



OPEN Extreme migratory connectivity and apparent mirroring of non-breeding grounds conditions in a severely declining breeding population of an Afro-Palearctic migratory bird

Máire Kirkland¹, Nathaniel N. D. Annorbah^{2,3}, Lee Barber¹, John Black¹, Jeremy Blackburn⁴, Michael Colley⁴, Gary Clewley^{1,4}, Colin Cross⁴, Mike Drew⁵, Oliver J. L. Fox⁴, Vicky Gilson¹, Steffen Hahn^{6,11}, Chas Holt^{1,7}, Mark F. Hulme^{1,8}, John Jarjou⁴, Dembo Jatta⁴, Emmanuel Jatta⁴, Kevin Leighton¹, Ernestina Mensah-Pebi², Chris Orsman⁹, Naffie Sarr⁴, Roger Walsh⁴, Leo Zwarts¹⁰, Robert J. Fuller¹, Philip W. Atkinson¹ & Chris M. Hewson¹✉

Understanding the distribution of breeding populations of migratory animals in the non-breeding period (migratory connectivity) is important for understanding their response to environmental change. High connectivity (low non-breeding population dispersion) may lower resilience to climate change and increase vulnerability to habitat loss within their range. Very high levels of connectivity are reportedly rare, but this conclusion may be limited by methodology. Using multiple tracking methods, we demonstrate extremely high connectivity in a strongly declining, peripheral breeding population of a long-distance migrant, the Common Nightingale in the UK. Non-breeding population dispersion is lower than for previously tracked populations of this and other species and likely lower than can usually be detected by light-level geolocation, the main tracking method for small bodied species. Extremely low levels of population mixing were also detected, so any impacts on this population on the non-breeding grounds are unlikely to be shared with more distant breeding populations, corresponding to the observed patterns of European population change. According to a species distribution model using independent field data, this population's non-breeding grounds had lower suitability than others and likely declined before the period we were able to assess. These results support hypotheses that climatic and habitat-related deterioration of non-breeding grounds contributes to population declines in peripheral and high-connectivity breeding populations of long-distance migrants, including the one studied here.

Keywords Migratory connectivity, Migratory networks, Habitat suitability, Population decline, Afro-Palearctic migrants, Non-breeding grounds

¹British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK. ²Ghana Wildlife Society, Accra Conservation Education Centre, Independence Avenue, 078-8918 Ridge, Ghana. ³School of Natural and Environmental Sciences, University of Environment and Sustainable Development, Yilo Krobo, Ghana. ⁴Kartong Bird Observatory, Kartong, Kombo South, The Gambia. ⁵Anglian Water Services Limited, Lancaster House, Lancaster Way, Ermine Business Park, Huntingdon, Cambridgeshire PE29 6XU, UK. ⁶Swiss Ornithological Institute, Seerose 2, 6204 Sempach, Switzerland. ⁷Adonis Blue Environmental Consultants, Kent Wildlife Trust Group, Tyland Barn, Chatham Road, Maidstone, Kent ME14 3BD, UK. ⁸University of the West Indies, St Augustine, Trinidad and Tobago. ⁹Royal Society for the Protection of Birds, The Lodge, Sandy, Beds SG19 2DL, UK. ¹⁰Altenburg and Wymenga Ecological Consultants, Suderwei 2, 9269 TZ Feanwâlden, The Netherlands. ¹¹Lab of Ornithology, Institute of Biology, University of Latvia, Jelgavas Street 1, 1004 Riga, Latvia. ✉email: chris.hewson@bto.org

Migratory connectivity, defined as the link between breeding and non-breeding populations of migratory species such as birds, is a key factor determining the responses of populations to environmental change experienced through their annual cycles^{1–3}. Migratory networks, which are composite patterns of migratory connectivity across populations, determine which populations are impacted by local changes and how populations interact with one another, potentially regulating breeding populations at wider scales¹. Understanding the extent of migratory connectivity, its variability within and between species and the limits of its detection using commonly used methods, is therefore critical in understanding population declines⁴ and effectively planning conservation action at flyway scales⁵.

Since migratory connectivity determines the link between environmental change on the non-breeding grounds and population impacts on the breeding grounds, the degree of connectivity has been hypothesised to have causal relationships to population changes, as usually measured on the breeding grounds^{2,3}. High connectivity is defined as limited population dispersion, i.e. small average inter-individual distances in the non-breeding season. Such species or populations may be less able to respond to changes in environmental conditions that vary at a large scale, such as changing climate influencing the distribution of suitable habitat, as non-breeding dispersal⁶ is likely to be low and the close proximity of different individuals means there will be little variation in the conditions they experience⁷. In contrast, high connectivity populations have been considered to be more resilient to widespread, patchy habitat loss^{2,3} due to the increased chances that this occurred outside their non-breeding range. Where this last condition is not met, however, they will be vulnerable to both widespread habitat shifts and localised habitat loss.

Non-breeding environmental change may be especially likely to produce a detectable impact on specific breeding populations when breeding populations have low non-breeding dispersion and non-breeding areas do not overlap with those of other populations^{4,8}. Low connectivity is, however, considered to be common³, although the extent to which this is due to methodological constraints has not been widely considered. For instance, smaller-bodied species have so far been tracked mostly using light-level geolocation. Calibration errors may produce significant latitudinal offsets in light-level geolocation, especially in species for which variable shading of light sensors can be expected based on intermittent occupation of shaded microhabitats⁹, such as the Common Nightingale *Luscinia megarhynchos* (hereafter Nightingale)¹⁰. If, however, low connectivity is indeed common, it potentially reduces our ability to detect impacts of non-breeding conditions on populations¹¹, which may be spread widely across different breeding populations.

Migratory connectivity is often measured by the extent to which the distributions of breeding populations overlap in the non-breeding period, but this is sensitive to the spatial distribution of sites at which migratory behaviour is sampled^{8,12}, with, in general, less non-breeding overlap expected between more distant breeding populations. An alternative is to examine population dispersion of individuals in the non-breeding period^{3,8}. Both connectivity measures may be influenced by the error inherent in tracking methods, such as light-level geolocation⁹, which reduces the ability to detect high connectivity, as described above¹³.

Here, we use population level dispersion, as estimated by light-level geolocation, as our primary measure to assess migratory connectivity for a population of a long-distance migrant which has undergone severe decline, the Nightingale in the UK. We then assess the extent to which errors may be influential in our estimation using multiple sources of evidence¹³, including complementary tracking at the estimated non-breeding grounds of both our focal population and, as a control, two other previously tracked populations from eastern France and Italy¹⁴. The precise non-breeding distribution of the Nightingale, and hence the range within which locations can be expected, has not previously been well documented. Hence, we created a species distribution model (SDM) from independent presence-absence survey data (see methods) to provide a habitat suitability mask against which the observed distribution of estimated locations could be compared, and then use this to assess habitat suitability for this and previously tracked populations.

Tracking from the non-breeding grounds allows us to examine the migratory network in which the target population is embedded with reduced sampling bias⁸, as well as providing independent corroboration of estimated non-breeding areas. Although this approach has rarely been carried out, there are exceptions, including Whinchats *Saxicola rubetra* in Nigeria¹⁵ and reciprocal tracking to strengthen inference about connections between breeding and non-breeding populations and migratory networks in Wood Thrushes *Hylocichla mustelina*¹⁶. We leverage additional inference from ringing recoveries, which provide highly spatio-temporally accurate but limited connections between capture locations. Ringing recoveries are subject to biases in recovery rates that limit inferences between populations but can provide important information to supplement data from more indirect sources such as light-level geolocators¹⁷. Finally, we use a small sample of archival GPS tags deployed on the breeding and non-breeding grounds, which provide highly spatially accurate information independent of many of the recovery biases associated with ringing. All forms of tracking using archival devices may, however, still be subject to biases arising from differential survival, for example of birds using different migration routes¹⁸ or occupying non-breeding grounds or habitats of differing quality.

The Nightingale is a small territorial songbird with a small breeding population in the UK compared to adjacent countries¹⁹ at around 5–6,000 territorial males²⁰. It is restricted to southeast England, at the north-western fringe of the global range²¹. It has declined by 90% between 1967 and 2022²² with some range contraction towards the core of the range in the southeast^{23–25}. This contrasts with generally favorable status across most of Europe¹⁹, although there is evidence from countries adjacent to the UK of a long-term decline (but short-term stability) in Belgium and, briefly, a short-term decline in France¹⁹, which has now reversed²⁶. There has also been limited range loss at the northwestern end of the range in France adjacent to the UK²¹. The UK decline has been attributed in part to loss and degradation of the dense understorey and scrub habitat that it depends on²⁷. However, the presence of empty suitable habitat²⁸ and population contraction towards the core of the range²⁵ suggest a possible role for wider scale factors such as climate change or changes in the non-breeding areas²⁷. Population decline and range contractions at the northwestern edge of the species range are, however, counter

to predictions based on the direct influence of breeding grounds climate change^{25,29}, despite climate being the major driver of the species' distribution²¹. Although indirect effects of climate change may have contributed to habitat degradation for the species via increased deer browsing and grazing^{30,31}, there is no evidence that breeding grounds climate has driven the declines³². Whilst the UK deer population differs from adjacent continental Europe due to the presence of the invasive Reeve's Muntjac (*Muntiacus reevesi*), deer populations have also increased substantially in France in recent decades³³, further suggesting that conditions elsewhere may be responsible for the decline of the Nightingale. By assessing the degree of connectivity of, and non-breeding habitat suitability for the UK population, we aim to provide further assessment of whether limitation in the non-breeding period is likely to be playing a role in the population decline.

