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Article type : Original Paper

Assigned Associate Editor: Colleen Downs

Low and annually variable migratory connectivity in a long-distance migrant: Whinchats *Saxicola rubetra* may show a bet-hedging strategy

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Keywords: climate change, long-distance migrant, migrant declines, migratory spread, Palearctic, serial residency hypothesis.

Running head: Low and variable connectivity in Whinchats

The spatial scale of non-breeding areas used by long-distance migrant animals can vary from specific, relatively small non-breeding areas for each independent breeding population (high connectivity) to a distribution over a large non-breeding area with mixing of breeding populations (low connectivity). Measuring variation in the degree of connectivity and how it arises is crucial to predict how migratory animals can respond to global habitat and climate change because low connectivity is likely to be an adaptation to environmental uncertainty. Here, we assess whether use of non-breeding areas in a long distance migrant may be stochastic by measuring the degree of connectivity, and whether it is annually variable. Twenty-nine wintering Whinchats tagged with geolocators over two years within 40 km^2 in central Nigeria were found to be breeding over 2.55 million km^2 (26% of the land area of Europe), without an asymptote being approached in the relationship between area and sample size. Ranges differed in size between years by 1.51 million km^2 and only 15% of the total breeding range across both years overlapped (8% overlap between years when only first-year birds were considered), well above the range size difference and below the proportion of overlap that would be predicted from two equivalent groups breeding at random locations within the observed range. Mean distance between breeding locations (i.e. migratory spread) differed significantly between years (2013, 604 + 18 km; 2014, 869 + 33 km). The results showed very low and variable connectivity that was reasonably robust to the errors and assumptions inherent in the use of geolocators, but with the caveat of having only two years' ranges to compare, and the sensitivity of range to the breeding locations of a small number of individuals. However, if representative, the results suggest the scope

for between-year variation (cohort effects) to determine migrant distribution on a large scale. Furthermore, for species with similarly low connectivity, we would predict breeding population trends to reflect average conditions across large non-breeding areas: thus, as large areas of Africa become subject to habitat loss, migrant populations throughout Europe will decline.

Understanding how breeding and non-breeding sites are connected (migratory connectivity) is crucial for successfully predicting the response of migratory populations to environmental change (Bauer *et al.* 2016, Webster *et al.* 2002), particularly in the light of the widespread decline of migratory animals and increasing habitat loss and degradation (Gilroy *et al.* 2016, Flockhart *et al.* 2015, Costa *et al.* 2012, Vickery *et al.* 2014). Indeed, strategies to address declines of migratory species are often based on the idea that migrant populations will have connected breeding and non-breeding (or wintering) ranges and that the identification of these ranges is a priority (Runge *et al.* 2014, Runge *et al.* 2015, Martin *et al.* 2007). However, the scale of connectivity within and between populations of migrants and how this scale arises are still poorly known (Bauer *et al.* 2016).

The spatial scale of use of non-breeding areas by long-distance migrant animals can vary from high connectivity, with specific non-breeding areas for each independent breeding population, to low connectivity, with a spread over a large non-breeding area and therefore mixing across breeding populations (Webster *et al.* 2002, Newton 2008). High connectivity is thought to arise from deterministic, targeted migration that allows population specialisation, but which reduces the resilience of a breeding population to changes in the distribution of non-breeding habitat, and so should only be selected for when the location and suitability of non-breeding sites are highly predictable and stable (Reilly & Reilly 2009, Cresswell 2014). In contrast, low connectivity is thought to arise from bet-hedging - untargeted migration which allows populations to deal with unpredictable environmental conditions (Reilly & Reilly 2009, Cresswell 2014, see also Botero *et al.* 2015). Breeding populations that are distributed over a large area during the non-breeding season should have greater potential to encounter suitable habitat over a larger range, even as this shifts due to climate change (Cresswell 2014). Furthermore, breeding populations that mix during the non-breeding season are likely to respond synchronously to changing conditions outside the breeding season, whereas highly connected populations will respond independently (Esler 2000).

Long-distance migration of birds between northern Europe and sub-Saharan Africa is a recently evolved adaptive response to dynamic global climatic conditions (Cresswell *et al.* 2011, Fryxell & Holt 2013), suggesting that a bet-hedging strategy of individuals from the same brood migrating to geographically separate non-breeding sites might actually be the norm because of the resilience this strategy grants against dynamic conditions (Botero *et al.* 2015, Reilly & Reilly 2009). Consequently, migrants are most likely selected to be generalists within their wintering habitat (Ivande & Cresswell 2016), with low and variable migratory connectivity (the serial residency hypothesis - Cresswell 2014). A recent analysis of all migratory tracks that were available from tagged birds from 45 ecologically diverse land-bird species (including Passeriformes, Apodiformes, Falconiformes, Cuculiformes and Coraciiformes) in both the Europe-Africa and the Americas flyways showed that connectivity at a large scale was the strategy used by most species (Finch *et al.* 2017). Here, we test whether use of non-breeding areas in a long-distance migrant is likely to arise from a bet-hedging strategy by measuring the degree of connectivity and whether it is annually variable.

Testing theories of migratory connectivity on a sufficiently large scale has recently become possible because of advances in tracking technology such as satellite and GPS tags. Geolocators (light-level loggers) now allow animals of relatively small body size to be tracked at global scales for the first time (Bridge *et al.* 2013). We measured and tested migratory connectivity in the Whinchat *Saxicola rubetra*, a common but declining Afro-Palearctic long-distance migrant bird (Müller *et al.* 2005, Britschgi *et al.* 2006). Uniquely, we measured connectivity (i) from a location on the wintering grounds to the breeding grounds, which allows much greater precision of locations (because of more variable daylength at higher latitudes, and because birds are highly likely to be stationary during the breeding period (Lisovski *et al.* 2012), (ii) in two separate years, (iii) with relatively large sample sizes (for geolocator studies; Bridge *et al.* 2013), (iv) in a system where we know there are no effects of tagging (Blackburn *et al.* 2016), and (v) where there is very high non-breeding site fidelity (Blackburn & Cresswell 2016b). We tested two predictions that arise directly if non-breeding site selection has an important bet-hedging or stochastic component for first year birds, followed by site fidelity for adults to the sites which allowed their non-breeding survival (Cresswell 2014): first that there will be an extensive range (on the scale of >1000 km) of breeding locations sampled from individuals sampled at a single wintering location (Fig. 1), and second that there will be differences in breeding ranges between years when comparing samples from the same wintering location (Fig. 2). This may be particularly pronounced when comparing cohorts (i.e. first-year birds only) because, in each year, we would expect birds from spatially closer breeding populations to be affected in a similar way by conditions on migration (and so tending to end up in similar non-breeding areas), but for these conditions to vary between years (particularly because of large-scale annually variable timing of breeding or possibly variation in departure post-breeding) so that these non-breeding areas might shift in location annually.

We tested these predictions by mapping annual ranges and comparing how these differed in terms of size, overlap and mean distance between individuals, with the expectation that annual ranges will be large but variable between years.

