



A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird

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ABSTRACT

Aim The extent to which individuals from different breeding populations mix throughout the non-breeding season (i.e. ‘migratory connectivity’) has important consequences for population dynamics and conservation. Given recent declines of long-distance migrant birds, multipopulation tracking studies are crucial in order to assess the strength of migratory connectivity and to identify key sites *en route*. Here, we present the first large-scale analysis of migration patterns and migratory connectivity in the globally near-threatened European roller *Coracias garrulus*.

Location Breeding area: Europe; passage area: Mediterranean, sub-Saharan Africa, Arabian Peninsula; wintering area: southern Africa.

Methods We synthesize new geolocator data with existing geolocator, satellite tag and ring recovery data from eight countries across Europe. We describe routes and stopover sites, analyse the spatial pattern of winter sites with respect to breeding origin and quantify the strength of connectivity between breeding and winter sites.

Results We demonstrate the importance of the northern savanna zone as a stopover region and reveal the easterly spring loop (via Arabia) and leapfrog migration of rollers from eastern populations. Whilst there was some overlap between individuals from different populations over winter, their distribution was non-random, with positive correlations between breeding and autumn/winter longitude as well as between pairwise distance matrices of breeding and winter sites. Connectivity was stronger for eastern populations than western ones.

Main conclusions The moderate levels of connectivity detected here may increase the resilience of breeding populations to localized habitat loss on the winter quarters. We also highlight the passage regions crucial for the successful conservation of roller populations, including the Sahel/Sudan savanna for all populations, and the Horn of Africa/Arabian Peninsula for north-eastern rollers.

Keywords

Bird migration, conservation, *Coracias garrulus*, migratory connectivity, roller.

INTRODUCTION

Migratory birds are potentially more vulnerable to environmental change than sedentary species because they rely on resources at a series of sites separated by hundreds to thousands of kilometres (Newton, 2004). It is therefore unsurprising that birds that migrate from temperate breeding grounds to tropical winter quarters are declining faster than their sedentary counterparts (Sanderson *et al.*, 2006; Hewson & Noble, 2009; Vickery *et al.*, 2013). Recent evidence suggests that the mechanisms driving these declines are population-specific combinations of potentially interacting factors acting on the breeding, passage and/or wintering grounds (Morrison *et al.*, 2013; Vickery *et al.*, 2013). Disentangling the mechanisms that limit migrant populations to guide their conservation therefore requires an understanding of their spatio-temporal distribution throughout the annual cycle.

A growing body of tracking studies are now identifying the sites used and threats encountered by migrants during the non-breeding season. These studies also reveal a range of migration strategies and patterns, including migratory divides (Reichlin *et al.*, 2008), narrow-front (Willemoes *et al.*, 2014) and broad-front migration (Schmaljohann *et al.*, 2012), leap-frog migration (Panuccio *et al.*, 2013), loop migration (Tøttrup *et al.*, 2012) and convergence at ecological barriers (Strandberg *et al.*, 2009). Of particular value (but also scarcity) are multipopulation tracking studies from across a species' range examining intraspecific variation in migration strategy. Multipopulation studies also provide insight into migratory connectivity, that is, the extent of mixing of different breeding populations during the non-breeding season (Stanley *et al.*, 2014; Trierweiler *et al.*, 2014). Migratory connectivity is described along a continuum from complete segregation ('strong' connectivity) to complete mixing ('weak' connectivity) of different breeding populations during the non-breeding season (Webster *et al.*, 2002). The strength of connectivity is expected to underpin the response of populations to habitat loss (Martin *et al.*, 2007; Taylor & Norris, 2009; Iwamura *et al.*, 2013) with strong connectivity increasing their vulnerability, as any local deterioration in non-breeding conditions will be felt by all members of a breeding population (Dolman & Sutherland, 1992; Jones *et al.*, 2008; Cresswell, 2014). Although migratory connectivity is typically measured between breeding and winter populations (Ryder *et al.*, 2011; Fraser *et al.*, 2012; Cormier *et al.*, 2013), the mixing of individuals *en route* and at stopover sites is arguably just as important, particularly given that mortality is often greatest during migration (Sillert & Holmes, 2002; Lok *et al.*, 2015). Connectivity across the annual cycle therefore has strong implications for conservation management, and its estimation is an important precondition for its effective delivery.

The European roller *Coracias garrulus* (hereafter 'roller') is a near-threatened long-distance migrant that has declined by 20–30% globally over the last decade (Baillie *et al.*, 2004). The species is classified as vulnerable in Europe, having gone extinct in several central and northern territories (Burfield &

Bommel, 2004; Kovacs *et al.*, 2008). Most authors attribute this decline to the degradation of the open agricultural habitats in which rollers generally breed (e.g. Avilés & Parejo, 2004; see also Kovacs *et al.*, 2008). However, with 'migration and wintering grounds' identified as a knowledge gap for this species (Kovacs *et al.*, 2008), the influence of non-breeding conditions on roller population dynamics remains unknown. Three recent tracking studies have revealed the year-round movements of rollers from the western extremes of the breeding range (Catry *et al.*, 2014; Emmenegger *et al.*, 2014; Rodríguez-Ruiz *et al.*, 2014), but further tracking studies from across the range are necessary to broaden our understanding of roller migration and population structure.

