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Migratory connectivity of barn swallows in South Africa to their Palaearctic breeding grounds

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Abstract

Aim: To demonstrate that the population of barn swallow *Hirundo rustica* in South Africa in the austral summer is not a pan-mixture of birds from their vast Palaearctic breeding range and to estimate proportions of barn swallows in four South African regions migrating to three breeding ground zones.

Location: South Africa and Eurasia.

Methods: We analysed citizen science barn swallow ringing records, obtained between 1954 and 2011 in South Africa, and their recoveries made in Eurasia. We used the "division coefficient" method to model the spatial variability of the recovery process and to estimate proportions of barn swallows ringed in four regions of South Africa (KwaZulu-Natal, Gauteng, eastern part of Northern Cape and the Western Cape) migrating to three zones in the Eurasian breeding grounds: western (west of 10°E), central (10°–60°E) and eastern (east of 60°E).

Results: The percentages of barn swallows migrating from KwaZulu-Natal to the eastern and central Palaearctic zones were estimated at 54.0% and 46.0%, respectively. The percentages from Gauteng to the central and western zones were 80.5% and 15.7%, from the Northern Cape to the central and western zones were 43.7% and 56.3% and from the Western Cape to the eastern, central and western zones were 30.8%, 35.4%, 33.8%. The estimate of the observer process suggested that reencounter rates per 10,000 swallows ringed increased from east to west: 32 reencounters per 10,000 in the eastern zone, 36 in the central zone and 50 in the western zone.

Main conclusions: These results provide the first quantitative estimates of the composition of barn swallow populations in four regions of South Africa, relative to their Palaearctic breeding zones.

KEYWORDS
African–Palaearctic migrant, barn swallow, division coefficient, *Hirundo rustica*, migratory connectivity, ringing recovery

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1 | INTRODUCTION

Migratory connectivity indicates where migratory populations spend different seasons of the year and different stages of the life cycle; this knowledge is essential for conserving migratory birds (Webster & Marra, 2004; Webster, Marra, Haig, Bensch, & Holmes, 2002). Hundreds of millions of birds of several hundred species migrate between their breeding and nonbreeding grounds twice every year, creating a vast network of ecological connections (Moreau, 1972). Bird migration is intrinsically complex in its ecology, biology, diversity, temporal and spatial patterns (Moreau, 1972), its mechanisms and constraints (Berthold, 1996), its capacity to transport disease (Peterson, Benz, & Pape, 2007; Webster et al., 2002) and the capacity of species to cope with human-induced environmental threats, including climate change (Knudsen et al., 2011). Patterns of anthropogenic climate change have revealed large geographic variability (Simmons et al., 2017; Vose, Easterling, & Gleason, 2005), as have ecological responses to climate change (Ahas, Aasa, Menzel, Fedotova, & Scheifinger, 2002; Both et al., 2004; IPCC, 2014; Knudsen et al., 2011; Menzel, Estrella, & Fabian, 2008; Menzel et al., 2006; Sparks & Menzel, 2002; Walther et al., 2002). Coincidentally with rapid climate change since the 1970s, bird populations have declined throughout the Northern Hemisphere, some catastrophically (Vickery et al., 2014). There are many potential causes for these declines, including multidecadal droughts (Walther, Van Niekerk, & Rahbek, 2011). Human-induced habitat loss, agricultural intensification, hunting, pollution, loss of migration routes and climate change all threaten species, and their cumulative effects impact resilience to individual threats (Vickery et al., 2014). Rapid climate changes, including altered timing of the seasons, and their immediate and delayed effects ("seasonal interactions", Webster & Marra, 2004), could make bird survival and adaptation increasingly difficult (IPCC, 2014, Vickery et al., 2014). Climate change causes population declines in migrants that cannot respond sufficiently (Møller, Rubolini, & Lehikoinen, 2008), or by disrupting the synchrony between populations and the conditions on which they depend, including their prey availability (Jones & Cresswell, 2010). Understanding migratory connections is therefore crucial for assessing the contribution of climate change to population declines, particularly when there is also evidence of phenological change.

