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High site fidelity in Northern Wheatears *Oenanthe oenanthe* wintering in Africa revealed through colour marking

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Summary

Wintering Northern Wheatears *Oenanthe oenanthe* in the Sahel region of Northern Nigeria held small (c. 70 m diameter) distinct territories during the study period, and territory size did not differ between adult and first winter birds. Evidence suggests that Wheatears may maintain small territories for a significant duration of the winter, similar to many other migrants.

The decisions migrant birds make during the non-breeding period can carry over to influence many aspects of their population dynamics (Norris et al., 2004, Newton, 2010, Reudink et al., 2009, Newton, 2006, Pulido, 2007, Sherry and Holmes, 1996, Baillie and Peach, 1992, Both et al., 2006, Studds et al., 2008). Many migrant species are site faithful (territorial) during the non-breeding season (King and Hutchinson, 2001, Salewski et al., 2000, Sauvage et al., 1998, Holmes and Sherry, 1992, Marra, 2000, Mcneil, 1982, Cresswell, 2014, Blackburn and Cresswell, 2015, Warkentin and Hernandez, 1996); a decision which can have substantial consequences for survival (Monroy-Ojeda et al., 2013), the degree of migratory connectivity (Cresswell, 2014), how susceptible a species is to the loss or alteration of one or more wintering sites (Newton, 2010, Sutherland, 1998), gene flow, and the conservation of distinct populations (Iverson and Esler, 2006). Knowing whether species are site faithful during winter thus has numerous consequences for the conservation of migrants, many of which are declining (Warkentin and Hernandez, 1996, Jones and Cresswell, 2010, Vickery et al., 2014, Sherry and Holmes, 1996).

Here we establish the extent to which the Northern Wheatear *Oenanthe oenanthe*, a long-distance migrant, is site faithful on its wintering grounds in West Africa, and give estimates of winter territory size. Although winter territoriality has been documented for this and other *Oenanthe* species (for example: Panov, 1999, Khoury et al., 2012, Cornwallis, 1975, Sharland, 1967), the scale of this within-winter site fidelity has not been explored in detail. Here we use colour ringing to closely track individually identifiable birds. We also examine age-dependent effects because aspects of migrant wintering ecology may differ with age (e.g. Marra, 2000).

45 Although population trends vary throughout the Northern Wheatear's range, the
46 European breeding population (25-49% of the global range) has experienced a
47 significant moderate decline since 1980 (Birdlife International, 2004).
48
49 The study took place in the winter of 2011 in Katsina state in the Sahel region of
50 Northern Nigeria, bordering Niger (13°00'56.9"N, 7°07'22.6"E). The study site was a
51 dry and rocky open area with patches of scrub, *Acacia* trees and bushes, and
52 boulders, intersected with a dry riverbed (Fig. 1). We captured and colour-ringed 41
53 Northern Wheatears over an area of approximately 1.3 km^2, between 15th
54 November and 8th December, with the exception of two individuals that were
55 captured earlier in mid-October during a preliminary visit to the site. Birds were
56 captured using baited spring traps with conspecific playback and each uniquely
57 colour-ringed, sexed, aged as adult or first winter (Jenni and Winkler, 2004), and
58 biometrics recorded (maximum wing chord, tarsus, mass, fat and pectoral muscle
59 scores). We resighted colour-ringed birds on 17 visits to the site between 3rd and 14th
60 December of the same winter. We resighted between dawn (~06:00 h) and 11:00 h,
61 and/or 16:00 h until dusk (~18:30 h) using binoculars to locate birds (Swarovski SV
62 8x32) and a spotting scope to read combinations (Zeiss Diascope 65 mm with 25x
63 eyepiece). Approximately 55 hours in total were dedicated to resighting ringed birds.
64 The average number of resighting visits made to the site after a bird had been ringed
65 was 15.7 visits (± 0.3, range = 11 – 17; although note that not every territory was
66 necessarily visited during a resighting visit). We attempted to locate all birds before
67 they were disturbed and scored each sighting regarding whether the bird had been
68 disturbed before being sighted. In the majority of cases, only one resighting location

was recorded for each bird per site visit or only if at least 3 hours after a previous resighting, site visits were separated by at least c. 5 hours, and Wheatears could cross their territories in seconds; therefore we are confident that resighting locations are reasonably independent. Locations of ringed individuals were recorded with a GPS device (Garmin GPSMAP 64). Coordinates were converted to UTM units (Zone 32N) for analyses. Resightings were 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).

