characteristic	<i>n</i>	<i>t</i> / <i>V</i>	df	<i>p</i>	<i>Bonferroni</i> adjusted <i>p</i>	Mean (start)	Mean (end)
% Bare ground *	14	5.5		0.0035	0.0045	8 (±2.5)	22 (±5.3)
% Long grass #	14	3.9	13	0.0017	0.0042	25 (±3.8)	10 (±1.9)
% Litter #	14	-1.2	13	0.15		41 (±5.3)	53 (±4.3)
% Herbs #	14	3.4	13	0.0051	0.0056	15 (±2.4)	8 (±1.1)
% Shrub *	13	25		0.075		10 (±2.7)	7 (±1.7)
Shrub leaf score:							
No leaves *	14	0		0.0059	0.0063	0.06 (±0.063)	8.8 (±3.0)
Leaf cover = 1-24% *	14	13.5		0.17		3.0 (±1.3)	7.2 (±2.3)
Leaf cover = 25-49% *	14	65		0.045		10.3 (±4.4)	1.9 (±0.52)
Leaf cover = 50-74% *	14	66		0.0038	0.0050	8.3 (±2.9)	1.2 (±0.73)
Leaf cover = 75-100% *	14	0		0.034		0.44 (±0.30)	1.7 (±0.66)
Average shrub leaf score	12	2.7	11	0.021		2 (±0.10)	1.4 (±0.29)
Amount of grazing *	13	0		0.0060			

Table 5. The range of habitat characteristics observed within habitat plots across all territories according to age and sex ($n = 83$, although sample sizes vary because age and sex was unknown for some individuals) plus results of t -tests (#) and Wilcoxon tests (*) to assess differences between territories of males (♂) and females (♀), and first-winter and adult birds. Degrees of freedom are given for t -tests and sample sizes for Wilcoxon tests. Note that shrub cover, vegetation cover and vegetation clumping are variables derived from principle component analyses (see *Methods* and Figures B & D for the scale and variation of these variables)

	Average ($\pm$ SE)					
Habitat characteristic				1 st winter		Adult
Shrub density	-0.079 (± 0.37)		0.096 (± 0.41)	-0.52 (± 0.35)		0.25 (± 0.40)
Vegetation cover	0.072 (± 0.14)		0.034 (± 0.23)	-0.083 (± 0.22)		-0.0072 (± 0.19)
Vegetation clumping	0.077 (± 0.15)		-0.051 (± 0.17)	-0.047 (± 0.13)		0.0090 (± 0.18)
Plant diversity (<i>Shannon index</i>)	1.43 (± 0.062)		1.26 (± 0.087)	1.27 (± 0.078)		1.44 (± 0.062)
% Farmland <i>if present</i>	50.0% (± 13.5)		56.3% (± 11.2)	55.0% (± 10.6)		53.0% (± 12.3)
<i>...of which</i> : % maize	55.0% (± 21.9)		59.2% (± 14.4)	57.9% (± 15.3)		53.3% (± 21.3)
% other crop	45.0% (± 18.9)		35.0% (± 16.1)	42.5% (± 14.8)		52.5% (± 12.5)
	vs.			1 st winter vs. Adult		
	<i>t</i> / <i>W</i>	<i>df</i> / <i>n</i>	<i>p</i>	<i>t</i> / <i>W</i>	<i>df</i> / <i>n</i>	<i>p</i>
Shrub density #*	-0.3	72	0.75	590	75	0.23
Vegetation cover **	621	74	0.55	756	75	0.58
Vegetation clumping ##	0.6	72	0.58	-0.3	65.2	0.80
Plant diversity *#	1.7	74	0.10	-1.7	73	0.087
% Farmland						
(all territories) **	640	74	0.59	828	75	0.072
% Maize (all territories) **	619	74	0.30	774	75	0.21
Amount of herbs **	772.5	74	0.21	771.5	75	0.38
Level of grazing **	761	74	0.30	656	75	0.57

Table 6. Results from General Linear Models exploring predictors of territory size of Whinchats during winter. The first model (the initial maximal model of: territory size ~ age + sex + bird size + shrub density + vegetation cover + vegetation clumping + presence of maize + % non-maize crops + main land type + plant diversity) is presented as the results from a dredge analysis averaging the top 16 models (within 3 AIC of the top model*), along with the minimal top model. Residual SE for top model = 7.48 on 79 df; adjusted R-squared = 0.26; $F_{2,79} = 15.2$; overall p -value = <0.0001. The interaction between age and sex was not significant. Note that the reference category for main land type is pasture; $n = 78$ and 82 for dredge analysis and minimal model, respectively (five and one cases excluded from full and minimal model respectively due to missing data)