Results

Location of non-breeding grounds of UK-tagged Nightingales

We estimated 32 primary non-breeding locations (the first stationary locations occupied south of the Sahara) and midwinter non-breeding locations (the locations occupied on 31st December) for 26 individual Nightingales tagged with geolocators in the UK (four birds were tracked twice and one was tracked three times). All were in a small area of West Africa, mostly on or near the coast, concentrated in Senegal, The Gambia and Guinea Bissau (Fig. 1a). In total, they spread between northern Sierra Leone and southern Mauritania, at the northern limit of suitable habitat according to our SDM (Fig. 1b). Comparing these locations to those from France, Italy and Bulgaria in a previous study¹⁴, the estimated initial and midwinter non-breeding locations of UK-tagged birds are to the northwest of, and did not overlap with, the non-breeding locations of birds tracked from eastern France and thus the spatial relationships between the four breeding populations were maintained (Mantel correlation 0.907, $P < 0.001$, $n = 42$).

Dispersion of UK-tagged Nightingales during the non-breeding period

The estimated population dispersion (mean inter-individual distance for initial non-breeding locations) of UK-tagged Nightingales was 268.5 km. After correcting for sample size (see Methods) it was 369.7 km, which was lower than for any of the 98 populations of 45 species reported by Finch et al.³. For the population with the next lowest population dispersion (Wood Thrush breeding in Pennsylvania, USA) sample size corrected dispersion was 355.9 km according to data in Finch et al.³, but there was no difference in the raw inter-individual distances between these two populations (Mann–Whitney U $W = 38,724$, $P = 0.360$). The Afro-Palearctic migrant population with the smallest population dispersion was for Black Kites breeding in Spain, for which the population dispersion was 387.1 km, according to data in Finch et al.³.

Amongst the UK-breeding Nightingale population and the French, Italian and Bulgarian populations reported in Hahn et al.¹⁴, the mid-winter inter-individual distances (see Methods; Supplementary Table S1) differed significantly, both when including a potential outlier in the Bulgarian population (Kruskal–Wallis $H_{3,475} = 85.75$, $P < 0.001$) and when excluding it (Kruskal–Wallis $H_{3,439} = 67.36$, $P < 0.001$). Pairwise comparisons indicated that individual distances were significantly lower for the UK Nightingale population than for the other three populations, despite its larger sample size (Dunn's test adjusted $P \leq 0.004$, Supplementary Fig. S2), with no differences between the other three populations (adjusted $P \geq 0.122$).

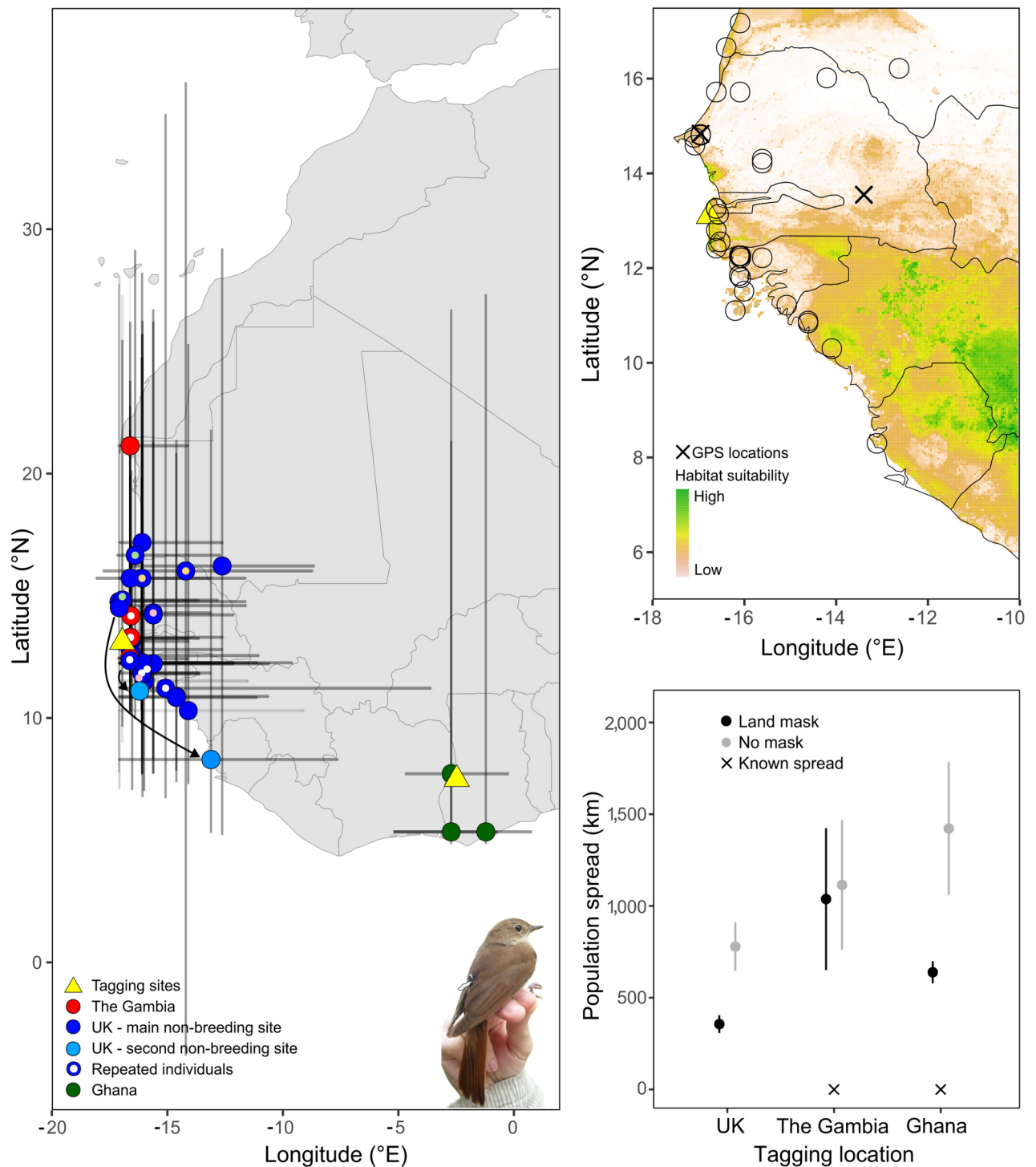
The actual dispersion of UK Nightingales in the non-breeding period may be even lower than our estimates suggest. There was no significant difference between the raw inter-individual distances of UK-tagged birds in the non-breeding grounds and the estimated inter-individual distances of Nightingales tagged in The Gambia or at the control site in Ghana (Supplementary Table 1), for which known dispersion was close to zero. This was true for the initial non-breeding sites (Kruskal–Wallis $H_{2,356} = 2.02$, $P = 0.364$) and the mid-winter sites (Kruskal–Wallis $H_{2,330} = 0.429$, $P = 0.513$). Furthermore, after application of a land mask (which restricts estimated locations to land and prevents them from being positioned in the sea), the sample size-corrected population dispersion estimates for UK birds were lower than the others (Fig. 1c, Supplementary Table S1). Together, these results indicate that the observed level of non-breeding dispersion for UK birds is at or below the lower limit detectable using these methods on this species. The greatest dispersion was for Ghana without a land mask (Fig. 1c, Supplementary Table S1), likely due to the shallower daylength gradient around this site due to its lower latitude.

Breeding grounds of Nightingales tagged in The Gambia and Ghana

Six estimated breeding locations for four individual Nightingales tagged with geolocators in The Gambia all fell in the UK and northern France except for one which fell in north central France (Fig. 2a). Several lines of evidence suggest, however, that all the Nightingales found in The Gambia are likely from the UK breeding population:

First, the distribution of all but one of these estimated breeding locations for birds tagged in The Gambia fall within the range of the ten estimated breeding locations of Nightingales tagged at four sites in the UK (Fig. 2a). The single outlier, which fell in north-central France, was one of three breeding location estimates for this bird in different years and their average falls within the range of locations estimated for the known UK breeders. This likely indicates its breeding location more accurately given the species' known high breeding site fidelity³⁴. Furthermore, the longitude of the estimated breeding locations of Gambia-tagged birds, which is calibration-independent and can be estimated more accurately than latitude⁹, closely matches the main concentrations of the species' UK breeding distribution.

Second, the estimated population dispersion at the breeding grounds of birds tagged in The Gambia was almost identical to the dispersion of UK-tagged birds in the breeding season estimated from geocator data (see below and Fig. 2c), for which known population dispersion was 91 km, indicating that they are likely restricted to a similarly small area.