We used an index to illustrate an estimate of territory size instead of the conventional method of Minimum Convex Polygons (MCP), which requires many resightings for accurate descriptions of space use and is subject to several biases (see Hansteen et al., 1997, Börger et al., 2006). For each individual, we averaged the location of all resightings scored as undisturbed to find the centre of the bird's territory. We then calculated the distance of each resighting to the territory centre, and averaged this distance to give the mean distance of each resighting from the territory centre. This value was then doubled this to give a measure of territory size. Full methods are described in Blackburn and Cresswell (2015a). Because territory size estimates calculated from very few resightings were likely to be less accurate, we then repeated the above for birds only with at least five resightings in an attempt to reduce the influence of increasing resighting sample size on estimates of territory size (Börger et al., 2006), whilst still maintaining adequate sample sizes. 15 birds had at least five independent resightings. Although coordinates recorded with GPS devices have an error of approximately ± 5 m (our device gave an accuracy of

93 approximately ± 2 – 3 m in Nigeria), we assume here that this error was similar
94 across all recorded points and did not adjust for GPS inaccuracy when calculating our
95 index of territory size. We used Analysis of Variance (ANOVA) to explore the
96 influence of age (adult vs. first winter) on territory size, a General Linear Model to
97 test whether the estimate of territory size was influenced by the number of
98 resightings for birds resighted at least five times, and Logistic Regression (GLM) to
99 test whether the probability of resighting a bird was related to the number of
100 resightings visits made after it was ringed. Analyses were carried out in R version
101 3.0.1 (R Development Core Team, 2013). Mean values are presented as means ± one
102 standard error in all cases. A statistical significance level of p <0.05 was chosen to
103 reject null hypotheses.
104
105 Of the 41 Northern wheatears ringed, 33 were resighted at least once after capture
106 (mean number of resightings per individual = 4.6 ± 0.5, range = 1 – 13). The number
107 of resighting visits made after ringing a bird was the same for birds that we never
108 resighted compared to those that were resighted (GLM of resighted (y/n) ~ number
109 of resighting visits after ringing: β = 0.10 ± 0.18, z = 0.5, p = 0.60, n = 41); therefore
110 the eight birds that were not resighted after capture may have been transients.
111 Resighted birds were last seen between 4 and 53 days after capture (mean = 14.0 ±
112 2.2 days). All resighted individuals were observed to hold small, distinct territories
113 during the entirety of the study (Fig. 1). The two individuals ringed in late October
114 during the first visit were re-sighted 50 and 53 days later at their exact capture
115 locations. Mean territory diameter was 73.5 m across all birds resighted at least
116 twice (the minimum number of locations to calculate a territory size; ± 7.2 m, range

25.2 – 220.0, n = 27; Fig. 1). For birds resighted at least five times, mean territory size was 69.4 m (± 5.4 m, range 35.0 – 114.1, n = 15). The number of resightings had no influence on our estimates of territory size for birds resighted at least five times (lm of territory size~number of resightings: p = 0.93, $F_{1,13}$ = 0.25, n = 15). There was no difference in territory size between adult and first winter birds (lm of territory size~age: p = 0.97, $F_{2,23}$ = 0.03, n = 25, of which 20 = adult, 5 = first winter).

By following individually identifiable birds during part of the wintering period, we show that the Northern Wheatear, a long-distance migrant, is territorial for at least part of the wintering period. Our study period was relatively short, yet both wheatears ringed during an earlier visit were resident in the same territories at least until the end of the study period (50 and 53 days). Furthermore, it was evident that territories were already established on our arrival in early- to mid-winter. This suggests that wheatears are territorial for a large part, if not all, of the wintering period. Individuals responded strongly to playback, and territorial behaviour (singing, chasing neighbouring birds) was observed throughout the study. Although eight birds were not resighted after ringing and so may have been transient birds that did not overwinter in the study area, resightings were not extensive in effort or time, and we cannot be certain that this was the case. Our findings therefore agree with other studies documenting strong winter territoriality and site fidelity in several *Oenanthe* species, including Northern Wheatears (e.g. Panov, 1999, Khoury et al., 2012, Cornwallis, 1975, but see Smith, 1971); for example for Northern Wheatears wintering in Egypt and at stopovers during migration (Arizaga et al., 2011), and for Black-eared Wheatears *Oenanthe hispanica* wintering in Nigeria (Sharland, 1967),

but it should be noted than many of these accounts are anecdotal and did not closely follow individually identifiable birds.