METHODS

The study took place between February 2013 and November 2013 (Year 1), and February 2014 and April 2015 (Year 2) during the dry season (early September to late April) on the Jos Plateau in the guinea savannah zone of central Nigeria, West Africa (09° 53' N, 08° 59' E, approximately 1250 m altitude). Some colour-ringed only Whinchats were captured outside these months (i.e. earlier in the wintering period or were colour-ringed birds that had returned from previous winters) to evaluate whether the geolocators affected survival (Blackburn *et al.* 2016). Whinchats were captured within an area of approximately 5 x 8 km; full site details are described in Blackburn and Cresswell (2016b). Capture areas 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 (Hulme & Cresswell 2012, Blackburn & Cresswell 2015). The study area represents typical wintering habitat for this species in the region (open savannah) and has high densities of Whinchats.

Whinchats were caught with spring traps and mist nets in late February and March in 2013 or 2014 (birds in 2014 were on average tagged 10.3 + 3.3 se days earlier than in 2013, $F_{1,27} = 3.2$, $P = 0.004$). Birds were aged and sexed (Jenni & Winkler 1994), ringed with unique combinations of colour-rings, and fitted with a geolocator. In Year 1, we deployed 49 and in Year 2 we deployed 131 geolocators fitted using leg-loop Rappole-Tipton (also called backpack) harnesses. Full details of tag and harness design are given in Blackburn *et al.* (2016), but importantly for this study, there was variation between years in the length of light stalks of the tags. In 2013, all tags had a 10 mm length light stalk, whereas in 2014 tags had either no light stalks, 5 mm or 10 mm length light stalk (see below). Tags weighed on average 0.63 g (0.01 se), representing 4.1 % of average body mass. There was no overall significant reduction in between-year resighting rate (our proxy for survival; Blackburn & Cresswell 2016b) comparing tagged and untagged birds in either year (Blackburn *et al.* 2016).

Attempts were made to recapture any returning tagged bird resighted in the following winter. Upon recapture, geolocators were removed by cutting the harness and birds were released unharmed after briefly assessing body condition (Blackburn *et al.* 2016). Sample sizes of breeding locations used in this paper are less than the number of individuals that returned with geolocators because 18/39 returning birds in 2014 could not be recaptured (because many had become extremely wary of spring-traps and mist-nets), two individuals had lost their loggers because of harness failure, and several loggers in 2013 suffered battery failure before the birds reached the breeding grounds. Overall, we include all possible data from 29 individuals (12 in 2013 and 17 in 2014 – any individual was tracked only in one year); data came from eight females and 21 males (sex ratio was not significantly different by year, Fisher's exact test $P = 0.41$), and 13 adults (see Supplementary Online Fig. S2 for the locations of these individuals), 13 first years and three that could not be aged confidently (ratio of known age birds was not significantly different by year, Fisher's exact test $P = 0.43$). In 2014, of the recaptured birds, 4 had tags with no light stalk (see Fig. S2 for the locations of these individuals), 8 with 5 mm light stalks and 5 with 10 mm light stalks.

Analyses

Raw data were downloaded, viewed and preliminarily cleaned using the BASTrack software suite (British Antarctic Survey, Cambridge, UK; see Fox 2010 for an overview of the following processes). We adjusted for clock drift, assuming that any drift was linear. We used the Transedit2 software that is part of the BASTrack software to view raw data as light curves over time. We used a threshold value of two to define sunrise, which is close to civil twilight. False twilight events due to shading from weather or vegetation were identified and removed with the 'minimum dark period' filter (we used four hours), which removes any impossible sunrise and sunset events (for a review and exploration of the effects of enviromental factors on geolocator data, see Lisovski *et al.* 2012). Data were then visually inspected to ensure that only one sunrise and sunset occurred within any 24-hour period.

Further analyses were then carried out using R 2.13.1 (R Development Core Team 2014). We used the LoessFilter in the R package *GeoLight* (Lisovski & Hahn 2012) to validate twilight events and identify those influenced by shading events at dawn and dusk: a polynomial regression of twilight events identified residuals that were greater than three times the interquartile range and were therefore likely to be erroneous (Lisovski & Hahn 2012). Identified outliers were checked within the original data and were retained because large movements resulting from migration were sometimes incorrectly identified as outliers, and outliers were reasonably normally distributed in the winter and summer periods analysed (and so their effects cancelled out when calculating mean locations).

Because conditions away from the wintering grounds are unknown, we carried out two calibrations to determine the correct sun elevation angle value (SEA, which influences the determined latitude) for winter (SEAw) and summer (SEAs). For SEAw, we used the LocatorAid software from the BASTrack software suite, which uses known residency times and wintering location to calculate the corresponding wintering ground SEA value. We attempted to find the correct summer angle using the Hill-Ekstrom (H-E) calibration method (Hill & Braun 2001, Ekstrom 2004, Tottrup *et al.* 2012) in which we selected the SEA value that gave the least amount of variation in latitude. If the calibration was not successful, we used the mean value for all of the loggers for which the calibration had been successful, calculated for each year separately (see Fig. S1 for a mapped description of which birds were affected; four in 2013 and 12 in 2014, and the locations associated with each SEA value used). Because the mean SEA value may have differed between years (e.g. because of inter-annual differences in cloud cover), we also simply used the same average SEA value for all birds regardless of year in a further analysis, but with little change to the results (see below). In further sensitivity analyses (see below), we also varied the SEA value for these ‘mean value’ birds over the range of observed values from the Hill-Ekstrom calibration for that year to demonstrate that this uncertainty (and the assumption of using mean values for those birds where the calibration did not give clear results) made little difference to the results (see below). Once a corresponding SEAw and SEAs value was known for each logger, noon and midnight locations for a two week period when variance in locations was minimal (and all Whinchats should have been stationary on their breeding grounds in any case) were derived from sunrise and sunset times using the *coord* function in the *GeoLight* package (Lisovski & Hahn 2012). Breeding location was further confirmed from visual inspection of latitude and longitude changes with date and through identification of stationary periods using *GeoLight*. We used the mean of all summer locations (calculated using SEAs values) for the first two weeks in June for all birds except two that showed evidence of some small movement in June where we used the last two weeks in May, and one bird that showed evidence of major movement in June, to a new stable location in July (perhaps after breeding failure) where we used the first two weeks in

July (‘Best’ Analysis 1). All two week ‘most’ stationary locations identified were at very similar locations to the mean of all locations from mid-May to mid-July for all but the three birds that moved during this period, and for these three birds, the ‘second’ location was then stable for several weeks afterwards probably indicating breeding. Using these ‘best’ most stationary periods, or simply all locations from each bird in June gives very similar results for all analyses (See Tables S1 and S2, compare results for Analysis 1 & 4); other periods between mid-May to the end of July gave similar results (unpubl. data).

Maps were plotted using the *raster*, *rgdal*, *rgeos* and *mapproj* libraries in R. Minimum convex polygon areas, overlaps of these polygons and distances (considering the curvature of the earth) were calculated using the *alphahull* and *geosphere* libraries in R. Areas were calculated for both years combined and for 2013 and 2014 separately; the range overlap between the two years as a percentage of the overall range (PHR) was also calculated. More sophisticated analyses using kernels generated from the density of points were not appropriate because we had only a single breeding location for each bird (albeit with variation due to geolocator errors in precision and SEA assumptions) and so sample sizes of overall points split by year were too small for meaningful calculations of probability density functions.