Third, both birds tracked with archival GPS tags from The Gambia bred in southern England (Fig. 2a). These tracks show the precise location and extent of their breeding home range and provide certainty about breeding location.

Last, 110 individual Nightingales captured at Kartong Bird Observatory (KBO) in The Gambia included four that had previously been ringed in England, whilst two ringed in The Gambia were subsequently recaptured in southern England, 303 km apart (Fig. 2b). Although ringing recoveries suffer from multiple biases, there have been no exchanges between The Gambia (or any other country in tropical Africa) and European countries adjacent to the UK, despite the larger number of Nightingales ringed in those countries (Fig. 2b)³⁵. The only other exchanges of ringed Nightingales between the European breeding and African non-breeding grounds are three exchanges between Italy and Ghana (two) and Togo (one)³⁶.

These results strongly indicate that the overwhelming majority of Nightingales found in The Gambia during the non-breeding residency period are from the UK breeding population, although we cannot rule out the

◀ **Fig. 1.** (a) Estimated non-breeding locations ($n = 32$) of 26 Nightingales fitted with geolocators in the UK between 2009 and 2017 (dark blue circles = primary sites, light blue circles = sites occupied at midwinter where different, repeated tracks for individuals indicated by centre colours), compared with six estimated non-breeding locations of four birds fitted with geolocators in The Gambia (red circles) at one site, KBO (see Methods) (yellow triangle). Bars show 95% confidence intervals of location estimates. See Supplementary Fig. 3a for locations without application of the land mask; (b) Estimated non-breeding locations for UK-tagged Nightingales (open circles) overlaid onto a habitat suitability map derived from an SDM based on independent survey data (see Methods), indicating their relative position within the non-breeding range. Two initial non-breeding locations from GPS tags are also shown (crosses) (See Methods); (c) Comparison of population dispersion at non-breeding grounds (mean distance between pairs of estimated locations, corrected for sample size) of Nightingales tagged with geolocators in the UK ($n = 26$), The Gambia ($n = 4$) and Ghana ($n = 3$). Bars show 84% confidence intervals, so non-overlap indicates significance at $P < 0.05$ ⁷. Population dispersion for UK birds is based on the first or sole wintering location. Known dispersion at African tagging locations was close to 0 and is indicated by a cross. Differences between known dispersion and observed dispersion can be attributed to error in light-level geolocation estimation of sites. Estimates are shown with and without the application of a land mask, demonstrating the impact that proximity to a coast has on dispersion estimates, which is considerable for birds tagged in the UK and Ghana (see Supplementary Fig. S3).

possibility that a small number may breed in northern France (see below for further details of migratory network in The Gambia).

Breeding grounds population dispersion of Nightingales tagged in The Gambia and Ghana

The breeding grounds population dispersion of birds tagged with geolocators during the non-breeding period was extremely similar to that for estimated breeding locations of birds tagged in the UK (which had a known population dispersion of 91 km) (Fig. 2c, Supplementary Table S1). This was much lower than the population dispersion of birds tagged with geolocators at the control location in Ghana (Fig. 2c) whose population dispersion was 1,162.8 km and 1,127.0 km greater, respectively, after correcting for sample size, than that of those tagged in The Gambia and the UK (difference across populations: Kruskal–Wallis $H_{2,53} = 11.98$, $P = 0.003$; difference between Ghana and The Gambia ($z = -3.46$, adjusted $P = 0.002$ and UK tagged birds ($z = -2.71$, adjusted $P = 0.010$).

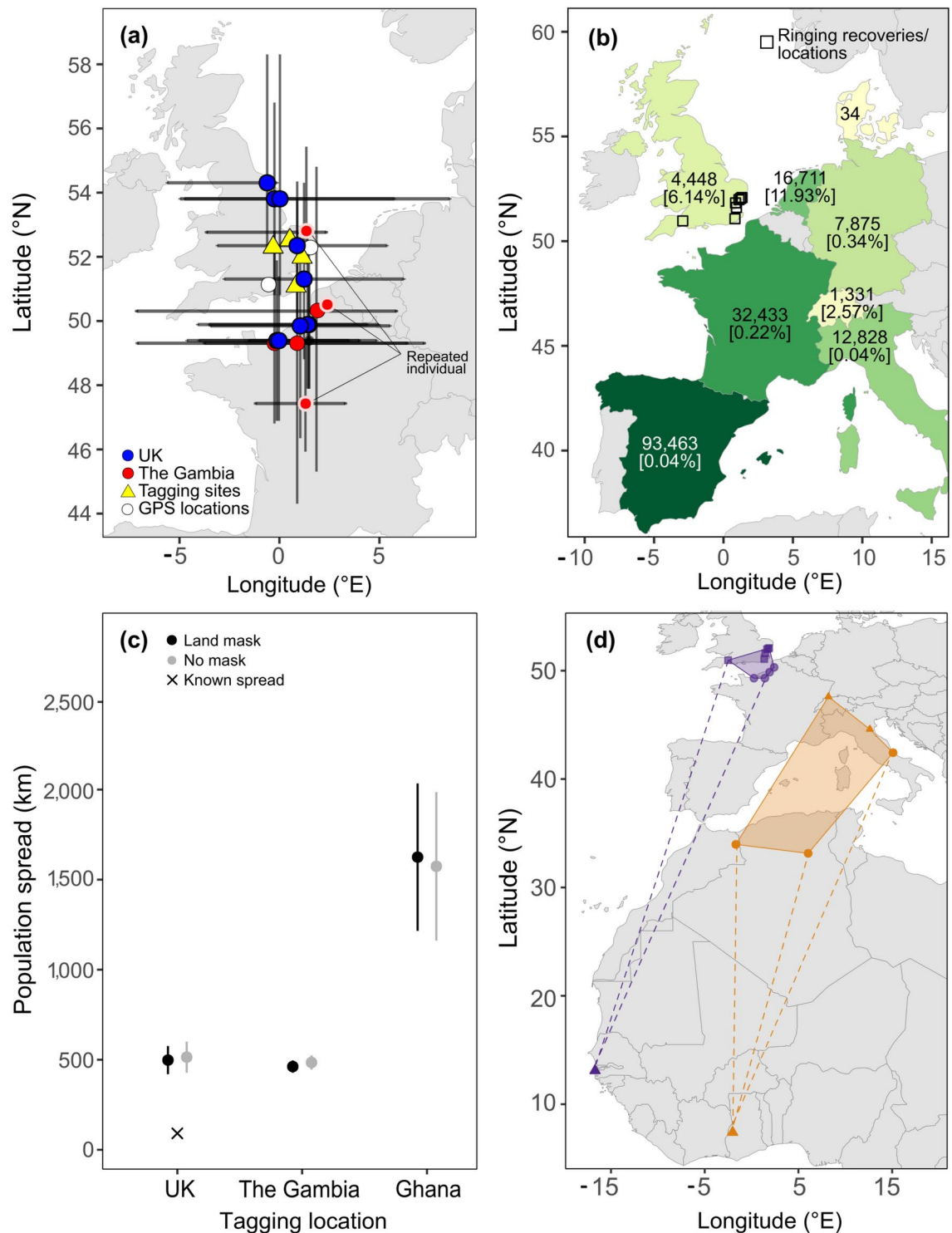
Migratory networks of Nightingales in The Gambia and Ghana

To assess the minimum migratory networks at the two sites where tagging was carried out in the non-breeding grounds, we combined information from all available sources, including the previous tracking study by Hahn et al.¹⁴. Using an average location for the repeatedly tracked individual, the breeding locations of four birds tagged in The Gambia with geolocators and two birds tracked with GPS tags were all in the UK and northern France (and are consistent with all being in the UK). The breeding locations of birds tracked from The Gambia should be proportional to their abundance in that non-breeding population, so these results provide good evidence of the constituency of that non-breeding population. Additionally, six ringing exchanges between The Gambia and the breeding grounds from 110 birds trapped at KBO since 2001 were all with the UK. The rate of exchange with each country will depend on their proportion in the non-breeding population in The Gambia and the proportion of birds that are trapped in the breeding country (see Fig. 2b and see Methods for explanation). These results are therefore consistent with the non-breeding population in The Gambia consisting only of birds from the UK, as is the overall high rate of ringing exchanges. Due to the low proportion of birds trapped in France and Spain (Fig. 2b), however, few exchanges would be expected with those countries, so these results do not exclude the possibility of the presence of a small number of birds from these countries.

The breeding locations of birds tracked from Ghana were in Italy, Morocco and Algeria. Additionally, the tagging location there is within the overlap zone of the non-breeding locations of birds previously tracked from northern Italy and eastern France¹⁴ (Fig. 2d). The total area of land encompassed by the 100% minimum convex polygon of birds present in the non-breeding period in The Gambia is 43,031 km², compared to 501,909 km² for the Ghanaian population (Fig. 2d). The observed migratory network in Ghana is therefore considerably more complex than that in The Gambia, creating a much more diffuse link between breeding and wintering grounds and demonstrating that there can be considerable intra-specific variation in migratory networks.