Here, we use South African ringing data for the barn swallow *Hirundo rustica* to estimate migratory mixing in this species. The European subspecies of the barn swallow *Hirundo rustica rustica* (hereafter "barn swallow") decreased in abundance in Europe west of Russia between 1980 and 2009 by 18% (total decline in estimated population size over the period) (Vickery et al., 2014). The barn swallow breeding grounds stretch from Ireland in the west to Siberia in the east; within this longitudinally broad range, its life cycle timing (phenology) has changed to different extents and in opposite directions (Møller, 2004; Sokolov, Markovets, Shapoval, & Morozov, 1998; Sparks & Braslavská, 2001; Sparks & Tryjanowski, 2007). Similarly, there were geographically variable phenological changes at the nonbreeding grounds in South Africa

during the 1990s and 2000s, with estimated shifts of up to two weeks in migration and moult phenology (Altwegg et al., 2012; Møller, Nuttall, Piper, Szép, & Vickers, 2011). Also in South Africa over this period, the mean start of primary feather moult shifted six days earlier (in Gauteng, north-eastern highlands) and seven days later (in the Free State, central highlands), with intermediate or no shifts in the other zones (Eastern Cape, Western Cape, and KwaZulu-Natal), and in some zones, the start of premigratory fuelling shifted in similar directions to the timing of moult and migration (Burman, 2016). Although these changes in different hemispheres might have many causes, Northern Hemisphere climate change is thought to be a key factor (Altwegg et al., 2012; Møller et al., 2011).

Migratory connectivity can be measured according to the strength of the connections between breeding and nonbreeding populations— that is, the extent to which separate breeding populations mix at the nonbreeding grounds, or vice versa (Webster et al., 2002). Stronger connectivity equates to weaker mixing (Supporting information Figure S1 in Appendix A) (Webster et al., 2002). A bird ring that is recovered at the breeding grounds, from a recaptured or dead bird that was originally ringed at the nonbreeding grounds, provides evidence of a migratory link between the sites (hereafter, "recovery" refers to all ring reencounters). Recoveries of barn swallows have revealed connections between the breeding and nonbreeding grounds, and the geographic distributions of these recoveries have been used to describe migratory connectivity (de Bont, 1970; den Brink, Bijlsma, & van Have, 1997; Davis, 1965; Drost & Schüz, 1952; Loske, 1986; Mead, 1970; Moreau, 1952, 1972; Oatley, 2000; Rowan, 1968; Zink, 1970). However, raw numbers of recoveries are not a quantitative estimate of migratory connectivity, because they do not take account of the observation process—the likelihood that a ringed bird will be encountered and reported, which depends on human population density and public awareness of how to report a ringed bird (Perdeck, 1977). A basic statistical method ("division coefficient method") to describe the observation process was developed by Busse and Kania (1977) and Kania and Busse (1987). This method simultaneously estimates the "ring reencounter rate" (birds recovered as a proportion of the total ringed) and the division coefficients—the proportion of birds from each source area estimated to migrate to each destination during the study period (Busse & Kania, 1977; Kania & Busse, 1987; Korner-Nievergelt, Schaub, Thorup, Vock, & Kania, 2010). The division coefficient method was applied to the song thrush *Turdus philomelos* (Busse, 1981; Busse & Maksalon, 1978, 1986; Kania, 1981) and chaffinch *Fringilla coelebs* (Kania, 1981). We believe this is an efficient and underutilized method in the study of migratory connectivity, and here, we apply it to test the earlier hypothesis (Oatley, 2000; Rowan, 1968) that although barn swallows from the entire Palaearctic breeding grounds mix at their nonbreeding grounds in South Africa, they do not form a pan-mixture. Rowan (1968) and Oatley (2000) based their hypothesis on raw numbers of recoveries and were limited to qualitative statements about migratory connectivity. We aim here to quantify the levels of mixing of barn swallow breeding populations at nonbreeding grounds in South Africa.