Here, we expand these single-country studies into a pan-European analysis by combining all existing published data with new data from rollers tagged in Portugal, France, Austria, Montenegro, Latvia and Cyprus. We identify and compare migratory strategies and wintering grounds of rollers breeding across Europe and quantify the strength of connectivity between breeding and winter sites. This multipopulation study provides a crucial step towards better understanding the population dynamics of the roller, a prerequisite for its successful conservation.

METHODS

We combine new data from 17 solar geolocators with geocator ($n = 9$) and satellite tag (6) data from three existing studies (Catry *et al.*, 2014; Emmenegger *et al.*, 2014; Rodríguez-Ruiz *et al.*, 2014) and the only sub-Saharan ring recovery. Our data were collected from breeding populations in Portugal ($n = 4$ individuals), Spain (10), France (8, with 1 individual tracked over two years), Austria (1), Montenegro (3), Latvia (4), Bulgaria (1 ring recovery) and Cyprus (1), spanning 3600 km longitude and 2500 km latitude and providing good coverage across the western half of the roller's global breeding distribution (Birdlife International & NatureServe, 2013; Fig. 1). All devices were deployed on breeding rollers captured at or near the nest site, towards the end of incubation or during chick rearing.

Geocator data

In total, 113 solar geolocators mass = 1.4–3.1 g; 0.7–2.9% of adult roller mass (Cramp, 1985) were deployed across eight countries between 2009 and 2013 (see Table S1 in Supporting Information). After accounting for return of tagged birds (48/113 = 42%), successful recapture (43/48 = 90%), tag loss (13/43 = 30%) and total electronic failure (4/30 = 13%), data were successfully downloaded from 26 tags. Of these, three failed before the onset of spring migration, but after arrival to the winter quarters.

We employ the standard 'threshold model' of geolocation, which involves estimating latitude from day/night length and longitude from the timing of solar noon/midnight and yields two positions per 24-h period. Sunrise and sunset (hereafter