Habitat suitability at non-breeding grounds across Nightingale populations

Based on independent presence/absence field survey data collated from various sources, we created a habitat suitability coverage using an SDM (see Methods). Evaluation metrics indicated good model performance: mean area under the receiver operator curve and true skill statistic were 0.920 and 0.671, respectively³⁷. The most important variables (Fig. 3d) were related to vegetation state at the height of the dry season (minimum NDVI), as well as elevation, drought severity (PDSI), those related to the amount of precipitation in the rainy season and maximum ambient temperature. This fits with prior knowledge of Nightingale distribution, i.e. that they occupy humid savanna ecosystems, reaching highest densities in the transition zone between the Guinea savanna and forest zones (see e.g. Dowsett & Dowsett³⁸). Based on knowledge of recent occurrence patterns, there may be some over-prediction in the north of the range, although it is possible that change in habitat structure have decoupled climatic and habitat-related suitability in recent decades (see Discussion). Surprisingly, no land cover variables were included amongst the most important variables, the most important being mosaic natural vegetation, which had a mean decrease in accuracy of 11.9%, with the other four being the least important



variables of all, with mean decrease in accuracy well below 10% (Supplementary Fig. S4). Land cover variables may not have been very informative because whilst they are indicators of presence of natural habitat, they are not necessarily informative about the specific habitat structures selected by Nightingales. These include low bushy vegetation intermixed with grass and residual trees, which may be found in various landcovers but may not necessarily be present in significant amounts in any of them.

The suitability of non-breeding locations for birds tagged in the UK was lower than for birds from both the French and Italian breeding populations in both 2001 and 2020 (Table 1, Fig. 3a,c). The average suitability for the UK population was $65.0 \pm 9.8\%$ lower than for the French and $64.6 \pm 18.5\%$ than the Italian population by 2020, whilst the peak suitability was considerably lower for the UK population compared to the other populations (Fig. 3c). Repeating the analysis excluding locations that contained no suitable habitat within a 100 km buffer yielded very similar results (Supplementary Table S2).

Fig. 2. (a) Estimated breeding locations ($n = 6$) of four Nightingales fitted with geolocators in The Gambia during the non-breeding periods of 2018–19 and 2019–20 (red circles, repeated tracks for individuals indicated by pale pink outline) compared with ten estimated breeding locations of ten birds fitted with geolocators during the breeding season (blue circles) at four sites in the UK (yellow triangles). Bars show 95% confidence intervals of location estimates. Two breeding locations of birds tagged in The Gambia with archival GPS tags are also shown (white circles); (b) The UK locations of six birds involved in ringing exchanges between KBO (The Gambia) and the UK. Countries in the background map are coloured from light to dark green by increasing national ringing totals between 2000 and 2022 (see Methods), indicated by the numbers plotted on each country. The figures inside the square brackets represent average annual ringing totals as a percentage of breeding population size (see Methods). Countries coloured in grey have no available data; (c) Comparison of population dispersion at breeding grounds (mean inter-individual distances, corrected for sample size) of Nightingales tagged with geolocators in the UK ($n = 10$), The Gambia ($n = 4$) and Ghana ($n = 3$). Bars show 84% confidence intervals, so non-overlap indicates significance at $P < 0.05$ ⁷. Known dispersion at UK breeding locations is c.91 km and is indicated by a cross. Differences between known dispersion and observed dispersion can be attributed to error in light-level geolocation. Estimates are shown with and without the application of a land mask, demonstrating the impact of proximity to coast on dispersion estimates, which is small in this instance (see Supplementary Fig. S3); (d) Source breeding populations of Nightingales found in the non-breeding period at sites in The Gambia (KBO) and Ghana (Nsuaatre). Polygons are 100% minimum convex polygons around breeding sites derived from geolocator data (circles; using an average location for one bird with three estimated breeding locations), combined with UK capture locations of birds involved in ringing exchanges with KBO and breeding locations of two birds fitted with archival GPS tags there (both squares), plus breeding grounds tagging locations of populations in Italy and France whose non-breeding range overlapped the site in Ghana¹⁴ (triangles).

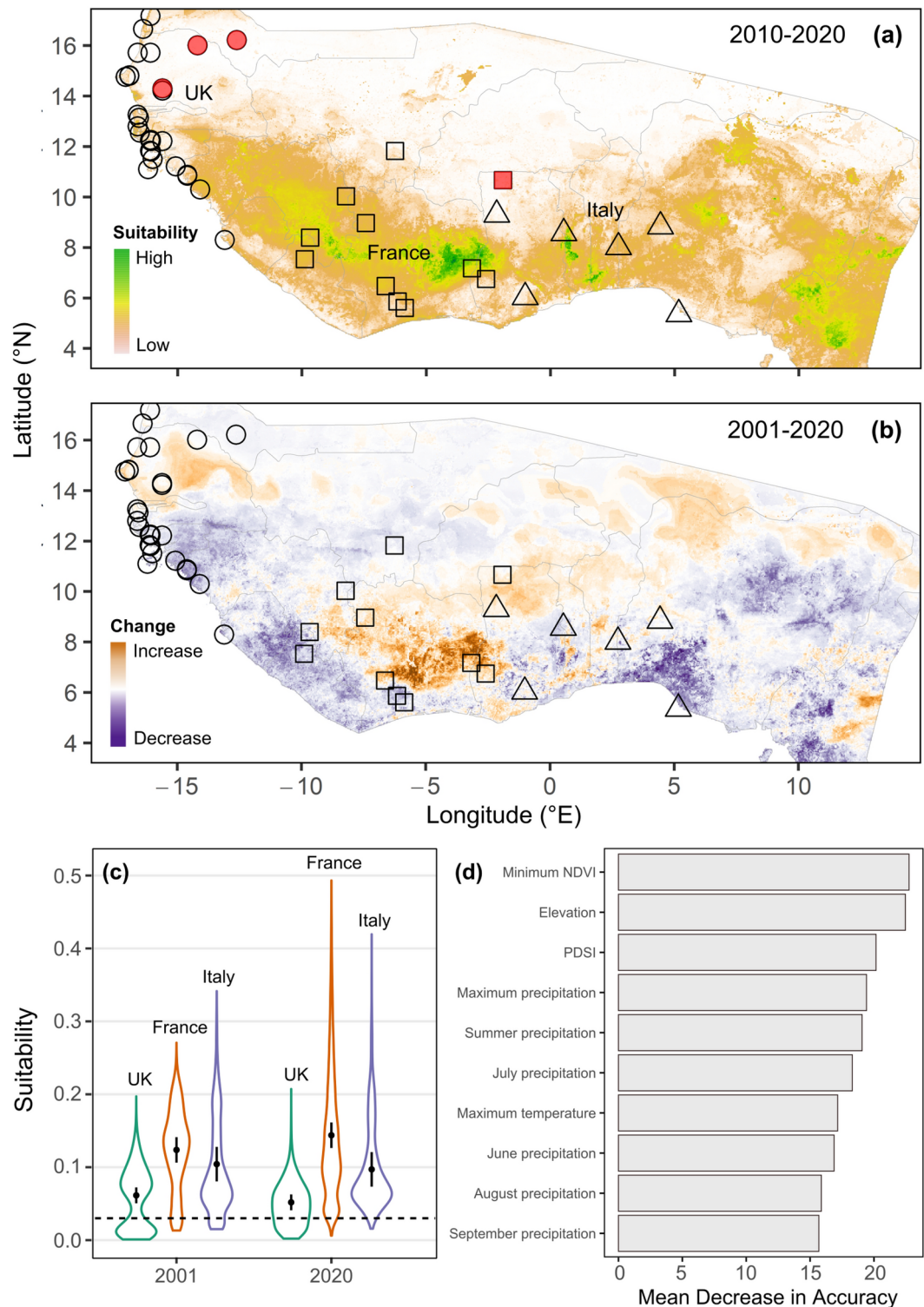
Between 2001 and 2020, there was no change in habitat suitability across the entire region but there was some evidence of an increase in habitat suitability for the French population when including all data (Table 1, Fig. 3b) and of a decrease for the UK population when excluding unsuitable locations (Fig. 3b, Supplementary Table S2). For the UK, this is despite an increase in suitability in the north of the non-breeding area (Fig. 3b), likely due to amelioration of drought conditions which persisted in that area from the late 1960 through to the end of the twentieth century³⁹, which has to some extent offset decreases in habitat suitability in the core non-breeding area further south.

Discussion

Our results demonstrate an extremely tight connection between a strongly declining Nightingale population at the northwestern extremity of the breeding range, in the UK, and the northwestern extremity of the non-breeding range in coastal West Africa (in Senegal, The Gambia and Guinea Bissau). The level of non-breeding dispersion observed for this breeding population is amongst the lowest so far documented in any tracking study of birds and it is clearly lower than for previously tracked breeding populations of the Nightingale, which spend the non-breeding season further east. Our UK-tagged sample contains only male Nightingales, compared to both sexes in the other samples, which could potentially reduce variation in non-breeding locations. Sex differences in connectivity have not, however, been previously studied in long-distance migrant land birds. On the other hand, our sample of non-breeding locations is larger than the other studies and was collected across multiple years, with more scope for between-year environmental effects impacting locations, so they should be highly representative of overall non-breeding distribution. As observed dispersion was equivalent to the level of observed locational error for this species using light-level geolocation, the true level of dispersion may be even lower than we have estimated.