2 | METHODS

Barn swallow ringing records from October to April, the main period when the species is present in South Africa, were extracted from the South African Bird Ringing Unit (SAFRING) database for 1954 to 2012 (Underhill & Oatley, 1994), with additional information about ringing totals for 1963–1968 from Rowan (1968). Barn swallows were trapped at roosts mostly in the evening using mist nets (de Beer et al., 2001). Years refer to the periods starting in October of the year named and ending in April the following year. The first and last ringing dates varied from year to year, so we do not give exact starting and ending dates. Five of the nine provinces of South Africa had adequate volumes of data: Western Cape (WC), Northern Cape (NC), Free State (FS), Gauteng (GP), KwaZulu-Natal (KZN) (Figure 1a).

Recoveries (of dead birds) and recaptures of live birds ringed in South Africa were extracted from the SAFRING database (Underhill & Oatley, 1994). The barn swallows which migrate to South Africa breed north of the Sahara Desert, and almost exclusively north of the Mediterranean Sea (Roselaar, 1988; Turner, 2006). Our interest was in birds recovered at or near their breeding grounds, and we thus used recoveries north of 36°N, which provides an approximate southern border for the breeding grounds (this excluded six reencounters from northern Africa and the Middle East). We grouped recoveries into three Palaearctic longitudinal sections ("zones"): west of 10°E ("western"), between 10°E and 60°E ("central"), and east of 60°E ("eastern") (Figure 1b). The western zone includes the British Isles and part of western Europe and Scandinavia, and the central zone covers the rest of western, eastern, southern Europe and Scandinavia as well as the Eastern European Plain (35°E to 45°E) as far east as the Ural Mountains at c. 60°E. The eastern zone covers Siberia east of the Ural Mountains. These zones cover the breeding range, which extends as far east as the Yenisei River Basin in Siberia (Roselaar, 1988) at about 92°E, of the barn swallows which migrate to Africa. We took into account the longitudinal distribution of recoveries when deciding on the divisions. According to the division coefficient method (Kania & Busse, 1987) there can be as many destination zones as source areas, but not more. We used three destination zones because further subdivision would have created zones with too few recoveries from some of the four regions in South Africa. We assumed that all barn swallows were recovered or retrapped in their breeding zones and that there was minimal migration between zones; we therefore included all available reencountered rings in the analysis.

The division coefficient method (Busse & Kania, 1977; Kania & Busse, 1987) was used to estimate the "ringing-recovery ratios" and division coefficients for the Palaearctic zones (Supporting information Appendix B). The ringing-recovery ratio for a destination is the estimated number of birds which need to be ringed to produce one recovery at the destination area; the inverse is the ring reencounter rate, and the division coefficients are the proportions of birds estimated to migrate from each source to each destination. To assess whether dead recoveries had different ring reencounter rates to all ring reencounters pooled together, we analysed the dead recoveries separately and used a chi-squared test to compare the two sets of division coefficients.

The division coefficients for each source zone should sum to unity (100% of birds ringed in that zone), if all requirements and assumptions are supported by the data (Supporting information Appendix C). We therefore present the absolute value of the difference between the sum of the division coefficients and unity, as an indicator of support for the model's requirements and assumptions (hereafter referred to as "residual"). For comparisons between zones, we rescaled the division coefficients to sum to unity within each zone. We obtained 95% confidence intervals for the ring reencounter probabilities and division coefficients by taking 1000 bootstrap samples with replacement from the data set of ringing and recovery records (Korner-Nievergelt et al., 2010). The "birdring" package (Korner-Nievergelt & Robinson, 2014) in R version 3.1.2 (R Core Team, 2017) was used to estimate the division coefficients and bootstrapped confidence intervals.