Variable	Full model		All models $\Delta AIC < 3$			Top model			
	z	p	Model-averaged parameter estimate	SE	Relative weight	Parameter estimate	SE	t	p
(Intercept)	23.0	<0.0001	68.44	2.94		67.90	1.78	38.1	<0.0001
Shrub density	4.2	<0.0001	-3.63	0.85	1.00	-3.78	0.79	-4.8	<0.0001
Maize (present)	3.9	<0.001	-24.28	6.17	1.00	-24.09	5.48	-4.4	<0.0001
Land type: crop	1.4	0.16	10.59	7.40	0.39				
Land type: old farm	1.2	0.23	-10.91	8.91					
% Other crops	0.9	0.39	0.10	0.12	0.24				
Vegetation cover	0.9	0.39	-1.23	1.41	0.20				
Body size	1.0	0.35	2.01	2.19	0.22				
Plant diversity	0.5	0.59	-2.26	4.12	0.13				
Vegetation clumping	0.3	0.74	0.63	1.86	0.09				

*3 AIC chosen to give a representative number of top models

Table 7. Results from logistic regression analyses (GLMM) exploring predictors of presence or absence (i.e. favoured areas) *within* territories. The first model (initial maximal model of: presence ~ winter (study year) + presence of maize + % herbs + main land type + human disturbance + amount of grazing + shrub density + amount of grass + plant diversity score + shrub density*presence of maize, controlling for individual territory) is presented as is the results from a dredge analysis averaging the top 16 models (all models within 3 AIC of the top model*), along with the minimal top model. Significant values are shown in bold. Deviance for top model = 207.78 on 157 df; AIC = 213.8. Note that main land type = pasture and winter 1 are the reference categories, and that the density of perching shrubs increases as shrub density increases. For final model, number of complete pairs = 74 (note that for seven of 80 individuals, only absent plots were surveyed)

Variable	Full model		All models $\Delta AIC < 3$			Top model			
	<i>z</i>	<i>p</i>	Model-averaged parameter estimate	SE	Relative weight	Parameter estimate	SE	<i>z</i>	<i>p</i>
(Intercept)	0.4	0.66	-0.170	0.39		-0.079	0.17	-0.5	0.63
Shrub density	3.4	<0.001	0.326	0.095	1.00	0.29	0.09	-3.3	0.0010
Grazing	0.9	0.36	0.274	0.30	0.25				
Herbs	0.8	0.40	-0.024	0.03	0.17				
Disturbance	0.8	0.44	0.251	0.33	0.16				
Main land type (crop)	0.7	0.51	-0.392	0.59	0.07				
Amount of grass	0.7	0.51	0.091	0.14	0.11				
Plant diversity score	0.6	0.54	0.113	0.18	0.11				
Winter (2)	0.2	0.88	0.069	0.46	0.06				
Maize (present)	0.3	0.73	-0.401	1.15	0.10				
Maize (present) * shrub density	1.0	0.32	-0.827	0.82	0.05				

*3 AIC chosen to give a representative number of top models

FIGURE LEGENDS

Figure 1. Map of the six study sites and their location within Nigeria in West Africa (•). Sites A, B and C were used in all three winters; sites D and E in winters 2 and 3, and sites marked x used in winter 3 only (see *Methods*). Note sites exist for logistical reasons rather than representing biologically distinct areas, although they are considered because of variation in sampling time and effort with site

Figure 2. Change in habitat characteristics within territories from the start (white) to the end (grey) of the winter. The amount of bare ground, long grass and amount of herbs changed significantly (marked *), whereas the amount of leaf litter and shrubs remained unchanged (see Table 4 for sample sizes, means and statistical tests)

Figure 3. The range of **a)** plant diversity and **b)** shrub density amongst all territories, split by age and sex. Coloured lines (top charts) show kernel density; box plots (bottom charts) show the range between first-winter and adults, and males and females. Sample sizes vary because age and sex was unknown for some individuals

Figure 4. Territory size as a response of the amount of perching shrubs in the territory ('shrub density'), either if maize was present (open circles) or absent (solid circles) in the territory ($n = 82$; one case excluded due to missing data). A more positive shrub density represents more shrubs in the territory. Lines show predicted values of territory size index from the model presented in Table 6, both if maize was present (solid line) or absent (broken line) from the territory and shrub density average. Birds had larger territories if there were fewer shrubs and if maize was present within their territory

810 **Figure 5.** The probability of sighting a bird within an area of its territory ('present' plot) or
811 not seeing a bird within an area of its territory ('absent' plot) in relation to the amount of
812 perching shrubs within that area. Lines show values (solid line) and confidence intervals
813 (dashed lines) as predicted from the model presented in Table 7; histograms show the
814 distribution of shrub density amongst present and absent plots. Total number of complete
815 pairs = 74 ($n = 148$; note that for seven of 80 birds, only 'absent' plots were recorded)

FIGURES

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Appendix

Examples of study sites, showing typical conditions at the beginning (images A and B) and end (images C and D) of the wintering season. Note the variation between territories C and D, and the decrease in ground vegetation from grazing and dryer conditions as the winter progresses.