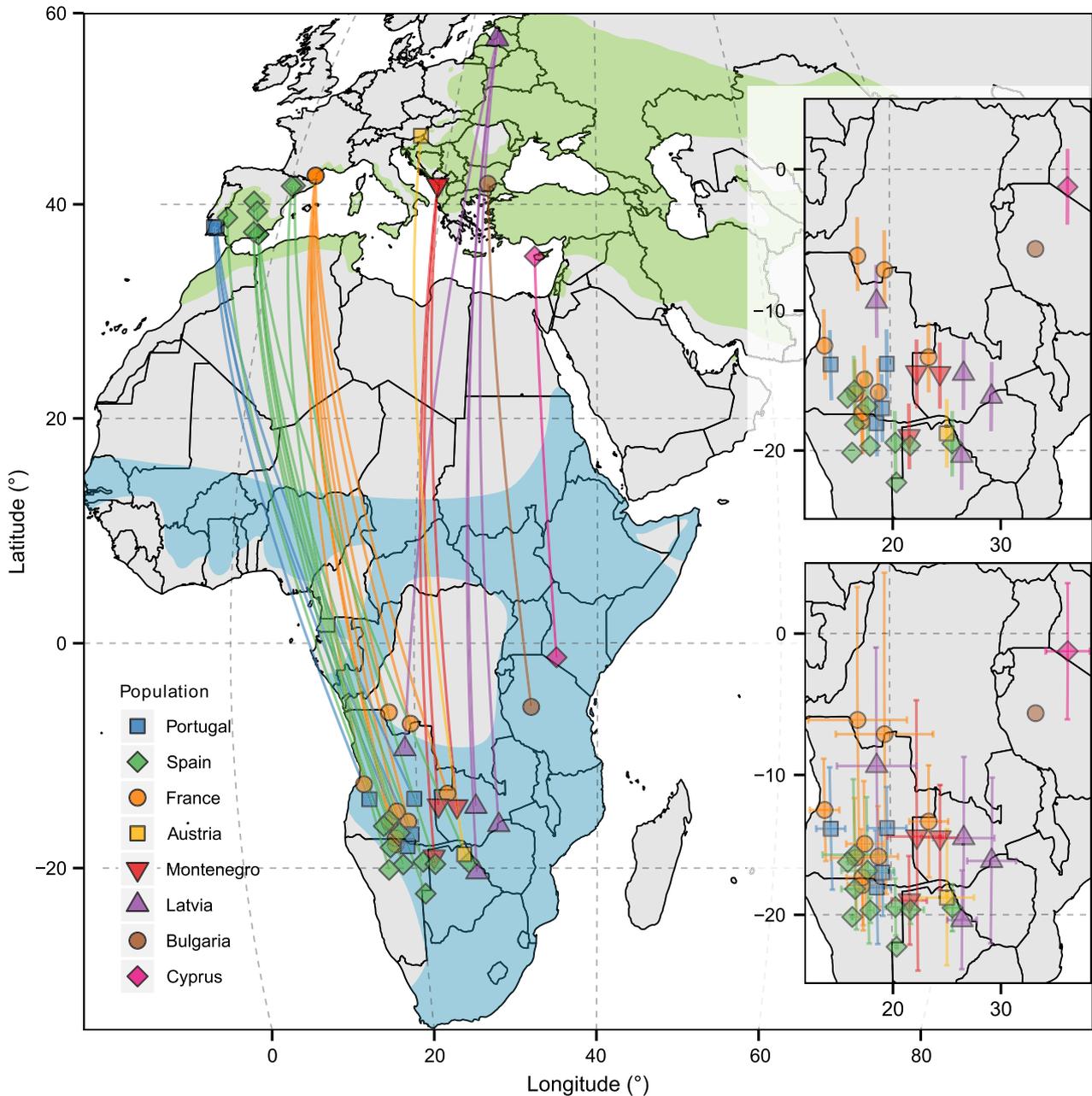


Figure 1 Migratory connectivity in the European roller (*Coracias garrulus*) revealed by geolocators, satellite tags and a ring recovery (Mollweide equal-area projection). Loxodromic lines (not intended to represent routes taken) connect breeding and winter sites of 33 European rollers from eight countries. Shaded areas show global breeding (green) and winter (blue) distribution of the European roller, from BirdLife International and NatureServe (2013). The south-east quarter of the breeding distribution, from Iraq and southern Iran to southern Kazakhstan, is occupied by the *semenowi* subspecies. Inset top: vertical lines represent latitudinal shift in mean winter position resulting from $\pm 1.0^\circ$ to sun elevation angle. Inset bottom: bars show variation (SD) surrounding mean winter locations.

‘transitions’, from which day/night length and timing of solar noon/midnight are derived) are identified when light intensity crosses a pre-defined threshold. Due to differences in light data output, the procedure for identifying sun transitions varies according to tag manufacturer. For BASTrak devices, initial data handling was conducted using the BASTrak software suite (British Antarctic Survey, 2008). We used a threshold of 2 arbitrary light units and identified and removed false transitions (due to shading during daylight)

by setting a minimum dark period of 4 h. Any remaining false transitions ($n = 18$ over 4 devices) were identified and removed manually. BASTrak devices record maximum light intensity over a model-specific logging period (2, 5 or 10 min), meaning that sunsets (but not sunrises) must be advanced by the length of this logging period. For SOI devices, and for all further analyses, we used the R (v3.1.2, R Development Core Team, 2014) *GeoLight* package (Lisovski & Hahn, 2012). A threshold of 3 units above the baseline

level was used, and false transitions were filtered out by fitting a LOESS curve to the transition data, removing transitions exceeding three interquartile ranges of the curve.

To estimate geographical position from sun transition timings, the sun angle to which the chosen light threshold corresponds must be determined (i.e. calibration). We employed ‘in-habitat calibration’ (Lisovski *et al.*, 2012) identifying for each tag the sun elevation angle that minimized latitudinal deviation from the known nesting location during the 21-day period following deployment (mean = -3.8° , min = -5.0° , max = -1.9°). The suitability of this angle is not necessarily constant in space and time because shading conditions (e.g. due to vegetation, cloud or topography) may vary, but this technique is commonly used in geolocator studies, and alternative calibration methods [e.g. Hill–Ekstrom (Lisovski *et al.*, 2012)] were not possible. We used the in-habitat angle to estimate twice-daily positions for all transition data from a given tag, but explored the influence of calibration angle on location estimates by recalculating mean winter and stopover (see next paragraph) latitudes using in-habitat angle $\pm 0.5^\circ$ and $\pm 1.0^\circ$ (calibration has no effect on longitude). Latitude estimates during the spring and autumn equinoxes – when latitudinal variation in day length is insufficient for successful geolocation – were discarded (mean period rejected per equinox = 20 days; min = 18, max = 52, depending on the calibration angle assigned to a given tag).

To separate stationary periods from periods of movement, we used the *changeLight* function [following Emmenegger *et al.* (2014)], which fits a changepoint model to sun transitions (quantile = 0.90, minimum stationary period = 5 days), allowing the detection of stationary periods throughout the annual cycle, including during the equinoxes when geographical positions are unavailable. For each individual, spatially overlapping and temporally adjacent stationary sites were aggregated manually and the mean (\pm SD) position of each site, in addition to the December–January (hereafter ‘winter’) period, was calculated. Individual route maps are presented in Fig. S1 for new geolocator data only ($n = 17$).

Satellite tag data

Twelve 5-g solar-powered Platform Transmitting Terminals (PTT-100; Microwave Telemetry Inc., Columbia, MD, USA) were deployed on breeding adult rollers from six sites across Spain in 2012 and 2013. After accounting for death or device failure, we were able to analyse the tracks of six individuals to their winter grounds and one on return migration. We randomly selected one ‘high-quality’ (up to 1.5 km accuracy) location per day and defined stopover and winter periods (mean \pm SD position) as all points reflecting <20 km movement in a 24-h period (see Rodríguez-Ruiz *et al.* (2014) for full details).

Ring recovery data

We are aware of only one sub-Saharan ring recovery of a European roller, a nestling ringed in Haskovo, Bulgaria, in July 1936

and found in Tabora, Tanzania, on 15 December 1936 (Pateff, 1942). Given that all tracked birds described in this study had reached their winter sites by early December, we assume that this ringed individual had reached its final destination upon recovery (although we have no information on whether migration schedules differ between juveniles and adults).

Analyses

Inferences about routes and precise phenology are limited by the latitudinal uncertainty of geolocator data during movement periods (and are of course impossible with our single ring recovery). We therefore present stopover sites (as defined above) and infer routes taken based predominantly on longitude data. Rather than presenting individual-level phenological data, we show median dates [with interquartile range (IQR)] of arrival to and departure from the breeding, autumn and winter sites, based on changepoint analysis of sun events.