3 | RESULTS

3.1 | Proportions migrating to different breeding zones

The data set consisted of 201195 barn swallow ringing records collected within the five source provinces in South Africa between October and April, from February 1955 to April 2012. Of those birds, 552 (0.27%) were recovered in the Palaearctic (27 per 10 000; Table S1). The estimated division coefficients for the period 1954 to 1986 (Table 1, Figures 1a, b) revealed that barn swallows from the three zones of the breeding grounds were present in each of the source areas of South Africa, but in varying proportions. Those from eastern South Africa (KwaZulu-Natal) migrated to the eastern (54.0%) and central (46.0%) zones, and those from Gauteng migrated to the central (80.9%) and western (15.7%) Palaearctic zones (Table 1, Figures 1a, b). Those ringed in central western South Africa (Northern Cape) migrated to the western (56.3%) and central (43.7%) zones (Table 1, Figures 1a, b). Western Cape barn swallows were distributed evenly across the three Palaearctic zones (33.8%, 35.4% and 30.8% respectively; Table 1, Figures 1a, b). These division coefficients reflect a similar distribution to the raw recoveries in the Palaearctic from 1954–1986 (Supporting information Table S1). For every 10 000 birds ringed in South Africa, the ring reencounter rates for the western, central and eastern zones of the Palaearctic were 50, 36 and 32 recoveries, respectively (Table 1).

3.2 | Change in recovery rates in the late 1980s

The recovery rates plotted by five-year period show that the reencounter rate was consistently greater before 1987, at 0.38% (38 recoveries per 10,000 ringed birds), than after 1987, when it was 0.08% (8 per 10,000; Supporting information Table S1 a, Appendix D; Figure 2). This change has the potential to introduce
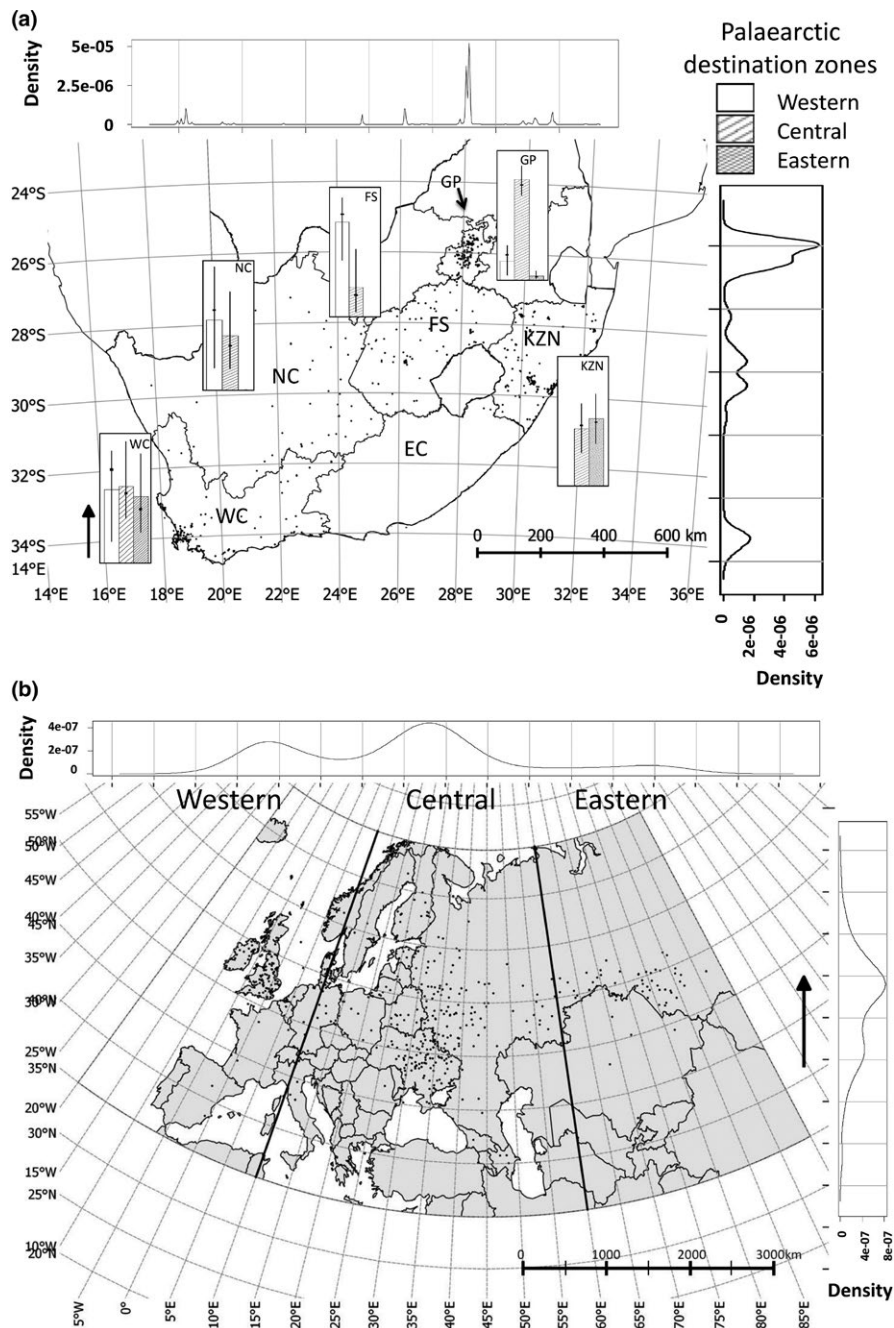
FIGURE 1 Locations of ringing (a) and recovery (b) of barn swallows ringed in South Africa in 1954–2011 (for provinces with enough data to analyse), and their spatial distributions shown by kernel density curves in the margins. a) Bar graphs show the proportions of birds estimated to migrate from the South African areas to each of the three Palaearctic zones shown in b, during 1954–1986, accounting for unequal recovery rates in the Palaearctic ("Division coefficients," Table 1). The height of the bars in each graph sums to 100%, and the graphs have the same