High site fidelity within winters appears to be common across migrants both in the Palearctic and Neotropics (for example: Blackburn and Cresswell, 2015, King and Hutchinson, 2001, Monroy-Ojeda et al., 2013, Wunderle Jr and Latta, 2000, Barg et al., 2006, Kelsey, 1989, Bates, 1992, Brown et al., 2000, Latta and Faaborg, 2001, Salewski et al., 2000, Rappole et al., 2003, Moreau, 1969). Likely, winter territoriality increases survival for these species. Moving during winter or not holding a territory is often associated with reduced survival (Rappole et al., 1989, Winker, 1998), whereas being territorial can increase survival probability through familiarity and predictability of food resources and surroundings (Förschler et al., 2010, Brown and Long, 2007).

Measures of territory size are scarce for Wheatears, but our findings are similar to winter territory sizes documented for Finsch's wheatears *Oenanthe finschii* (Khoury et al., 2012). Territory size did not differ between first winter and adult birds and the location of first winter territories was not distinct from that of adults (see Fig. 1), and there appears to be no spatial segregation according to age, unlike some Neotropical examples (e.g. Marra and Holmes, 2001, Stutchbury, 1994). However, the number of first winter birds in our sample is small, our measure of territory size is relatively crude and based on small sample sizes for each individual and we do not measure territory quality. Nonetheless, territory size, location and quality does not differ according to age and sex for Whinchats, a similar Palearctic migrant (Blackburn and

Cresswell, 2015). This suggests that – like Whinchats – Northern Wheatears probably do not exhibit strong dominance hierarchies according to age on the wintering grounds, in contrast to several Neotropical species which do (e.g. Stutchbury, 1994, Marra, 2000). Further work is required to confirm whether the absence of age or dominance effects on territoriality is the general case for Palearctic wintering passerines.

In summary, we accurately document high within-winter site fidelity in a long-distance Palearctic migrant and suggest that Northern Wheatears maintain territories throughout the wintering period. More detailed knowledge of winter residency and whether individuals are capable of relocating under changing conditions is essential for the effective conservation of migrants given the increasing anthropogenic-driven decline across wintering habitats (Vickery et al., 2014).

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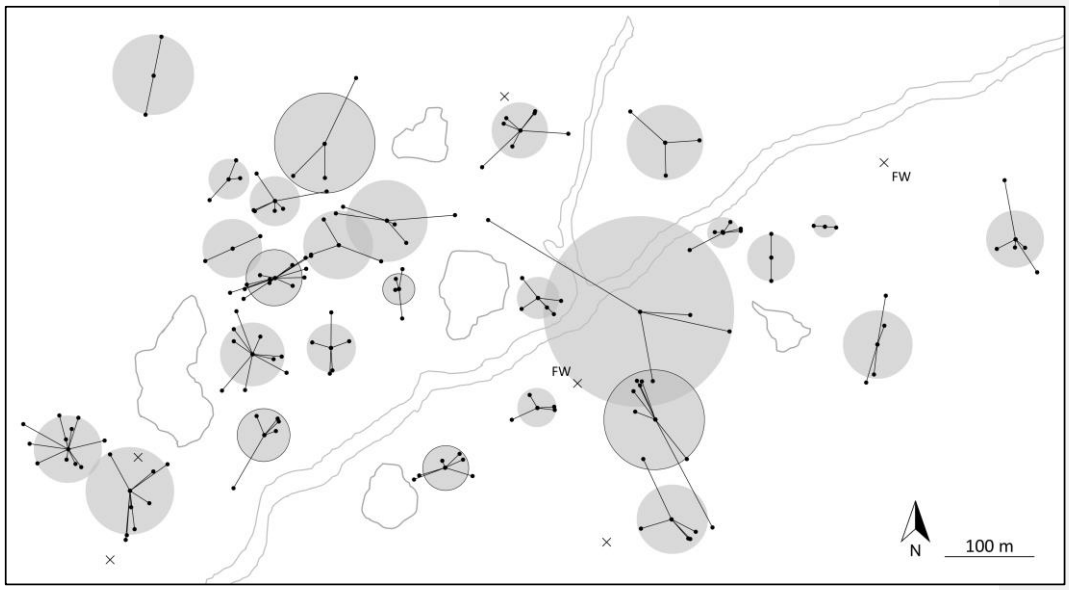
186 Fig. 1. Individual territories of 33 Northern Wheatears wintering in northern Nigeria.
187 Each point represents an undisturbed resighting, connected to the mean location of
188 all resightings for that individual. The grey shaded circles illustrate the territory size
189 for each individual resighted at least twice (*n* = 27 birds). Black crosses show the
190 location of birds resighting only once following capture (*n* = 6 birds). Territories
191 outlined in black and crosses with 'FW' show the territories of first winter birds.
192 Shapes with grey outlines show the location of rocky outcrops and a dry riverbed.
193 This figure shows that Wheatears held small, distinct territories throughout the
194 duration of the resighting period.

195 Fig. 1

196 

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