To examine migratory connectivity throughout the annual cycle, we combine data from all sources ($n = 33$, although lower for some analyses). Pearson’s correlation coefficients were calculated between (1) longitude of breeding and post-Saharan autumn stopover site, (2) longitude of breeding and winter site (where positive coefficients indicate a ‘parallel’ migration pattern), (3) breeding site latitude and orthodromic (great circle) migration distance and (4) latitude of breeding and winter site [where positive coefficients indicate sequential (‘chain’) migration and negative coefficients occur when northerly breeders winter furthest south (‘leapfrog’ migration)]. We also calculated the Mantel correlation coefficient (r_M , range -1 to 1) between pairwise (orthodromic) distance matrices of breeding sites and winter sites, where positive correlations indicate that individuals that breed close together also winter together (i.e. migratory connectivity; Ambrosini *et al.*, 2009). Tests were conducted across all individuals, as well as independently for western (Portugal, Spain and France) and eastern (east from Austria) subsets.

To account for uncertainty around the mean geolocator-derived positions of autumn stopover and winter sites, we repeated the analyses using a randomized iterative process, sampling new positions from the error distribution about mean positions (see Appendix S1 for details). Furthermore, to explore the implications of sample size for our analyses, we conducted resampling experiments in which each statistical test was performed on sequentially reduced data sets (see Appendix S2 for details).

RESULTS

Autumn migration

Median departure date from the breeding site was 21th August (IQR: 3rd August – 6th September). In the west, two autumn routes were apparent: rollers from south-west Iberia took a westerly route along the Atlantic coast of West Africa before bearing east along the savanna belt, whereas those

from north-east Spain and southern France flew directly across the Sahara (Figs 2 and S1). In the east, rollers migrated south over the Mediterranean Sea and Sahara; for Latvian birds, this southward movement occurred on a broad front with several Mediterranean crossing points.

Stopovers were detected in south-east Europe for Latvian rollers and West Africa for rollers from south-west Iberia, and all birds made a prolonged autumn stopover in the northern savanna [Table 1; median arrival = 20th September (IQR: 8th September – 29th September); median departure = 3rd November (IQR: 26th October – 14th November)]. There was a significant correlation between breeding and autumn stopover site longitude (Pearson's correlation: $r = 0.81$, d.f. = 29, $P < 0.001$; Fig. 3a). This association was nearly significant when using data only from eastern populations ($r = 0.63$, d.f. = 7, $P = 0.07$), but not with data from western populations alone ($r = 0.27$, d.f. = 20, $P = 0.22$). In addition to the main autumn stopover, some individuals also stopped south of the equator prior to reaching their winter

quarters. Median arrival to the winter quarters was 14th November (IQR: 3rd November – 21st November).

Winter quarters

All individuals spent the winter period in southern Africa, between the equator and 20–25°S (Table 1, Fig. 1). Data from the PTT devices suggest that at least some individuals make small-scale movements during the winter period (mean winter site SD = 46 km for latitude; 50 km for longitude) which are too small to detect with geolocators. There is no evidence of substantial variation in winter distribution between years (data not shown).

Great circle distances between breeding and winter sites (ignoring any deviations from the orthodromic route) ranged from 4050 to 8625 km (Table 1) and were greater for individuals from more northerly breeding grounds ($r = 0.66$, d.f. = 31, $P < 0.001$). When data for rollers from eastern and western Europe were tested separately, this association was significant for the eastern ($r = 0.90$, d.f. = 8, $P < 0.001$), but not the western subset ($r = -0.04$, d.f. = 21, $P = 0.85$), which is perhaps unsurprising given the limited latitudinal variation between western breeding sites. There was no overall correlation between breeding and wintering ground latitude ($r = 0.01$, d.f. = 31, $P = 0.94$). For western populations, this association was nearly significant and positive ($r = 0.37$, d.f. = 21, $P = 0.08$), and for eastern populations, it was non-significant but negative ($r = -0.45$, d.f. = 8, $P = 0.19$).

Rather than occupying discrete areas, the winter quarters of different breeding populations were large and often overlapping. However, there was a strong overall correlation between breeding and winter site longitude ($r = 0.75$, d.f. = 31, $P < 0.001$; Fig. 3b). When this analysis was repeated on data from just the eastern or western populations, it was significant for the former ($r = 0.69$, d.f. = 8, $P = 0.03$), but not the latter ($r = 0.02$, d.f. = 21, $P = 0.92$). There was also a strong correlation between pairwise distance matrices of breeding and winter sites (Mantel test; $r_M = 0.50$, $P = 0.001$), indicating that individuals which breed close together also winter close together. Again, when eastern and western populations were considered separately, the Mantel test was significant for the former ($r_M = 0.36$, $P = 0.02$), but not the latter ($r_M = -0.3$, $P = 0.68$).