Ranges are sensitive to sample size, with range increasing with sample size until an asymptote is reached when individuals from nearly all parts of the range are part of the sample. We tested the degree to which the ranges which we measured approached an asymptote, i.e. whether the range calculated from our small samples is likely to have approached the true range. The effect of sample size on the range recorded overall and in each year separately was tested by randomly sub-sampling the breeding locations for all birds, selecting four points up to n – 1 points overall and for the individual years, 1000 times and then calculating the range for each sub-sample. The relationship between mean range of the 1000 sub-samples and number of tagged birds was then tested with a GLM to determine the line of best fit, comparing linear and quadratic fits to determine if an asymptote in range with sample size had been reached.

We tested whether there was any significant difference in the size of the range and degree of overlap of range between the two years by creating comparison data sets of the range size and overlap that would occur if two groups of random points were selected from the total breeding range observed in the two years. Twenty-nine geographic points were selected randomly from the combined observed range plotted for all individuals across both years; the first 12 points were placed in group 1 corresponding to the first year's sample and the final 17 points in group 2 corresponding to the second year's sample. Minimum convex polygons for each group and the combined groups were calculated using the *alphahull* library in R; the area in each year and the difference in area between years, overall area and the overlap in area between the two groups as a percentage of this total area for both groups was then calculated. The procedure was repeated 1000 times to determine the 95% confidence intervals of area difference and overlap for randomly selected points (i.e. with random difference in location between years). We then repeated this analysis with 13 points randomly selected (seven in group 1 and six in group 2) to create a similar random comparison data set considering only the first-year birds.

We also measured the mean distance between breeding locations in each year (equivalent to migratory spread as calculated in Finch *et al.* 2017). A matrix of all possible pairs of distances was created and the distance between locations was calculated using the *distHaversine* function in R, and then the mean and standard error of these annual mean distances was calculated. We tested whether there was any significant difference in mean spread of locations between years using a *t*-test with degrees of freedom conservatively set to the number of original locations (i.e. n = 29 for all birds and n = 13 for first-year birds).

We tested for any systematic biases in latitude or longitude calculated with respect to variation in sex, age, stalk length, SEA value, and whether this SEA value was estimated using the H-E calibration or an average, in a GLM controlling for year. We also included interactions with year in this model to test whether any effects of these potential biases acted differently in the two years of the study. There were no significant effects (systematic biases that may have accounted for the results) in any variables or interactions apart from light stalk length (Tables S3, S4). A significant effect of light stalk length on latitude (but not longitude) was found so that more southerly latitudes were recorded from tags without light stalks, dependent on the SEA value considered (details in Table 2). Correspondingly, we adjusted all latitudes for the light stalk effect so that if a tag did not have a light stalk, we added the parameter estimate for light stalk (between +3.8 to +5.0 degrees of latitude – see Table 2) to the estimate of latitude: note this had the effect of reducing any differences between years, because 2014 locations were generally to the south of 2013 locations (see figures in Supplementary Material and particularly Fig. S2 which identifies those loggers that had no light stalks). Results using stalk length as a three-way factor, or as a two-way factor of light stalk presence or absence, were similar, and models which considered stalk length as a three-way factor were more than 2 AIC units worse than identical models with stalk length as a two-way factor. We therefore only considered the presence and absence of a light stalk when considering the potential confounding effects of tag design in detail. There was no significant variation in latitude with age or sex in any model and models were substantially (ΔAIC > 2) improved by the removal of these terms which allowed the full data set to be used (i.e. by including those birds that lacked age data; Tables S3, S4). Final adjustment of latitude was therefore calculated from a model including year and light stalk presence or absence (Tables S3, S4). The appropriate adjustment (i.e. depending on SEA value) was used for each analysis and its associated range of SEAs values (Table 2). Because of the potential confounding effect of light stalk between the years that we identified, all analyses were carried out on both the raw observed location data set (Table 1) and also the data set with locations adjusted for the absence of a light stalk (Table 2).

Because of uncertainty introduced by not knowing breeding location SEA value, we also analysed the data under a set of scenarios with different assumptions for the SEA value (Tables S1, S2). These analyses were: 1. ‘Best’ with summer SEAs values determined using the Hill-Ekstrom calibration, or the mean value from the calibrations for that year for birds where the calibration was not conclusive, for the two-week breeding season period with lowest variation in latitude; 2. Winter SEAw value for the 2 week breeding season period with the lowest variation in latitude; 3. Average SEA value - the mean location calculated for each bird for sun elevation angles 2 to 6 at 0.5 increments (i.e. nine mean locations), then averaged across these nine locations, applied to all birds regardless of year; 4. As analysis 1, but for *all* locations in June; 5. As analysis 1, but with the maximum or minimum SEA value observed for that year used for those birds where the Hill-Ekstrom calibration was not conclusive, so that the range for each year was minimised (i.e. an analysis to examine the minimum range possible under the uncertainty of the SEAs values); 6. As analysis 1, but with the maximum or minimum SEA value observed for that year used for those birds where the Hill-Ekstrom calibration was not conclusive, so that overlap for each year was maximised (i.e. an analysis to examine the maximum overlap possible under the uncertainty of the SEAs values).

In short, extensive sensitivity analyses (Tables S1 & S2, Figures S3 – S20), regardless of SEA value and light stalk adjustment assumptions, showed very similar results. The results presented here use the data set which we considered to be the most accurate (Analysis 1. ‘best’ data set), but these results are representative of other scenarios which vary the assumptions of sun elevation angle; these are also detailed in Tables S1 and S2.

Best models were identified on the basis of AIC, and models differing in AIC of less than 2 were considered as equally valid (Burnham & Anderson 2002). Model fits were evaluated from diagnostic model plots, and models were presented if assumptions were reasonably met (Crawley 2007). Mean values are presented with one standard error (se) in all cases; R^2 values were adjusted in all cases.

RESULTS

Overall range extent

Whinchats tagged within a 40 km^2 area of central Nigeria had a breeding range extent of up to 2.55 million km^2 (range 2.351 – 2.549 million km^2; note here and subsequently, range is calculated across the different SEA values, see Tables S1, S2), or 26% of the land area of Europe (Table 1, Fig. 3). The latitudinal range of the breeding grounds was approximately 16.3 degrees from Serbia to the southern border of Finland (a north to south distance of approximately 1700 km) and the longitudinal range was 35.9 degrees from Poland to the Ural Mountains in Russia (an east to west distance of approximately 2300 km; Fig. 3). When values were adjusted for the effect of light stalk absence, breeding range extent was 1.68 million km^2 (1.681 – 1.835 million km^2), or 17% of the land area of Europe (Table 2).

The total breeding range observed overall did not reach an asymptote with sample size. A straight line relationship between range and sample size for all birds unadjusted for light stalk absence gave a reasonable model fit (Fig. 4a). When latitudes were adjusted for the absence of light stalks, a quadratic fit was much better for the relationship between range and sample size, but although the relationship was becoming less steep, it did not approach an asymptote (Fig. 4b).