Reciprocal results tracking birds from the core of the identified non-breeding area strongly suggested that at least most of the birds present at this nonbreeding location are from the UK breeding population. Thus, the migratory network into which this breeding population is embedded during the non-breeding period appears to be extremely simple. This contrasts with the much more complex population structure identified from tracking results at a control site further east in Ghana, for which the identified source breeding area is more than ten times larger. This greater level of breeding dispersion from a single non-breeding location may be more common in general, based on the few connectivity studies that tagged long-distance migrants on the non-breeding grounds^{15,16}. Hence, the UK breeding population is not only extremely tightly clustered but also appears to be unusually completely separated from other breeding populations in the non-breeding grounds. Additional tracking from The Gambia and potentially the breeding populations in western France and Iberia are necessary to precisely quantify this. According to theory^{2,3}, low non-breeding dispersion leaves this population unable to adjust to changing climatic conditions, and vulnerable to even small amounts of habitat loss in the non-breeding area, whilst the limited population mixing means the impacts of non-breeding conditions can be detected specifically within this breeding population¹¹. In contrast, impacts of non-breeding conditions at the control site in Ghana would be less detectable, being spread out amongst breeding populations.

Habitat suitability of the non-breeding grounds was lower than for previously tracked populations of the species breeding in France and Italy and has recently declined in its core. Much of the huge population decline of the Nightingale in the UK, which began in the late 1960s^{22,40} had occurred by the early twenty-first century²² and thus largely predates both our main tracking period (2009–2020) and the period for which we were able to assess habitat suitability (2000–2020). Hence, we cannot be sure whether the size and habitat suitability of the non-breeding range has changed during the main period of population decline. Additionally, as we use archival



tracking only, it is possible that birds that did not return to the tagging areas may have used poorer quality non-breeding areas and/or habitats, so we may be over-estimating habitat quality for the UK (and potentially other) breeding populations.

Based on climatic relationships and known patterns of climate and habitat change, the current non-breeding range may be a relic of a larger previous range spreading to the north and possibly east. Densities in the non-breeding range must otherwise have been an order of magnitude higher at the start of the decline, likely requiring suitability to have been higher overall. It is notable that the decline in the UK began at the same time as that of many species which wintered in the arid Sahel zone further north, as well as some other species occupying more humid habitats⁴⁰. Although habitat suitability is declining in the south of the non-breeding range of the UK population, there was an increase in the north between 2000 and 2020, reflecting amelioration of the drought conditions that were present from the 1960s to the late twentieth century³⁹. The recent increases in apparent

◀**Fig. 3.** Habitat suitability for Nightingales in West Africa based on weighted averages of four random forest models. **(a)** Mean predicted suitability between 2010 and 2020. **(b)** Change in suitability between 2001 and 2020. Geolocator-derived non-breeding locations occupied at mid-winter for birds breeding in the UK (circles), France (squares) and Italy (triangles) are shown. Geolocator locations whose 100 km buffers do not encompass any suitable habitat (as determined by the mean threshold that maximised TSS) and therefore potentially reflect calibration errors resulting in inaccurate latitudes, are shown in red in **(a)**. **(c)** Distribution of suitability values within non-breeding location buffers for 2001 and 2020, the width of the shape corresponding with the frequency of data points at each value. Points indicate the mean with 84% confidence intervals (nonoverlapping confidence intervals significantly different at $P=0.05$)⁷. The dashed line indicates the threshold used to determine suitable habitat. **(d)** Mean Decrease in Accuracy⁶⁹ for the top ten variables determining suitability based on 40 random forests (see Methods). Climate variables are the averages between 2001 and 2020, apart from annual accumulated precipitation and the Palmer Drought Severity Index (PDSI), which were extracted for the year associated with the record. Values for the precipitation variables refer to the quadratic term.

Country	β	SE	P
Difference between years	− 0.002	0.006	0.644
Pairwise differences between years			
UK	− .010	0.007	0.163
France	0.020	0.012	0.087
Italy	− 0.007	0.016	0.648
Pairwise differences between countries			
2001			
UK–France	− 0.062	0.014	0.001
UK–Italy	− 0.043	0.018	0.051
France–Italy	0.020	0.020	0.602
2020			
UK–France	− 0.092	0.014	<0.001
UK–Italy	− 0.045	0.018	0.037
France–Italy	0.047	0.020	0.061

Table 1. Pairwise comparison of habitat suitability at the non-breeding grounds for three breeding populations of Nightingales in 2001 and 2020. Differences $P<0.05$ are shown in bold, differences at $P<0.1$ are shown in italics. Sample sizes were based on number of individuals per population.

suitability across much of Senegal according to our climatically-dominated SDM may, however, not have been realised on the ground due to on-going habitat degradation by a rapidly increasing human population⁴¹. Formerly, Nightingales may have occupied the most mesic habitats further north (e.g. adjacent to watercourses or lakes and floods etc.), but habitat degradation due to overgrazing and collection of firewood, exacerbated by drought, has likely reduced availability of suitable habitat structures within these regions⁴¹.

These results support the suggestion that historical deterioration of climatic conditions at the northwestern non-breeding range extremity is a contributory factor in the severe population declines and range contractions that have been observed at the northwestern extremity of the breeding range but largely not elsewhere¹⁹. This is consistent with the earlier finding that low abundance, peripheral populations of the Wood Thrush, a Neotropical migratory songbird that is broadly ecologically similar to the Nightingale, were more strongly linked to non-breeding climate than were core populations⁴². The same study demonstrated that multiple drivers are often important in determining breeding populations, which is also consistent with the observation of empty, apparently suitable habitat at the range periphery in the UK²⁸.

Demonstration of high migratory connectivity for a strongly declining Nightingale population is counter to a previous finding that in general, Afro-Palearctic migrant species with low non-breeding population dispersion had more positive population trends than species with high dispersion². This was attributed to high dispersion species being more vulnerable to widespread and uneven non-breeding grounds habitat loss than low dispersion species, due to increased chances of some individuals being impacted². Low dispersion populations may, however, be severely impacted by even a very small amount of localized habitat loss that occurred within their range especially if, for instance, the population is highly clustered at the site level and high-quality habitat is restricted. Whilst climatic factors were much more important than land cover in determining habitat suitability in our SDM, land cover variables likely do not identify the specific habitat structures that are important for Nightingales, which may be very specific for Afro-Palearctic migrants during the non-breeding season^{43,44}.

It has been suggested that non-breeding land availability impacts connectivity³. In the case of the UK Nightingale population, availability of suitable habitat is restricted by the shape of the West African continent and rainfall patterns. The non-breeding area is bounded by the Atlantic Ocean to the west and south, and more arid lands to the north and north-east. The population occupies the northwestern extremity of the humid

wooded savannas within the continent, with more suitable habitat for the species lying in the forest-savanna transition zone³⁸ to the southeast (Fig. 2a). Steep rainfall gradients in this area increase the proximity of habitat that is unsuitable due to both aridity (Sudan savanna and Sahel) and high rainfall (closed-canopy forest). Hence, suitable habitat is highly restricted in the area occupied. The distribution of other populations may also restrict habitat availability, as our results demonstrate that further into the range there are more complex migratory networks where competition is likely intense, especially given the much larger breeding populations in Spain and France¹⁹.

Inaccurate calibration in light-level geolocation due to shading⁹ may produce significant locational errors, even when using methods specifically designed for heavily shaded data⁴⁵. The low non-breeding dispersion for UK birds compared to birds tagged in The Gambia and Ghana (which had known dispersion close to zero) indicates that the actual dispersion is at or below the lower limit of non-breeding dispersion detectable using these methods on this and likely other species in which heavy and intermittent shading can be expected. Estimation of the true level of dispersion, and thus whether site-level conservation action may be required for this population to protect the most important habitats, will therefore require tracking methods with greater spatial accuracy, such as archival GPS tags⁴⁶ or multisensor geolocators⁴⁷.

The non-breeding dispersion of birds tagged in The Gambia fell just below the lower boundary of the modal dispersion found by Finch et al.³ for 98 populations of migratory birds (250–500 km), and that for birds tagged in Ghana fell in the next category (500–750 km) (all before correction for sample size). Many of the studies that paper reviewed contained data from light-level geolocator tracking, including from species in which heavy intermittent shading can be expected. It is therefore possible that increased use of tags enabling higher spatial resolution tracking, as they become miniaturised, will reveal that levels of connectivity are in general higher and that extreme connectivity levels are more common than initial tracking results suggested.