Spring migration

Median departure date from the winter quarters was 5th March (IQR: 14th February – 17th March). Spring routes differed from autumn routes for all individuals (Table 1), most strikingly for Latvian rollers, whose spring 'loop' reached as far as 45°E (Figs 2 and S1). Spring stopover sites were often difficult to identify given their close proximity to the vernal equinox. Nevertheless, all individuals stopped before reaching Europe, and in most cases, these stopovers appear to be in the sub-Saharan savanna zone (in others,

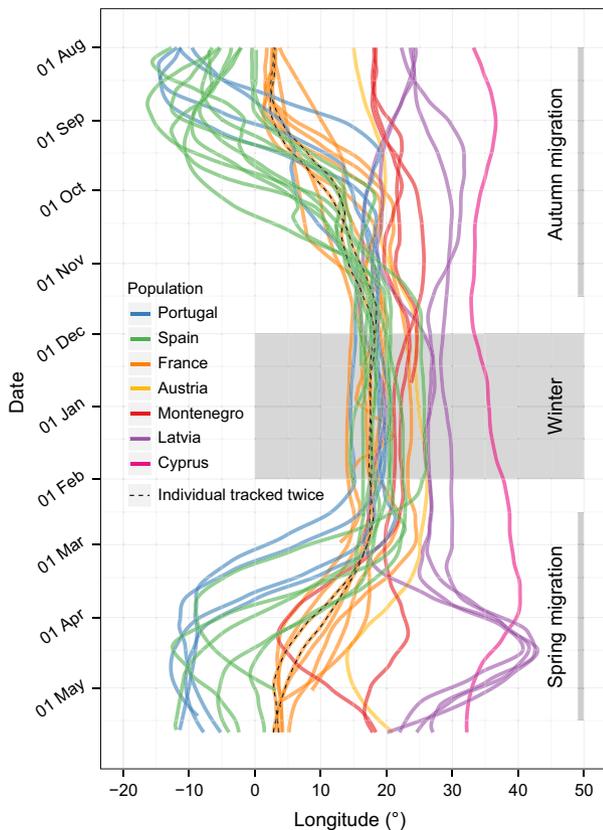


Figure 2 Smoothed longitudinal tracks of 32 European rollers (*Coracias garrulus*) from seven countries (LOESS regression, $\alpha = 0.25$). Note that time is on the y-axis, latitude is not represented and that, for obvious reasons, the Bulgarian ring recovery is not represented in this figure. Shaded box denotes winter period (December–January), and bars indicate approximate periods of autumn and spring migration. Dashed lines show the migration of a French roller tracked across two consecutive years.

Table 1 Country-level summary of the migration of 33 European rollers (*Coracias garrulus*) revealed by geolocators (GLS), satellite tags (PTT) and a ring recovery. Migration distance is measured as mean great circle distance between breeding and winter site. Spring–autumn displacement is the mean longitudinal difference between autumn and spring routes, with negative values indicating a westerly (clockwise) spring loop.

Country	<i>n</i>	Migration distance		Spring–autumn displacement (° ±SD)	
		(km ± SD)	Sub-Saharan stopover		
Portugal	4 GLS	6550 ± 271	Cameroon, Libya, Congo	Angola, Namibia	−5.4 ± 6.7
Spain	4 GLS 6 PTT	6800 ± 371	Nigeria, Cameroon, Niger, Chad	Namibia, Angola, Botswana	+2.2 ± 6.0
France	9 GLS	6450 ± 458	Chad, Niger, Nigeria, CAR	Angola, DRC, Namibia, Zambia	−4.2 ± 3.6
Austria	1 GLS	7350	Chad	Botswana	−4.0
Montenegro	3 GLS	6450 ± 287	Libya	Zambia, Botswana	−8.3 ± 5.3
Latvia	4 GLS	8050 ± 503	Chad, Sudan, Libya	Zambia, Botswana, Zimbabwe, Angola	+12.2 ± 5.0
Bulgaria	1 ring	5350	–	Tanzania	–
Cyprus	1 GLS	4050	Sudan	Kenya	+4.0