Annual variation in range extent

The breeding area of all Whinchats tagged in central Nigeria, unadjusted for light stalk absence, was much lower in 2013 (0.651 million km^2, range 0.503 – 0.744) than that in 2014 (2.157 million km^2, range 1.971 – 2.230; Fig. 5). The differences in unadjusted area between the two years were greater than expected by chance for all SEA analyses for all birds (Table 1, Table S1). The breeding area of all Whinchats tagged in central Nigeria in 2013 was much smaller than that of the range adjusted for light stalk absence in 2014 (1.650 million km^2, range 1.650 – 1.814); the differences in adjusted area between the two years were greater than expected by chance for all SEA analyses (Table 2, Table S2). For first-year birds only, the breeding area unadjusted for light stalk absence in 2013 (0.470 million km^2, range 0.429 – 0.518) was much smaller than that of the range in 2014 (1.199 million km^2, range 1.145 – 1.199; Fig. 3). The differences in area between the two years were greater than expected by chance for all SEA analyses of first year birds (Table 1, Table S1). For first-year birds only, adjusted for light stalk presence in 2014, the breeding area in 2013 was much smaller than that of the 2014 area (1.232 million km^2, range 0.829 – 1.232). The differences in area between the two years were greater than expected by chance for all SEA analyses of first-year birds, apart from when using the summer SEA for all locations in June (Table 2, Table S2).

Whinchat breeding ranges in the two years generally overlapped relatively little, although this was less clear in first-year birds. The breeding range of all Whinchats showed relatively little overlap between years: only 15% (range 8.7% - 27.1%) of the total range for both years was overlap, with all overlaps being lower than that expected by chance (Table 1, Table S1). For latitudes adjusted for light stalk absence, overlap was 37% (range 31% - 42%) with a trend (P = 0.03 to P = 0.07) for overlaps to be lower than that expected by chance (Table 2, Table S2). For first-year birds only, there was also a trend for relatively low overlap in the breeding ranges between years: 8% (range 2.7% - 18.9%) of the total range for both years overlapped, with overlaps only being lower than that expected by chance when using the summer SEA for all locations in June, and marginally significant for the ‘best’ analysis (Table 1, Table S1). For latitudes adjusted for light stalk absence for first year birds, however, there was reasonable overlap in the breeding ranges between years: 33% (range 3.3% - 39%) of the total range for both years overlapped, with all overlaps only being lower than that expected by chance when using the summer SEA for all locations in June (Table 2, Table S2).

The mean distance between breeding locations was greater in 2014. For all birds, the mean distance was 604 km in 2013 (range 591 – 631) and was 869 km in 2014 (range 839 – 903) and the difference was highly significant for all SEA analyses (Table 1, Table S1). For all birds, the mean distance adjusted for light stalk in 2014 was 820 km (range 817 – 828) and the difference was highly significant for all SEA analyses (Table 2, Table S2). For first-year birds, the mean distance was 598 km in 2013 (range 567 – 631) and was 1059 km in 2014 (range 1013 – 1060) and the difference was highly significant for all SEA analyses (Table 1, Table S1). The mean distance adjusted for light stalk in 2014, for first-year birds, was 1042 km (range 950 – 1042) and the difference was significant for all SEA analyses (Table 2, Table S2).

The total breeding range observed in each year separately did not reach an asymptote with sample size. For all birds, the relationship between range and sample size was dependent on sample size, but with different slopes dependent on year (interaction of year* sample size $t = 11.5$, $P < 0.0001$). There was therefore a significantly greater spread in breeding locations for 2014 (0.141 + 0.007) compared to 2013 (0.061 + 0.006), i.e. a much higher rate of increase in range per increase in sample size (Fig. 4c). The relationships between range and sample size were linear (overall model $R^2 = 0.99$). The same result was found using 2014 range adjusted for the effect of light stalk absence. For all birds adjusted for the effect of light stalk, the relationship between range and sample size was dependent on sample size, but with different slopes dependent on year (interaction of year*sample size $t = 11.7$, $P < 0.0001$): there was therefore a significantly greater spread in breeding locations for 2014 (0.109 + 0.004) compared to 2013 (0.061 + 0.004): i.e. a much higher rate of increase in range per increase in sample size (Fig. 4d). The relationships between range and sample size were linear (overall model $R^2 = 0.99$).

DISCUSSION

We made two predictions, that Whinchats wintering in Nigeria would have a large breeding range and an annually variable breeding range. Both were supported by our results, which indicate very low connectivity, i.e. connectivity only at a very large scale: Whinchats from a single wintering location were spread out over a continental scale in Europe (approximately 40% of the maximum east to west width of Europe). The reverse, that individuals from the same breeding location in Europe will be spread out over a large non-breeding area in Africa, is logically likely to apply (Fig. 1), especially in a species with such high non-breeding site fidelity (Blackburn & Cresswell 2016b), breeding ground site fidelity (Bastian 1992) and a non-breeding distribution across the whole of Africa, from Senegal to Tanzania. Whinchats from any local breeding population in the east of Europe are therefore likely to spread out over a similar continental scale in Africa (33% of the maximum east to west width of Africa at typical wintering latitude, 8 degrees). Furthermore, we suggest that the breeding distribution of a wintering population of Whinchats in Africa may also be annually variable, with potential shifts in average occurrence between years of the order of hundreds of kilometres.

Our results, at least in terms of the large scale of the ranges and variation we have described, seem reasonable. Although locations from geolocators have errors, these errors within individual stationary periods were reasonably normally distributed, as probably were errors between individuals through incorrectly assessing SEA value (e.g. some individuals will have lower and some higher SEAs values than they should, but these are likely to be random with respect to individual location on a large scale). There were, for example, no correlations between SEA value used in the 'best' analysis and latitude or longitude (model of SEAs ~ latitude + longitude; latitude 0.04 + 0.03, $t = 1.2$, $P = 0.24$, longitude -0.002 + 0.014, $t = -0.2$, $P = 0.86$; $F_{2,26} = 0.7$, $R^2 = 0$). Furthermore, our analyses (analyses 2 & 3, Tables S1, S2) that simply used an average value of SEA for all birds will have increased the randomness of the errors, and both gave very similar results to analyses which used the best available information to more accurately estimate SEA value. Consequently, range areas and range differences between years should be real, even if imprecise in location. Fundamentally, the scale of geolocator errors (Fudickar *et al.* 2012) is also relatively small compared to the scale of the ranges identified in this study. Our analyses, which used different assumptions regarding sun elevation angle values, breeding stationary period and effect of absence of light stalks, showed broadly similar results at the large scale of this study: despite variation in the individual breeding locations in each analysis, 2013 birds had a smaller spread and range than 2014 birds and there was reasonable evidence for a difference in range between years when comparing overlap.

Although the H-E calibration should have accounted for differences in shading between birds, locations and years, the effect of light stalk presence or absence on latitude demonstrated that this calibration was biased by shading (in this case, most likely through flight feathers covering the light sensor). Consequently, the latitudes of breeding locations in each year could have been biased by the degree and variability of weather shading in the period for which data was used in the calibration, especially when this was based on a short period (two weeks). This could potentially have caused spurious shifts in range between years. The difference in SEA between years after the H-E calibration was small (2014, -0.55 + 0.58, $t = -1.0$, $P = 0.37$) and would have shifted 2014 locations by about 0.6 degrees latitude to the south away from 2013 locations, thus the bias, if it was operating, would have increased any differences in range and overlap between years for the ‘best’ analysis (Analysis 1). It could not, however, completely explain the differences in spread of individuals between years because this also has a longitudinal component (albeit due to a few birds). In any case, any such bias was completely removed when using the same average SEA value for all birds regardless of year.