Application of a land mask reduced non-breeding dispersion of UK birds to lower than for the control birds tagged within this non-breeding area, i.e. in The Gambia (Fig. 1c). Hence, measured population dispersion is to some extent contingent upon proximity to sea. Whilst the area of available land influences dispersion levels at the macroscale³, it also impacts our ability to detect low dispersion using light level geolocators. As most studies do not present locations without application of a land mask, it is not clear to what extent land availability drives observed patterns versus facilitates their detection. In our case, the location of the non-breeding range at the western extremity of West Africa has facilitated estimation of the extremely low dispersion but given the tight longitudinal concentration of locations (Supplementary Fig. S3), which is not dependent on calibration, it is unlikely to have exaggerated it.

Our results demonstrate intraspecific variation in migratory connectivity and the complexity of the migratory networks in which populations are embedded. Neither has previously been well-studied but both are important determinants of population limitation^{1–3} and regulation¹. Understanding such variation within species may be important for understanding population declines as well as planning conservation action^{1,48}. We demonstrate a stronger connection between specific breeding and non-breeding locations than has so far been demonstrated for any similar long-distance migrant in either western or eastern hemispheres, since a population of Wood Thrushes that showed similar non-breeding concentration^{3,16} shared its non-breeding grounds with more disparate breeding populations. These findings suggest that future deterioration of conditions in non-breeding areas could be reflected in breeding grounds range loss in species and populations exhibiting high connectivity. This is especially likely in peripheral, low abundance populations and especially where breeding grounds conditions also deteriorate. High connectivity may be more common than so far appreciated in small long-distance migratory land birds and that may leave them more vulnerable to winter population limitation and drive negative trends.

Methods

Breeding grounds tagging

Study sites

We selected four study sites along a transect across the UK range of the Nightingale, covering an area of 170 × 105 km (Supplementary Figure S5). Sites were selected to allow sufficient birds to be captured to comprise both tagged and control cohorts and birds at all sites were considered part of a single UK breeding population. Within the core of the range were: Orlestone Forest (51.085 N, 0.834 E), wet ancient semi-natural woodland with rotationally managed coppice providing dense understorey ideal for Nightingales, and Alton Water (51.991 N, 1.115 E), open woodland and scrub fringing a reservoir. Towards the range periphery were: Rosedene Farm, Methwold Hythe (52.525 N, 0.484 E), intensively farmed arable land on peaty soils with willow hedges along irrigation ditches and tree lines along field boundaries, and Little Wood and Dudney Creek, Grafham Water (52.296 N, – 0.342 E), scrub fringing a reservoir and open woodland.

Capture and tagging

Nightingale territories were located through survey and capture attempts were made using mist nets in the core area of each territory. Playback of song was used, which means that males are much more likely to be caught than females, especially once incubation has begun. Consequently, due to the need to use playback to achieve acceptable capture rates and to maximise retrieval rates, we tagged only males from 2012 onwards. A total of 119 tags was deployed between 2009 and 2017 and 32 devices were retrieved in later years. The rate of device retrieval declined during the study, likely due to reduced recapture as well as return rates, but did not differ from the rate of recapture of ringed-only control birds. Deployments were made in 2009 (20 × 0.9g version of SOI-GDL1.0, 7 retrieved, 1 male track); 2012 (20 × BAS Mk20L, 13 retrieved), 2015 (20 × Intigeo-P55A1, 8 retrieved), 2016 (19 × Intigeo-P55Z11top621-11-DIP, 4 retrieved) and 2017 (40 × Intigeo-P50Z11-7-DIPv9, 6 retrieved). Except in 2009 where the tag was 0.9 g and 4–4.5% of body weight, tags were 0.55–0.7 g and 2.5–3.5% of body weight. In all

cases except where stated, non-breeding locations were obtained from data downloaded from each tag retrieved, although in 2015 only one of eight devices retrieved recorded throughout the core non-breeding period (i.e. to mid-February) and one failed to record through to midwinter. In total, we obtained geolocator data from 26 individuals and four non-breeding periods seasons, including three individuals that were tracked for two and one individual tracked for three non-breeding periods. In May 2023, six birds (1 at Orlestone Forest, 4 at Alton Water and 1 Rosedene Farm) were fitted with bespoke c.0.9 g Pathtrack Nanofix® GEO mini archival GPS tags programmed to allow long term tracking without solar recharging. Two from Alton Water were retrieved in May 2024 and contained data up to mid-October and early November, allowing assessment of initial non-breeding locations in each case. All tagging was carried out under license issued by the Special Methods Technical Panel of the British Trust for Ornithology Ringing Scheme, operating on behalf of the UK government Home Office, and following the relevant guidelines and practices set out in that license. The work in the paper was carried out in compliance with the ARRIVE guidelines for Animal Research.

Non-breeding grounds tagging

Study sites

We selected two sites (the number limited by logistical challenges and lack of resources)—one in the core of the identified non-breeding range of the birds tagged in the UK during the breeding season, and as a control, one in the overlap zone between the non-breeding ranges of the French and Italian populations tracked in a previous study¹⁴, allowing us to test the extent to which the migratory networks at the sites differed compared to the results of the tracking from the breeding grounds. Within the non-breeding range of the UK birds, we selected the vicinity of Kartong Bird Observatory (KBO), The Gambia (13.088 N, – 16.765 E), an area of coastal scrub. The control site was at Nsuatre, Ghana (7.418 N, – 2.485 E), an area of dense scrub and trees on spoil from road construction and grassland, scrub and farmland mosaic.

Capture and tagging

In February 2012, twelve Nightingales were fitted with BAS Mk20 geolocators with 10 mm light stalk (0.7 g) at Nsuatre and three were recaptured in February 2013, despite habitat clearance removing the territories of three tagged birds. In January 2019, five birds were tagged with Intigeo-P55Z11top621-11-DIP-COOL tags (0.7 g) at KBO, of which four were recaptured and devices retrieved in the following non-breeding period. In November 2019 and January 2020, six birds, including all four of the birds from which tags were retrieved, were tagged with the same tag model. Due to the covid-19 pandemic, retrievals were not possible during the following non-breeding period, but one tag was retrieved in March 2022. This tag contained data allowing two further, successive breeding locations to be estimated for this bird. In February 2023, five birds were fitted with bespoke 0.9 g Pathtrack Nanofix® GEO mini archival GPS tags enabled to allow long term tracking without solar recharging. Two were retrieved in January 2024 and included data covering the entirety of the 2023 breeding seasons in each case.

Data analysis

Geolocator analysis

We used the ‘preprocessLight’ function of the TwGeos package v0.1.2⁴⁹ to automate twilight event annotation of log-transformed, raw light-level data, using a threshold of 1, which represents an appropriate value above and below which to differentiate twilight events from noise. Dark periods shorter than four hours were excluded, thereby avoiding false dusk events caused by shading. Possible false dawn events were removed with the ‘loessFilter’ function from the GeoLight v2.0.1 package⁵⁰. We considered twilight times with residuals greater than three times the interquartile range as errors and removed these from further analysis.

We determined stationary periods using the ‘changeLight’ function of GeoLight, setting the minimal stopover period to three days. We used geolocator-specific quantile probability thresholds to identify movement between sites, selecting values between 0.90 and 0.96, since the optimal choice of this value is influenced by data quality. Higher values were used when noisier data led to outliers being regularly erroneously defined as a new stationary site. We used the Hill-Ekstrom calibration method via the ‘findHEZenith’ function of the GeoLocTools v1.0 package⁵¹ to calculate the optimal sun elevation angle (SEA) for the non-breeding period. We focussed on the non-breeding period between October and March. The Hill-Ekstrom calibration chooses the SEA that results in the highest precision (lowest variation) in latitude estimates of a stationary period. We then used the ‘mergeSites2’ function to combine consecutive sites within specific distance thresholds that the ‘changeLight’ function separates due to errors in twilight times, indicated by overlap of the 95% confidence intervals, specifying a gamma error distribution and the SEA for the entire non-breeding period. The twilight error distribution was calculated from in-habitat calibration when the bird was present at the deployment site using the ‘getElevation’ function of GeoLight⁵². We set the calibration period as the first 27 days from the earliest date in the dataset for each bird, and visually inspected plots of the log observed versus expected light levels for the deployment site over time. These steps were iterated over each bird using different distance thresholds (50 to 550 km at 50 km intervals). We aimed for maximum accuracy of non-breeding locations by using the Hill-Ekstrom calibration method to estimate SEAs for each stationary period and recalculating locations of stationary sites. For some short stationary periods, the Hill-Ekstrom calibration failed, so in these cases the SEA for the entire non-breeding period was used. SEAs during the non-breeding period ranged from – 7.9 to – 1.4. We estimated stationary periods with and without a land mask, the former estimating locations only on land. Higher, more conservative distance thresholds were used when large variation in estimates of latitude resulted in erroneous or overlapping stationary sites. This was assessed by visual inspection of the migration schedule inferred from ChangeLight and the estimated locations of stationary sites.