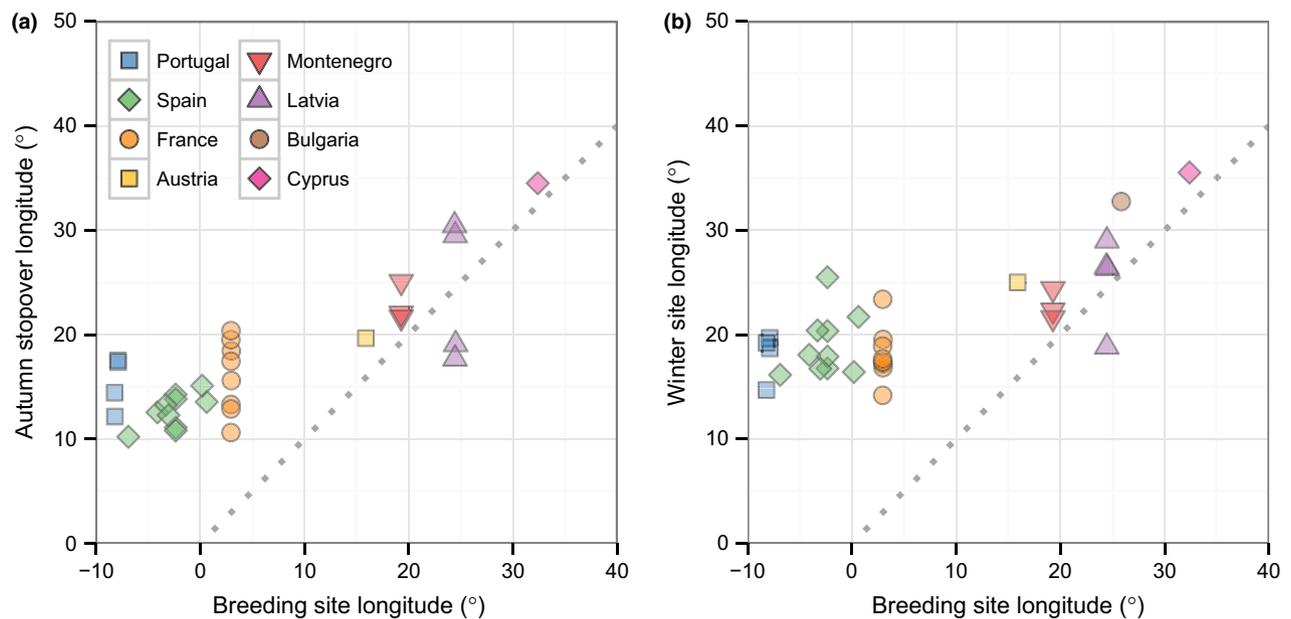


Figure 3 Relationship between (a) longitude of breeding site and first sub-Saharan autumn stopover ($r = 0.75$, d.f. = 31, $P < 0.001$) and (b) longitude of breeding site and winter site (Pearson's correlation; $r = 0.81$, d.f. = 29, $P < 0.001$). Dashed lines represent $x = y$.

latitudinal uncertainty was too large to tell; Fig. S1). Additional spring stopovers were made north of the Sahara by some individuals, as well as in West Africa by rollers from south-west Iberia. Median arrival date to the breeding grounds was 4th May (IQR: 29th April – 8th May), so rollers spent on average more than 8 months away from their breeding grounds.

We only successfully tracked one individual across multiple years, so are unable to make any quantitative conclusions regarding within-individual repeatability. However, the migration of this individual appears to be repeatable in space (see Fig. S1(b and f) and dashed lines in Fig. 2) and time; departure and arrival to and from winter and breeding grounds were consistent to within 6 days (but note the

potential uncertainty of geocator-derived phenological information).

Geocator-derived locations are inherently imprecise and potentially inaccurate, so an evaluation of the sensitivity of our conclusions to this source of uncertainty is crucial. Imprecision in estimated winter locations (SD = 540 km for latitude, 214 km for longitude) was small relative to the cross-hemispheric movements of this long-distance migrant, and our randomization tests show that our conclusions based on mean autumn and winter positions are robust; on only one occasion did an originally significant ($P < 0.05$) test have 95% confidence intervals overlapping zero, and this was only marginal (Appendix S1). Confidence intervals were wider for outputs of tests incorporating latitudinal

information than those based on longitude only, owing to the greater imprecision of the former. Whilst it is not possible to quantify the potential inaccuracy arising from the application of an inappropriate sun elevation angle, altering the chosen in-habitat sun angle by $\pm 0.5^\circ$ and $\pm 1.0^\circ$ resulted in average latitudinal displacements in mean winter position to the north (angle decrease) or south (angle increase) of 138 km and 275 km, respectively. Finally, our resampling experiments suggest that test coefficients stabilize by $n \approx 10$, with the inclusion of additional samples having no effect on coefficient precision (Appendix S2).

DISCUSSION

Knowledge of the year-round spatial distribution of migrant populations is critical for their conservation (Newton, 2008). To protect a specific breeding population, it is important to know not only where they migrate to and how they get there, but to what extent they mix with individuals from other populations (e.g. Jones *et al.*, 2008; Iwamura *et al.*, 2013). Here, we have performed the first wide-scale multinational analysis of migratory connectivity in the European roller, a charismatic and globally near-threatened migrant bird. New data from France and Portugal are broadly consistent with the two previous studies from these breeding populations (Catry *et al.*, 2014; Emmenegger *et al.*, 2014), with data on the previously unknown migration routes of Austrian, Montenegrin, Cypriot and Latvian rollers greatly extending our knowledge of this species' year-round movements.

Our randomization trials showed that analyses using latitudinal data were more sensitive to geolocator imprecision (arising due to day-to-day variation in shading) than those incorporating longitudinal information only, but in general, our conclusions are robust to this imprecision. The second component of geolocator uncertainty is calibration error, that is the application of an inappropriate sun elevation angle. This inaccuracy is not possible to quantify in our study (see Fudickar *et al.*, 2012; Lisovski & Hahn, 2012; McKinnon *et al.*, 2013) but affects latitude only and is only likely to be a concern if rollers experience considerable differences in shading conditions over winter compared to during the breeding season. We acknowledge this unknown potential for latitudinal inaccuracy (perhaps up to several hundred km), but note that our conclusions are predominantly based on east–west, rather than north–south, segregation. Finally, our resampling experiments suggest that the inclusion of additional data would not necessarily increase the robustness of our conclusions.

Autumn migration

In western rollers, autumn migration occurred on two fronts: rollers from the south-west of the region took a westerly route along the Atlantic coast of West Africa and then turned east along the savanna belt, whereas those from

north-east Spain and southern France took a more direct route across the Sahara (Catry *et al.*, 2014; Emmenegger *et al.*, 2014; Rodríguez-Ruiz *et al.*, 2014). This suggests a trade-off between the additional time and energy required to make a detour and the costs associated with the desert crossing, which is narrower and potentially more benign towards the coast (Alerstam, 2001; Rodríguez-Ruiz *et al.*, 2014). Similar detours are made by common swifts *Apus apus* and common redstarts *Phoenicurus phoenicurus* from northern Europe (Åkesson *et al.*, 2012; Kristensen *et al.*, 2013), suggesting that the factors driving the selection of this route may not be unique to the roller. Interestingly, individuals from both sides of this migratory divide eventually converged at similar autumn stopover sites and wintered in the same region of south-west Africa. For eastern rollers, there was no evidence of any detours shortening the southward Sahara crossing.