We still found variation when controlling for cohort effects, despite smaller sample sizes. The larger population contained both first-year and adult birds from previous years, each individual year having a likely different cohort range effect. Any comparison between two consecutive years that includes adult birds will therefore be conservative because, as more cohorts are included, the range in any one year will regress to the mean range of the population. This will act to blur any differences between years. However, Whinchat annual survival rate for this population is of the order of 54% (Blackburn & Cresswell 2016a), so even when considering adults, it was likely that over 75% of the population sampled in each year consisted of only two cohorts. Unfortunately, any convincing analyses of only adult birds – which should show less variation (this was the case, but not included here) - was precluded by only four adults being part of the 2013 sample versus nine in the 2014 sample (Fig. S2), so making any confirmation of the null hypothesis likely simply because of low power, regardless of any actual differences or not between years.

Although the results of the analyses are consistent regardless of assumptions, they rely on small sample sizes. Any range or migratory spread calculation will be dependent on its relatively few peripheral points, and the sample size for inter-annual comparisons is only two years. The overlap result is also difficult to interpret, being confounded by variation in size as well as a possible shift in location, although the study shows clear evidence of annual variation in measures that will affect overlap (i.e. migratory spread, and the relationship between range and sample size). The study clearly needs to be repeated, ideally tracking only first-year Whinchats from other areas in Africa in consecutive years to determine inter-annual variability in range, with sufficient breeding locations obtained to analyse range using probability density functions. Nevertheless, our results suggest that low and variable connectivity can occur in Whinchats. Our range estimates did not approach an asymptote with a sample size of 29 tagged birds and there were differences in range between years sufficient that conclusions about where Whinchats wintering in central Nigeria may have bred, or their degree of connectivity, would have differed on an international scale, if the study had been only conducted in a single year, or with a different sample size.

Our results show migratory spread consistent with the pattern just emerging from other studies. Long-distance migrant birds have high migratory spread regardless of phylogeny and flyway; the predicted average maximum distance between wintering individuals from the same breeding population, across 45 species, is of the order more than 3000 km (Finch *et al.* 2017). It should be noted, however, that all species lie on a continuum of connectivity and there are examples of particularly low connectivity species (e.g. Pallid Harriers *Circus macrourus* Terraube *et al.* 2012) and particularly high connectivity species (e.g. Nightingales *Luscinia megarhynchos* Hahn *et al.* 2013); Whinchats would appear to lie closer to the extreme end of low migratory connectivity. Inter-annual shifts in range are less well documented or tested, even in the few multi-year datasets, but Liechti *et al.* (2015) reported that Barn Swallows *Hirundo rustica* wintered 400 km to the north in one year compared to the population mean for the previous year, and Swainson's Thrush *Catharus ustulatus* (Delmore & Irwin 2014) and Semi-collared Flycatcher *Ficedula semitorquata* (Briedis *et al.* 2016) populations also probably show inter-annual variability in mean wintering location.

Although the low and variable connectivity suggested here could arise through a bet-hedging strategy, because first-year non-breeding site selection is to a degree stochastic, other mechanisms may have caused the pattern. As detailed in Figure 1, if migrants with wide breeding ranges in Europe have relatively small wintering ranges in Africa (e.g. Eleonora's Falcon Falco *eleonora* Gschweng *et al.* 2008, Kassara *et al.* 2012), effectively concentrating in a small non-breeding area, and they are then sampled in that small area, they will show apparently very low connectivity. This is unlikely to be the case for Whinchat, however, due to its very large non-breeding distribution in Africa. Variation in breeding success on a continental scale may also cause differences in breeding ranges when sampled in different years from Africa. For example, northerly breeding Whinchats in 2012 may have produced more first-year birds than southerly Whinchats, and vice-versa in 2013. Annual variation in settlement patterns for first breeding, particularly if a species has low or environmentally variable natal site fidelity (Studds *et al.* 2008), could also lead to the patterns observed here.

With the caveat that alternative explanations are possible, the results of this study are consistent with the predictions of the serial residency hypothesis, where low and variable connectivity emerges from juveniles having deterministic migratory directions varying around a mean 'approximate' migration direction and then subsequent non-breeding locations further varying due to annually variable events (e.g. breeding phenology and weather patterns during migration), followed by high wintering site fidelity of surviving adults (Cresswell 2014). Such a system makes sense in terms of the evolution of migration, which is an adaptation to large scale climate change and consequent shifting of suitable habitat (Cresswell *et al.* 2011, Fryxell & Holt 2013). As required resources or environments shift in location, at least some offspring from a brood will find survivable routes, thus a bet-hedging strategy, whereby some offspring migrate in slightly different directions and/or different times (Reilly & Reilly 2009), is adaptive when the location of suitable habitat is unknown and unpredictable (Cresswell 2014). As location of suitable conditions becomes more predictable, this bet-hedging strategy becomes less adaptive because a proportion of offspring will always miss the target and arrive in unsuitable habitat. Although adjustments within the wintering range can be made by further small or even large scale migratory movements, there may be costs because migration itself can represent a period of high mortality (Sillett & Holmes 2002, Strandberg *et al.* 2010).

A bet-hedging strategy is, however, unlikely to be adaptive if the availability of habitat declines, because an increasing proportion of offspring (or the population) will miss the target. Thus the connectivity optimum for climate change (bet-hedging leading to a wide non-breeding distribution) is the opposite of the connectivity optimum for habitat loss (with specific site or area selection leading to a narrow non-breeding distribution): migratory species cannot adapt to both. This creates an adaptive conflict in the face of both shifting habitat due to climate change and disappearing habitat because of rapidly increasing human populations in Africa. The many migrant species that apparently make a first naïve bet-hedging migration (i.e. excluding those relatively few species that use social learning and that migrate in mixed age groups) will have a wide non-breeding distribution and an annually increasing proportion of their populations arriving in unsuitable habitat on the wintering ground, thus reducing survival. The wide non-breeding distribution ensures that any reduction in habitat availability over a very wide area of the wintering grounds affects all populations over a very wide breeding area (Sutherland & Dolman 1994, Taylor & Norris 2010, Cresswell 2014). This general characteristic may then significantly contribute to the decline of so many populations of migratory species (Vickery *et al.* 2014), regardless of their location on the breeding grounds and their ecology.

A number of predictions arise from this framework with respect to population trends and distribution. First, population trends will be a function of a population's distribution or migratory spread on the non-breeding ground: at some point the proportion of first years that miss the target must reduce juvenile survival below the level of productivity/recruitment, although this will vary depending on the degree of non-breeding habitat/resource specialisation (i.e. how big the target is, or how costly it is to miss it). Species with low migratory spread will have favourable population trends where they winter in climatically stable areas and are likely to be habitat specialists; selection may act to reduce genetic variability in migration direction and/or to promote social learning of routes. Species with high migratory spread will have favourable population trends (e.g. Gilroy *et al.* 2016), particularly if they winter in climatically variable areas and are likely to be habitat generalists (e.g. Hulme & Cresswell 2012, Blackburn & Cresswell 2015); selection may therefore act to increase variability in migration direction. Consequently, species with intermediate migratory spreads and generalist habitat requirements might have more favourable population trends. Second, appreciating that there are cohort effects will greatly affect our understanding of distribution. Range should shift rapidly on the wintering ground so that range maps built from sight records over decades may not accurately reflect current range, or indeed the actual range in any year. Furthermore, models to predict the habitat requirements of migrants at a large scale will be subject to errors both from the false negatives from stochastic range shifts as well as the ‘false’ positives of juvenile cohorts in unsuitable areas with much lower survival.