We estimated six breeding locations for four birds tagged at Kartong, The Gambia, and three tagged in Nsuatre, Ghana. We used a distance threshold of 250 km to identify a single breeding location for each bird, since birds were not expected to move significantly within their breeding period (May and June). Any such movements would be truly exceptional in a small territorial songbird; lack of such movements is supported by the data from the four GPS tags retrieved in this study, as well as four retrieved in earlier years that only collected data during the breeding period. All eight birds remained on the breeding territory until at least late July. For two birds the Hill-Ekstrom calibration failed for the breeding season, so in-habitat calibration during non-breeding period was used to calculate the SEA. Using the median of 16 breeding grounds SEAs derived from robust H-E calibrations (six locations for four birds tagged in West Africa and ten in the UK—see below), which was -6.6 , produced quantitatively similar results for these birds.

We assessed the impact of errors in light-level geolocation on estimated dispersion of non-breeding and breeding locations in two ways. Firstly, we compared the dispersion of estimated non-breeding sites for UK-tagged birds with the dispersion of estimated non-breeding sites for birds tagged in West Africa. We also performed the same analysis for breeding sites of birds tagged in The Gambia, comparing their dispersion to that of estimated breeding sites of birds tagged in the UK. Secondly, we compared the dispersion of estimated non-breeding sites of birds tagged in West Africa and the estimated breeding locations of birds tagged in the UK with their known dispersions, which were close to zero for birds tagged at the two sites in Africa and 91 km for birds tagged in the UK.

Hill-Ekstrom calibration during the breeding season, the year the tag was deployed, failed for the majority of birds tagged in the UK, likely due to the short within-breeding season data series available from these tags, which were put on in one breeding season and removed the next. This may have been exacerbated by variations in behaviour at twilight within these truncated periods due to changes in singing and breeding activities and the fact that the remaining period is further away from the equinox in the year where the tag was, which reduces the accuracy of the calibration⁹. To avoid any biases, we discarded the data from the failed H-E calibrations, leaving only ten UK-tagged birds with robust estimates of breeding grounds for comparison with those from birds tagged in The Gambia and with their known dispersion. One breeding location for a bird tagged in The Gambia, which was one of three estimated for that bird (see Fig. 2a), was identified as a potential outlier, being further south than all other birds, in central France. Using the median SEA for other birds produced quantitatively similar results for this location.

Processing of geolocator data was done in R version 4.2.3⁵³.

Ringling data and national population size data

We compared the results of our geolocator analyses with ringing data from KBO, which were supplied directly. Numbers of Nightingale ringed in European countries were downloaded from the Euring website³⁵ to compare against the exchanges of ringed birds between KBO and those countries. We selected numbers for the period from 2000 to 2022, to match the period over which Nightingale ringing has been undertaken at KBO. We extracted national population sizes of Nightingales from Burfield et al. 2023¹⁹ for all countries for consistency. The proportion of Nightingales ringed in each country was estimated as the number ringed in each country divided by the population size, which is given in breeding pairs but more accurately refers to territorial males¹⁰. We divided the number of birds ringed by this estimate of population size to give an index of the proportion of birds ringed, since both will be biased towards males due to uneven sex ratios in breeding populations¹⁰ and sex-dependent differences in both detectability and capture probability (the latter due to behavioural differences including responses to tape luring).

Connectivity analysis

We followed the methodology of Finch et al.³ to derive a measure of population dispersion, calculated as the mean (great-circle) distance between individual non-breeding sites. We compared the population dispersion of our Nightingale population during the non-breeding period with the data on non-breeding areas compiled by Finch et al.³ comprising 43 species and 98 populations. We excluded species with data from only one individual and/or juvenile birds, and restricted our analyses to long-distance Afro-Palearctic or Neotropical migrants tagged during the breeding season in the northern hemisphere. Ten birds occupied two separate non-breeding sites, moving to a second more southerly site later in the non-breeding period. For direct comparison with the populations in Finch et al.³ we used the first non-breeding site to calculate population dispersion, matching their methods. For individuals that were tracked over more than one non-breeding period, none of which used more than one site in a non-breeding period, we took a single location by averaging the coordinates of available locations to reduce non-independence. To correct for the effect of sample size of individuals in each population on estimated population dispersion, we ran a linear mixed model, using the lme4 v1.1–35.1 package⁵⁴ with a random intercept of species identity. We assumed a non-linear relationship between sample size and population dispersion, so we modelled the natural log of the population sample size as the independent variable. There was a positive relationship between population dispersion and log-transformed sample size ($\beta = 137.42$, $SE = 52.54$, $P = 0.010$, $R^2_m = 0.057$, $R^2_c = 0.424$). We then predicted population dispersion assuming equal (maximum) sample sizes.

Three other Nightingale populations breeding in France, Italy and Bulgaria were included in the dataset, originating from the study by Hahn et al.¹⁴. They focussed on the period between the 15th November and 15th February and identified non-breeding sites of birds using individual kernel density plots of daily locations. For direct comparison with these populations, we therefore additionally calculated population dispersion taking the site occupied in the middle of the period defined from that study (31st December, referred to throughout as 'midwinter') which, in two cases, was not the first site occupied.

We quantified inter-population mixing as the Mantel correlation coefficient (ranging from -1 to $+1$) between pairwise distance matrices of individual breeding and non-breeding sites using the *vegan* 2.6–4 package in R⁵⁵. High values indicate that individuals that breed close together also spend the non-breeding period relatively close together and therefore inter-population mixing is low⁵. For this analysis, we used a combination of geolocator, tagging, ringing, and GPS data. As the Bulgarian population was tagged at two different sites c.150 km apart, we took the average across the two sites as the breeding grounds for this population as we did not know at which site individuals had been tagged.

Habitat suitability modelling

Presence absence records. Using the same core non-breeding period as Hahn et al.¹⁴, we compiled 12,592 Nightingale presence/absence records between 15th November and 15th February from 2001 onwards, 222 of which were confirmed Nightingale records. We collated records derived from scientific surveys and citizen science databases (Fig. 4). We used the target group approach to derive absences from scientific surveys. This approach uses all occurrences of a predefined species group i.e. the ‘target group’ collected with the same sampling design as the species of interest. It has been shown to improve the quality of model predictions. In our case, target-group absences were localities that were surveyed for Afro-Palaearctic migrants, but Nightingales were not found. To increase the range of environmental variables beyond those of the species’ known distribution, crucial for predicting the potential distribution of species, we included absence points derived from the surveys conducted by Zwarts et al.⁵⁶, primarily in the Sahel. We sampled two citizen science projects, eBird and the African Bird Atlas, using complete checklists to derive presence and absence points. Three quarters (73.8%) of all records were obtained from eBird.

Predictor variables. We preselected predictor variables based on a priori knowledge of species limits. These were: (1) monthly NDVI; (2) precipitation; (3) minimum and maximum temperature; (4) Palmer Drought Severity Index (PDSI); and (5) land cover type. NDVI data were obtained from the 250 m resolution US Geological Survey MOD13A3 and MOD13A3 V6.1 data products^{57,58}. We extracted mean NDVI for each month averaging across all years from 2001 to 2020. We extracted variables (2) to (4) from TerraClimate, a global dataset providing monthly bioclimatic data at a 4 km resolution. We chose this over the commonly used WorldClim dataset, since it covers our study period and better lends itself to temporal analysis that may be important for linking climate variability and climate impacts⁵⁹. We extracted the minimum and maximum temperature of the coldest and warmest month, respectively, and mean monthly accumulated precipitation between 2001 and 2020 to capture consistent differences between habitats (e.g. savanna versus forests) over the period covered by the presence/absence records. We also extracted accumulated precipitation and PDSI for the specific year associated with each record, capturing temporal variability in habitat suitability and the effect of dry versus wet years. If the record was dated between January and March, accumulated precipitation and PDSI from the preceding year was used, since most rainfall occurs during the summer. We obtained land cover information from one of the most recent and detailed land use products, the European Space Agency Climate Change Initiative (ESA CCI) Land Cover dataset⁶⁰, a continuous global dataset at annual time steps (1992–2020) at 300 m grid resolution. We used the legend provided by the ESA CCI⁶¹ to reclassify land cover types into 11 categories, matching non-agricultural vegetation types to the Intergovernmental Panel on Climate Change land categories (Table 2). We matched records to the closest land cover map in time. We obtained elevation data at a 90 m resolution from the Shuttle Radar Topography Mission v4 digital elevation dataset⁶². We used *terra* v1.7.55 package⁶³ in R version 4.2.3⁵³ to extract land cover data. The remaining variables were available on the Google Earth Engine Platform⁶⁴ and were extracted using the ‘*reduceRegion*’ function.

Modelling process. We used a machine-learning random forest algorithm to investigate habitat suitability points using the *randomForest* v4.7–1.1 package in R⁶⁵. The recent advancements in the machine-learning algorithms provide a powerful tool for building accurate predictive models of species distribution and their habitat relationships and are widely used to map species distributions. We used a longitudinal cut-off of 15°E to remove data points from under-sampled regions beyond Cameroon (Fig. 4) from the analyses. We randomly selected one record from each week from within roughly 4 km hexagons, using the R package *dggridR* v3.0.0⁶⁶. This mitigates, but does not remove, spatial and temporal bias in the occurrence data⁶⁷.