Given that the roller is predominantly a sit-and-wait predator (so unlikely to 'fly-and-forage') and an active, flapping flier, we expected migration to be punctuated by stopovers for refuelling (Alerstam & Hedenström, 1998), the locations of which are clearly important from a conservation perspective. Our study supports previous work identifying the northern savanna zone, particularly the Lake Chad basin, as an important autumn stopover site for rollers from western European populations (Catry *et al.*, 2014; Emmenegger *et al.*, 2014; Rodríguez-Ruiz *et al.*, 2014). We also show that individuals from eastern populations make use of this area. Although the longitude of breeding and autumn stopover sites were positively correlated (indicating 'parallel' migration), the longitudinal spread of the latter was narrower, suggesting convergence of rollers from across Europe. The northern savanna is an important site for many insectivorous migrants that winter further south (Morel, 1973), and recent tracking studies have demonstrated its importance for species including Eleonora's falcon *Falco eleonora* (Mellone *et al.*, 2013), red-backed shrike *Lanius collurio* (Tøttrup *et al.*, 2012), European bee-eater *Merops apiaster* (Arbeiter *et al.*, 2012) and common cuckoo *Cuculus canorus* (Willemoes *et al.*, 2014). Droughts in this region during the 1970s and 1980s reduced the survival and population size of several European visitors, presumably due to reduced prey abundance (e.g. Peach *et al.*, 1991; Baillie & Peach, 1992). Given that rollers from across Europe converge on this region, in both autumn and spring, any environmental degradation (e.g. Held *et al.*, 2005; Zwarts *et al.*, 2009) would likely have widespread population consequences. Currently, only the Chadian portion of Lake Chad is designated as an Important Bird Area, with no protection afforded in north-east Nigeria or in the surrounding basin.

Winter quarters

All tracked rollers wintered in the tropical grasslands, savannas and shrublands (Olson *et al.*, 2001) of southern Africa, 4000–8600 km away from their breeding sites. The roller's arrival in southern Africa coincides with the southward

movement of the Intertropical Convergence Zone (ITCZ) and the return of the wet season to this region, whilst the northern savannas are entering the dry season (Barry & Chorley, 1992). Our data conform to the official species distribution map (Fig. 1; Birdlife International & NatureServe, 2013), although none of our tracked rollers wintered as far south as South Africa (which is perhaps occupied by rollers from the far east of the breeding range, including the *semenowi* subspecies). Given that none of the 24 rollers from western Europe wintered in West Africa, we suspect that the species occurs here only on passage and suggest that a revision of the current distribution be considered. However, further research is necessary, particularly given the unknown winter quarters of the small north African breeding population.

Although the winter ranges of different (and often distant) breeding populations overlapped, the distribution of wintering rollers with respect to their breeding origin was significantly non-random. In addition to strong longitudinal correlations between breeding and winter sites, there was a correlation between pairwise distance matrices of breeding and winter sites. These results suggest that migratory connectivity is neither absent nor strong, but somewhere in the middle of the 'weak-strong' continuum defined by Webster *et al.* (2002). This moderate level of connectivity ($r_M = 0.50$) is similar to that measured by Trierweiler *et al.* (2014) in their study of Montagu's harriers *Circus pygargus* from northern Europe ($r_M = 0.56-0.60$), although such interspecific comparisons should be made with caution due to the scale dependence of connectivity measurements. The fact that rollers from discrete breeding populations spread out over a larger area during the non-breeding season may increase their (population-level) resilience to deterioration of local environmental conditions on the non-breeding grounds. On the other hand, it could dilute the strength of interseasonal density effects (Norris & Marra, 2007). For instance, if a population suffers a locally catastrophic breeding season but mixes with individuals from across Europe over winter, the expected density-dependent reduction in per-capita overwinter mortality may not be realized.

Migratory connectivity appears to be stronger for eastern populations compared to western ones, as demonstrated by significant correlations between (1) breeding and winter site longitude and (2) pairwise distance matrices of breeding and winter sites for the former, but not the latter. Similarly, Rodríguez-Ruiz *et al.* (2014) found no evidence for connectivity in Spanish rollers. Whilst these differences may reflect the different spatial structure of eastern (mean pairwise distance between breeding sites = 1202 km) versus western (536 km) study sites, an alternative explanation for this disruption to connectivity in the west may be the easterly circumnavigation of the Gulf of Guinea. In contrast, eastern birds are able to make a southerly, 'parallel' migration, thus maintaining their longitudinal structure. This intriguing possibility points to the potential importance of continental configuration as a driver of connectivity patterns in other

species. Stronger connectivity in eastern populations may increase their vulnerability to loss of non-breeding habitat compared to western ones (Jones *et al.*, 2008), a possibility that deserves attention in the face of strong population declines in the east (Kerus & Račinskis, 2008; Kovacs *et al.*, 2008).