Testing such predictions is essential if we are to respond to the extremely rapid decline of migratory species across global flyways. Whether we adopt species-specific and local site specific land sparing solutions, rather than widespread land sharing solutions likely depends on degree of connectivity and how it affects survival.

The study was carried out in Nigeria where no licences are required for the procedures used. Nevertheless this study was carried out under the ethical guidelines of the AP Leventis Ornithological Research Institute Scientific Committee (APLORI is the only ornithological research institute in Nigeria) based on the Association for the Study of Animal Behaviour guidelines and those of the British Trust for Ornithology’s ringing scheme. All personnel involved in fieldwork, either catching, colour-ringing or tagging birds, had BTO ringing licences. MB had been previously licensed to fit geolocators in the UK. This work was supported by the Chris Goodwin, A.P. Leventis Conservation Foundation, AP Leventis Ornithological Research Institute, the British Ornithologists’ Union and the Linnean Society. This is paper number (to be completed at proof stage) from the AP Leventis Ornithological Research Institute.

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Table 1. Observed area and overlap (million square kilometres) of breeding locations compared to a random sample (lower and upper 95% CI), and mean distance (+ 1 se km) between breeding locations for all birds (a) and first year birds (b) with 'best' summer sun elevation angle values (SEAs). See Table S1 for a comparison of these values when using different sun elevation angle values: all are reasonably similar regardless of assumptions of sun elevation angle value.

	Overall	2013	2014	Difference 2014 - 2013	Lower 95% CI value for the random sample	Upper 95% CI value for the random sample	*P*-value
a. All birds	*n* = 29	*n* = 12	*n* = 17				
Area	2.549	0.651	2.157	1.506	-0.612	1.225	0.01
Overlap	14.7				32.4	76.2	0.01
Mean distance		604 + 18	869 + 33	$t_{28} = 5.2$			0.0001
b. First-year birds	*n* = 13	*n* = 7	*n* = 6				
Area	1.700	0.470	1.199	0.729	-0.857	0.589	0.02
Overlap	7.9				3.8	56.8	0.06
Mean distance		598 + 40	1059 + 72	$t_{12} = 4.1$			0.0010

Table 2. Observed area and overlap (million square kilometres) of breeding locations compared to a random sample (lower and upper 95% CI), and mean distance (+ 1 se km) between breeding locations for all birds (a) and first-year birds (b) with 'best' summer sun elevation angle values (SEAs), latitudes adjusted for the effect of no light stalks on four birds in 2014. Latitude adjustments for each analysis are given in italics. Sample sizes as in Table 1. See Table S2 for a comparison when using different sun elevation angle values: all are reasonably similar regardless of assumptions of sun elevation angle value.

	Overall	2013	2014	Difference 2014 – 2013	Lower 95% CI value for the random sample	Upper 95% CI value for the random sample	*P* value
a. All birds	*Light stalk adjustment for latitude -4.45 + 1.6, $F_{1,26}$ = -2.7, P = 0.010*						
Area	1.681	0.651	1.650	0.999	-0.440	0.814	0.01
Overlap	36.5				35.2	77.8	0.06
Mean distance		604 + 18	820 + 29	t_{28} = 4.5			0.0001
b. First-year birds	*Adjustment as for all birds above*						
Area	1.275	0.470	1.232	0.762	-0.651	0.486	0.01
Overlap	33.2				4.2	60.3	0.51
Mean distance		598 + 40	1042 + 63	t_{12} = 4.3			0.001

Figure legends

Figure 1. How sampling at any one point on the non-breeding ground can result in sampling birds over a large breeding range (i.e. low connectivity arises from wide migratory dispersal). This model assumes high natal (Greenwood & Harvey 1982) and non-breeding (Cresswell 2014) site fidelity. The model also assumes that the non-breeding range of a migrant is at a very large scale (as it is with the Whinchat and most other Afro-Palearctic migrants which have non-breeding ranges that encompass much of Africa), where migrants may have small, concentrated, non-breeding areas thus tagging from these areas will also result in sampling birds over a large breeding range.

Figure 2. How sampling at any one point on the wintering ground in different years can result in sampling birds with different breeding ranges (i.e. inter-annual variation in connectivity arises through stochastic cohort effects such as, for example wind conditions during migration varying between years). This model assumes high natal site fidelity (Greenwood & Harvey 1982) and high non-breeding site fidelity if a first year bird has found a non-breeding site that allowed survival (the serial residency hypothesis; Cresswell 2014).

Figure 3. Breeding locations and range for 29 Whinchats tagged at Jos Nigeria (A) in 2013 (black circular points, white fill) and in 2014 (white triangular points and darker grey fill). Each point is plotted at the mean of all latitudes and longitudes recorded over the least variable two-week stationary period during mid-May – mid-July; +/- 2 Standard Errors from the mean location are also plotted but only the highly variable locations are clearly visible at this scale. All birds plotted at the ‘best’ estimate locations, unadjusted for light stalk absence (see Table 1).

Figure 4. Mean range plotted for 1000 random subsamples of points, each of different sample size. a. All birds and years pooled, unadjusted for light stalk absence. A linear fit is plotted with 95% CI plotted as dotted lines (range = (0.097 + 0.003*(sample size)) + (– 0.03 + 0.04), $F_{1,12} = 37.2$, $P < 0.0001$; $R^2 = 0.99$; ΔAIC = + 0.2, compared to a quadratic model including the square of sample size which gives a near identical plot). b. All birds and years pooled, adjusted for light stalk absence. Line of best fit is quadratic, 95% CI plotted as dotted lines (range = (0.094 + 0.005*(sample size)) + (-0.0011 + 0.0002*(sample size^2)) + (– 0.04 + 0.03), $F_{1,11} = 1010$, $P < 0.0001$; $R^2 = 0.99$; ΔAIC = - 19.8 better than a linear model without the square of sample size). c. All birds, years plotted separately, unadjusted for light stalk absence. Lines of best fit are linear (1 standard error plotted as dotted lines)

and the gradients of the two lines are highly significantly different. d. All birds, years plotted separately, adjusted for light stalk absence. Lines of best fit are linear (1 standard error plotted as dotted lines) and the gradients of the two lines are highly significantly different.

Figure 5. Breeding locations and range for Whinchats tagged in 2013 (black circular points, white fill, *n* = 12) and in 2014 (white triangular points and darker grey fill, *n* = 17). Each point is plotted at the mean of all latitudes and longitudes recorded over the least variable two-week stationary period during mid-May – mid-July (*n* = 28 locations), +/- 2 Standard Errors from the mean location are also plotted but only the highly variable locations are visible at this scale. a. All birds plotted at the 'best' estimate locations, unadjusted for light stalk absence (i.e. an enlarged version of Fig. 3). b. All birds plotted at the 'best' estimate locations, adjusted for light stalk absence. c. First-year birds plotted at the 'best' estimate locations, unadjusted for light stalk absence. d. First-year birds plotted at the 'best' estimate locations, adjusted for light stalk absence. Ranges that arose from varying the assumptions with respect to sun elevation angles (see Tables 1 and 2) are broadly similar and are illustrated in Figures S3 – S20).