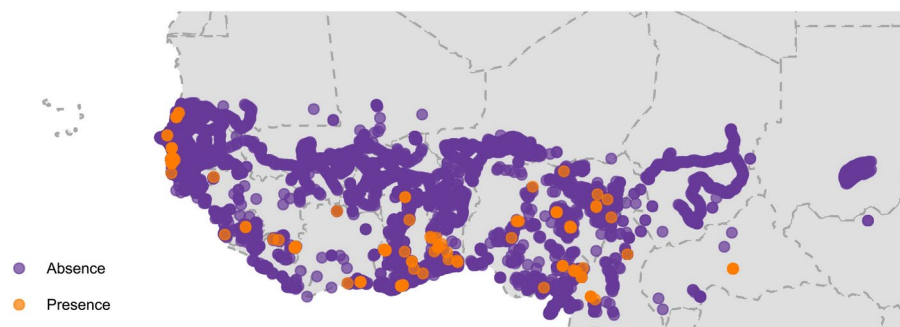


Fig. 4. Presence ($n = 222$) and absence ($n = 12,370$) records of Nightingales between 15th November to 15th February in West Africa. Data originate from 2001 onwards and were obtained from structured surveys and citizen science databases.

CCI code	CCI name	IPCC classification	Our classification
10	Cropland, rainfed	Agriculture	Cropland, rainfed
11	Herbaceous cover	Agriculture	Cropland, rainfed
12	Tree or shrub cover	Agriculture	Cropland, rainfed
20	Cropland, irrigated or post-flooding	Agriculture	Cropland, irrigated or post-flooding
30	Mosaic cropland (> 50%) / natural vegetation (tree, shrub, herbaceous cover) (< 50%)	Agriculture	Mosaic cropland
40	Mosaic natural vegetation (tree, shrub, herbaceous cover) (> 50%) / cropland (< 50%)	Agriculture	Mosaic natural vegetation
50	Tree cover, broadleaved, evergreen, closed to open (> 15%)	Forest	Forest
60	Tree cover, broadleaved, deciduous, closed to open (> 15%)	Forest	Forest
61	Tree cover, broadleaved, deciduous, closed (> 40%)	Forest	Forest
62	Tree cover, broadleaved, deciduous, open (15-40%)	Forest	Forest
70	Tree cover, needleleaved, evergreen, closed to open (> 15%)	Forest	Forest
71	Tree cover, needleleaved, evergreen, closed (> 40%)	Forest	Forest
72	Tree cover, needleleaved, evergreen, open (15-40%)	Forest	Forest
80	Tree cover, needleleaved, deciduous, closed to open (> 15%)	Forest	Forest
81	Tree cover, needleleaved, deciduous, closed (> 40%)	Forest	Forest
82	Tree cover, needleleaved, deciduous, open (15-40%)	Forest	Forest
90	Tree cover, mixed leaf type (broadleaved and needleleaved)	Forest	Forest
100	Mosaic tree and shrub (> 50%) / herbaceous cover (< 50%)	Forest	Forest
110	Mosaic herbaceous cover (> 50%) / tree and shrub (< 50%)	Grassland	Grassland
120	Shrubland	Shrubland	Shrubland
121	Evergreen shrubland	Shrubland	Shrubland
122	Deciduous shrubland	Shrubland	Shrubland
130	Grassland	Grassland	Grassland
140	Lichens and mosses	Sparse vegetation	Sparse vegetation
150	Sparse vegetation (tree, shrub, herbaceous cover) (< 15%)	Sparse vegetation	Sparse vegetation
151	Sparse tree (< 15%)	Sparse vegetation	Sparse vegetation
152	Sparse shrub (< 15%)	Sparse vegetation	Sparse vegetation
153	Sparse herbaceous cover (< 15%)	Sparse vegetation	Sparse vegetation
160	Tree cover, flooded, fresh or brackish water	Forest	Forest
170	Tree cover, flooded, saline water	Forest	Forest
180	Shrub or herbaceous cover, flooded, fresh/saline/brackish water	Wetland	Wetland
190	Urban areas	Urban	Urban
200	Bare areas	Bare area	Bare area
201	Consolidated bare areas	Bare area	Bare area
202	Unconsolidated bare areas	Bare area	Bare area
210	Water bodies	Water	Water

Table 2. Reclassification of European Space Agency Climate Change Initiative (ESA CCI) Land Cover types in line with Intergovernmental Panel on Climate Change (IPCC) land categories.

We retained 80% of occurrence data for model training, and 20% for model testing. To reduce the dependence of our predictions on the choice of predictors, we ran competing models creating different variables from monthly rainfall and NDVI, which were expected to be most closely related to ecological productivity in tropical ecosystems and therefore Nightingale habitat suitability. We identified important variables from all candidate variables using the wrapper feature selection algorithm from the Boruta 8.0.0 package in R⁶⁸. This identified seven land cover types as unimportant. The final variables included in the models are shown in Table 3. This process was repeated ten times for each model, resulting in a total of 40 models. We used the area under the receiver operation curve (AUC) and the true skill statistic (TSS) as a threshold-independent and threshold-dependent measure of model performance³⁷. Habitat suitability was predicted using model averaging weighted by the AUC. We resampled all rasters to a 1 km resolution. We measured variable importance as Mean Decrease in Accuracy, ranging from 0 to 100, which indicates the decrease in the accuracy of classifications if the variable is removed.

We modelled changing habitat suitability between 2001, which was the lower limit of our predictor variable datasets, and 2020. We did not include the population breeding in Bulgaria, because the non-breeding area for this population fell outside of the area encompassed by our habitat suitability map. To provide an index of the suitability of habitat available for each population, we drew 100 km buffers around geolocator-derived non-breeding locations occupied during midwinter, thereby incorporating some uncertainty around positions whilst avoiding sampling very large areas around the best-estimate locations, and quantified changes within the buffer regions. Potentially erroneous locations that did not overlay any suitable habitat were determined by the

Variable	Description	Scale (m)	Unit	Link
NDVI				
Monthly NDVI	Mean NDVI for each month of the year between 2001 and 2020	250	–	https://lpdaac.usgs.gov/data/
Maximum NDVI	Maximum monthly NDVI	250	–	https://lpdaac.usgs.gov/data/
Minimum NDVI	Minimum monthly NDVI	250	–	https://lpdaac.usgs.gov/data/
Climate				
Precipitation				
Maximum precipitation	Mean accumulated precipitation during the wettest month between 2001 and 2020	4000	mm	https://www.climatologylab.org/terraclimate.html
Minimum precipitation	Mean accumulated precipitation during the driest month between 2001 and 2020	4000	mm	https://www.climatologylab.org/terraclimate.html
Summer precipitation	Mean accumulated precipitation from June to October between 2001 and 2020	4000	mm	https://www.climatologylab.org/terraclimate.html
Winter precipitation	Mean accumulated precipitation from November to February between 2001 and 2020	4000	mm	https://www.climatologylab.org/terraclimate.html
Monthly precipitation	Mean accumulated precipitation for each month of the year between 2001 and 2020	4000	mm	https://www.climatologylab.org/terraclimate.html
Annual precipitation	Accumulated precipitation of a given year	4000	mm	https://www.climatologylab.org/terraclimate.html
Temperature				
Maximum temperature	Mean maximum temperature during the warmest month between 2001 and 2020	4000	°C	https://www.climatologylab.org/terraclimate.html
Minimum temperature	Mean minimum temperature during the coldest month between 2001 and 2020	4000	°C	https://www.climatologylab.org/terraclimate.html
PDSI	Palmer Drought Severity Index for a given year	4000	–	https://www.climatologylab.org/terraclimate.html
Elevation	–	30	m	https://srtm.csi.cgiar.org/
Land cover				
Cropland, rainfed	–	300	–	https://www.esa-landcover-cci.org/?q=node/164
Mosaic natural vegetation	–	300	–	https://www.esa-landcover-cci.org/?q=node/164
Forest	–	300	–	https://www.esa-landcover-cci.org/?q=node/164
Shrubland	–	300	–	https://www.esa-landcover-cci.org/?q=node/164
Urban	–	300	–	https://www.esa-landcover-cci.org/?q=node/164

Table 3. Description of predictors variables used in habitat suitability models.

weighted mean threshold that maximised TSS, values below this threshold indicating unsuitable habitat. We measured and compared habitat suitability both including and excluding these locations.

We modelled differences in suitability between years and populations via linear mixed models with individual as a random effect, using lme4. We also ran a simplified model of suitability as a function of year with individual and population as nested random effects, to assess changes across the region as a whole.

Data availability

Data, code and instructions to access data can be found at: <https://zenodo.org/records/14393013>.

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Author contributions

All authors critically reviewed and commented on the manuscript. Chris Hewson conceived the study, acquired funds, carried out and coordinated fieldwork, designed analyses and wrote the paper. Maire Kirkland designed and carried out analyses and co-wrote the paper. Philip Atkinson and Robert Fuller acquired funds. All other authors contributed to collection of data or provision of existing data.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to C.M.H.

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