There was no overall relationship between breeding and winter site latitude, but the non-significant tendency for high-latitude eastern breeders to winter at more southerly latitudes suggests a leapfrog migration, with a significant positive relationship between breeding latitude and migration distance. Rollers from the relict (Kerus & Račinskis, 2008) Latvian population wintered 800–2000 km south of the roller from the increasing (Burfield & Bommel, 2004; but see Pomeroy *et al.*, 2013) Cypriot population, despite breeding ~2400 km further north. Whilst this conclusion largely relies on a single data point from Cyprus and is based on latitudinal patterns that are prone to uncertainty, the Bulgarian ring recovery adds further support to our hypothesis. Leapfrog patterns have been described in a number of migrants, including many wader species (e.g. Duijns *et al.*, 2012) yellow wagtail *Motacilla flava* (Bell, 1996) and barn swallow *Hirundo rustica* (Ambrosini *et al.*, 2009), and may reflect competitive differences or different optimal time allocation strategies between northern and southern breeding populations (Greenberg, 1980; Bell, 1996; Alerstam & Hedenström, 1998). Further multipopulation tracking studies are necessary to explore the generality of leapfrog migration, in addition to its causes and consequences.

Spring migration

The northern savanna zone also appears to be used on spring migration, when stopovers were generally south of their autumn equivalents (although note large latitudinal uncertainty due to proximity to equinox and equator), as expected given that the northern savanna becomes increasingly dry over winter. All individuals exhibited, to some extent, a loop migration. French and Montenegrin rollers had a small clockwise loop, whereas Latvian rollers had a large anticlockwise loop, taking them to the Horn of Africa and along the Arabian Peninsula. This route, proposed by Hogg *et al.* (1984) and presumably driven by regional variation in foraging and/or wind conditions (Pearson & Lack, 1992), is supported by the recovery of a Latvian-ringed roller on spring migration in Saudi Arabia (data not shown). The recovery of ringed Serbian and Hungarian rollers in Arabia suggests that other eastern populations also use this route (Stanković, 2011; Tokody, B. pers. comm.). Recent tracking of red-backed shrikes (Tøttrup *et al.*, 2012) and Eleonora's falcons (Mellone *et al.*, 2013) shows that this route is not unique to rollers, but may be important for many insectivorous migrants. In contrast, common cuckoos (Willemoes *et al.*, 2014) and Montagu's harriers (Trierweiler *et al.*, 2014) perform a clockwise loop, with spring migration displaced to the west. All three ringed rollers recovered in Arabia were

shot, and anecdotal evidence suggests that large numbers of rollers are killed by hunters in this region (e.g. Del Hoyo *et al.*, 2001). Having been separated by up to 1000 km on autumn migration and over winter, the spring migration of Latvian rollers occurred in a synchronous and narrow front, so any threats present in this region will likely affect all members of the population.

CONCLUSIONS

Our study supports existing data on the migration of rollers from western Europe and describes new routes from eastern Europe, including a large synchronous loop migration (via Arabia) performed by Latvian rollers, and a putative leapfrog pattern in the east. It also highlights the importance of the northern savanna zone as a stopover region for this species. We perform the first pan-European quantification of migratory connectivity in this species, finding a non-random spatial structure despite some mixing of individuals from different breeding populations. Any conservation actions in southern Africa would therefore have wide-ranging but diffuse effects. Connectivity appears to be stronger for eastern populations, many of which have undergone severe declines in recent decades. Whilst it is unclear exactly what the consequences of the level of connectivity detected here will be for roller population dynamics, we are now in a position to start exploring explicit hypotheses.

Although our findings appear robust to the inherent imprecision of geolocator data and our relatively small sample sizes, future studies should aim at more precisely elucidating the sites used; we are currently limited to making only large, international-scale conservation recommendations. We expect many of our findings to be consistent across other flapping, insectivorous, terrestrial birds faced with similar environmental constraints. For example, if driven by prey availability and weather conditions, migration routes (e.g. detours to shorten the Sahara crossing, stopovers in the northern savanna) should be fairly conserved across species. More broadly, we suggest that continental configuration plays a role in shaping patterns of connectivity. The development of migration strategies at the individual level is also predicted to be important in determining connectivity patterns (Cresswell, 2014), so studies of juvenile migration and adult route fidelity are crucial. We also recommend research into differential migration in relation to sex, and spatial and temporal patterns of mortality during the non-breeding season. This information should be combined with genetic analyses to examine the interplay between migratory connectivity and the structure and isolation of breeding populations to further inform conservation management.

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SUPPORTING INFORMATION

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

Table S1 Summary of solar geolocator deployment and recovery.

Figure S1 Migration route of 17 European Rollers revealed by solar geolocators.

Appendix S1 Results of randomised iterative procedure exploring the sensitivity of our analyses to geolocator imprecision.

Appendix S2 Results of resampling experiments exploring the influence of sample size on the precision of our results.

DATA ACCESSIBILITY

Raw light files for new solar geolocators ($n = 17$) are available on Movebank (<http://www.movebank.org>, study name 'Migratory connectivity in the European roller (data from

Finch *et al.* 2015)') and are published in the Movebank Data Repository with DOI 10.5441/001/1.874gb577.

BIOSKETCH

Tom Finch is a NERC-funded PhD candidate at the University of East Anglia. He is interested in the links between environmental change, behaviour, demography, and population dynamics, especially in migratory birds. His PhD explores these issues in the European roller (project website: <http://www.coracias-research.co.uk/>).

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