Figure 1:

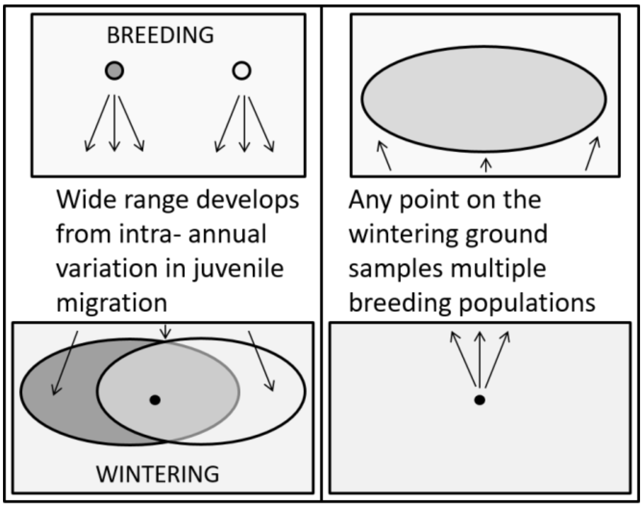


Figure 2:

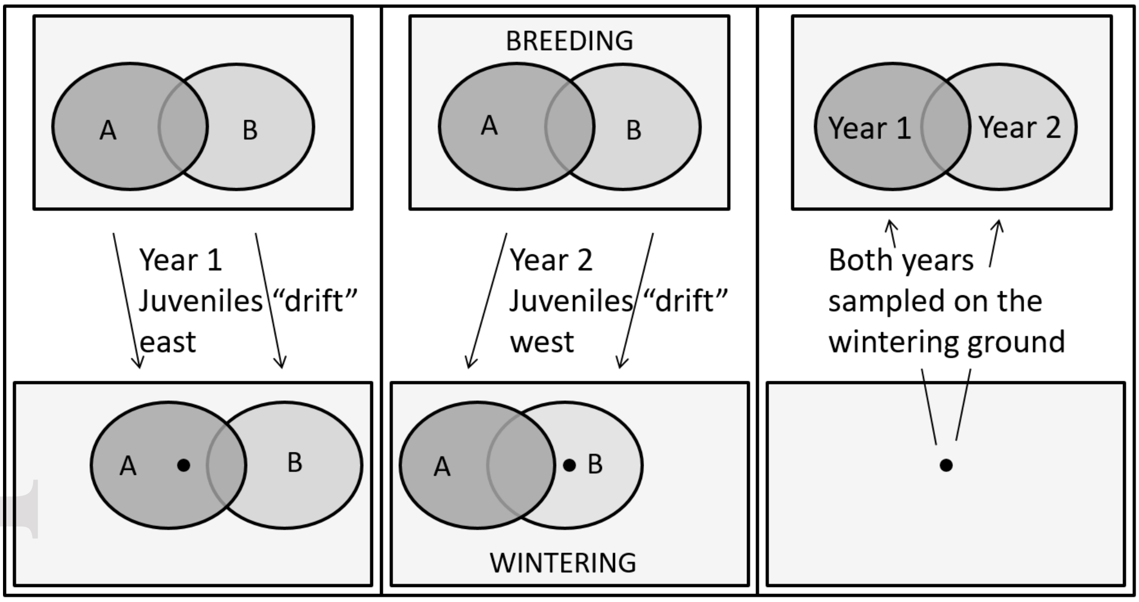


Figure 3

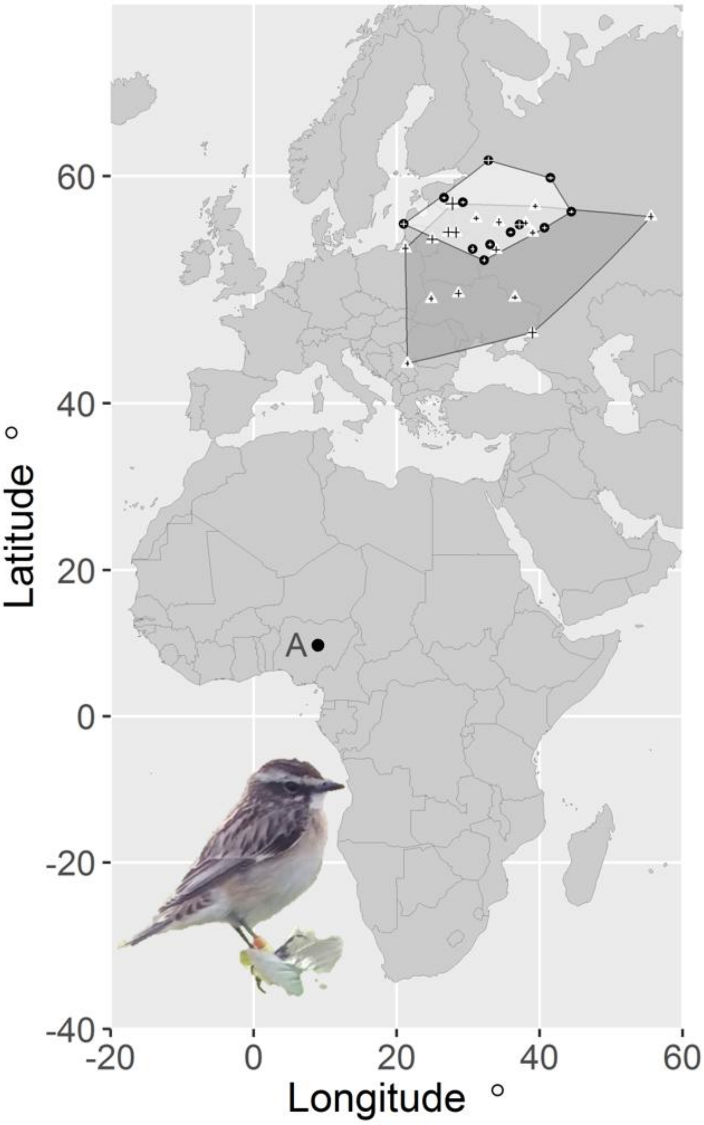


Figure 4

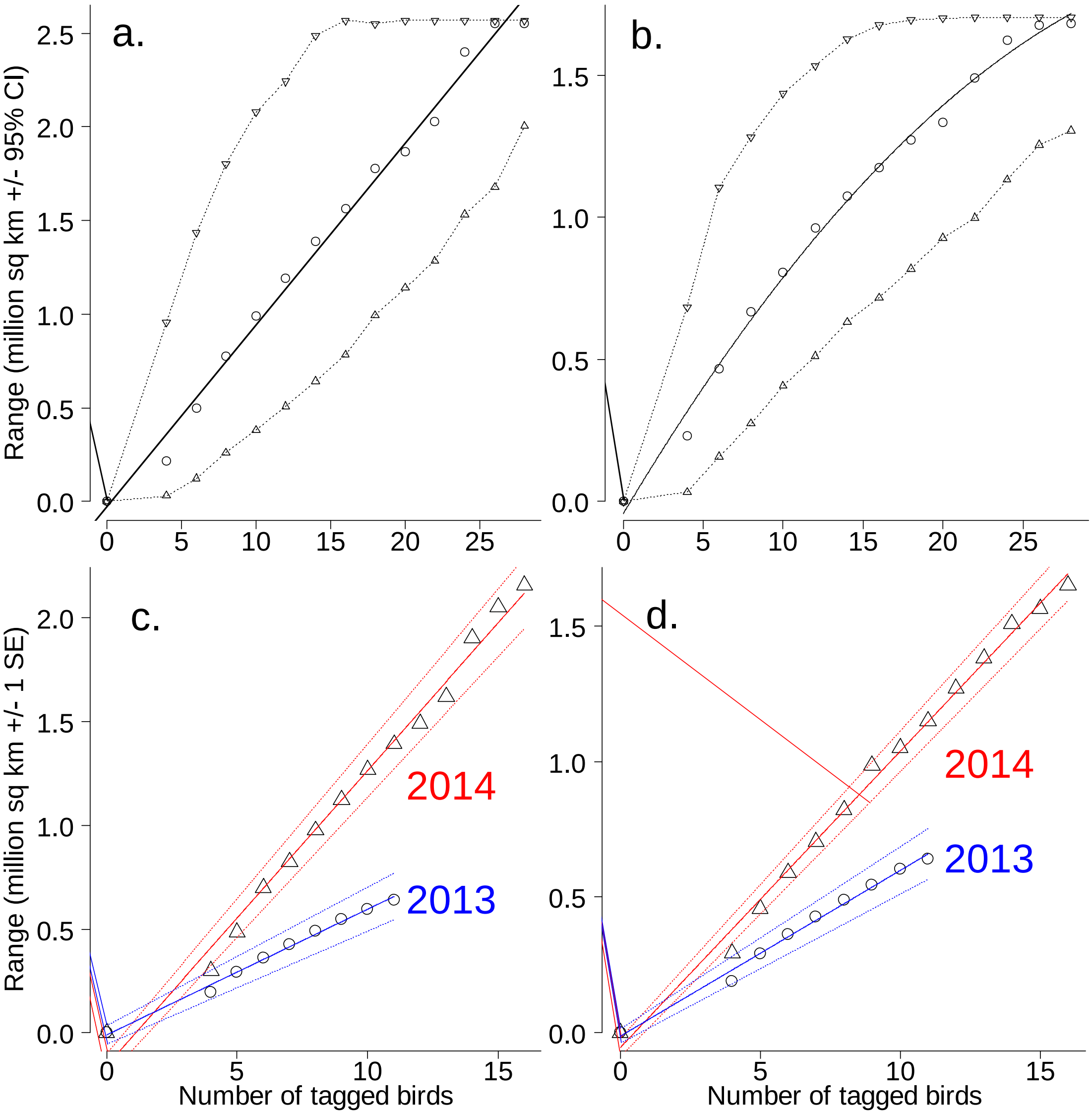
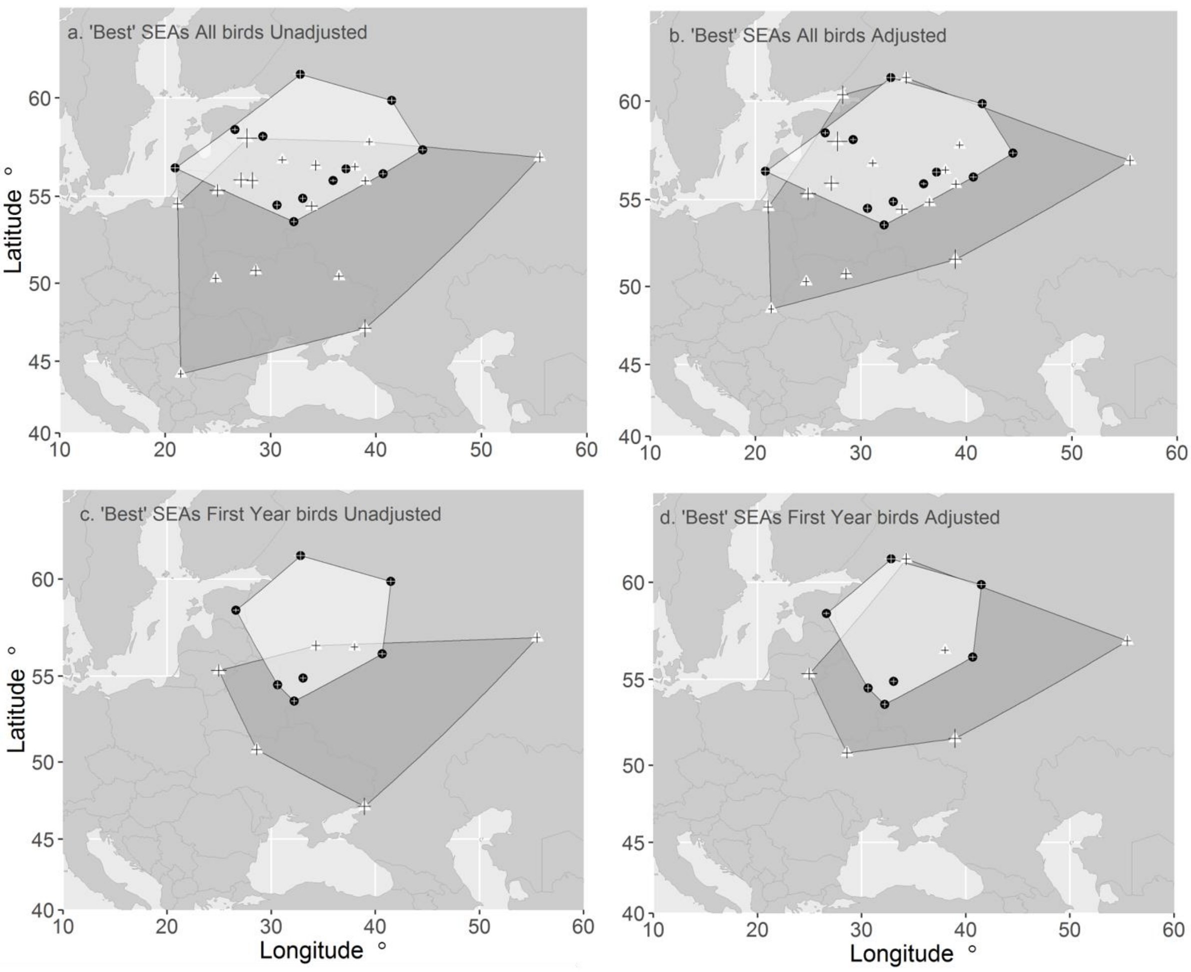

a.
b.
c.
d.
Range (million sq km +/- 95% CI)
Range (million sq km +/- 1 SE)
0.0
0.5
1.0
1.5
2.0
2.5
0
5
10
15
20
25
2014
2013
Number of tagged birds
Number of tagged birds

Figure 5


a. 'Best' SEAs All birds Unadjusted
b. 'Best' SEAs All birds Adjusted
c. 'Best' SEAs First Year birds Unadjusted
d. 'Best' SEAs First Year birds Adjusted
Latitude °
Longitude °
40
45
50
55
60
10
20
30
40
50
60