scale. Source areas: KZN: KwaZulu-Natal, GP: Gauteng, FS: Free State, NC: Northern Cape, WC: Western Cape, EC: Eastern Cape (not analysed due to insufficient data). Vertical error lines are nonparametric 95% confidence intervals. For the Free State, virtually all recoveries were after 1987 (Supporting information Table S1a), and its division coefficients (Supporting information Table S4) were estimated separately to the others shown here; hence, comparison between this and the other zones must be treated with caution. b) Palaearctic zones—western zone: west of 10° E; central zone: 10°E to 60°E; eastern zone: east of 60°E. The projection is Albers Equal Area, customized for (a) southern Africa and (b) Eurasia—the maps can therefore be divided into equal area grid cells of (a) 200 km^2 and (b) 1000 km^2 in extent (these gridlines are not shown, but their positions are reflected by the tick marks along the top and right of each map). The kernel densities in the margins are calculated based on the location of the records on the equal area projection and are therefore aligned to the equal area tick marks

an unknown error into the division coefficient estimates, because the method assumes that the reencounter rate does not change during the study period (Busse & Kania, 1977; Kania & Busse, 1987). To investigate the effect of this apparent change, we estimated division coefficients both for all years in the data set (1954–2011) and for a subset of years (1954–1986). Most (64%) birds

were ringed before 1987, and of those, 87% were ringed between 1962 and 1971 (Supporting information Table S1a, Figure 2).

Considering the period 1954–2011, the central Palaearctic zone had the most recoveries (61%) as well as highest recovery rate among the Palaearctic zones, at 0.17% of all barn swallows ringed; the eastern Palaearctic zone, comprising 11% of recoveries, had the lowest (0.03%) recovery rate (Supporting information Table S1a; for dead recoveries only, refer to Table S1b). The former USSR/Russia contributed the most recoveries (327) followed by Great Britain with 113 (Supporting information Table S2).

Using only the data for 1954–1986, the residuals ranged from 0% (Gauteng) to 2.7% (Northern Cape), whereas for the pooled data (1954–2011), the residuals were as high as 53.8% for the Free State (Supporting information Table S3). After rescaling the division coefficients for the entire period to 100%, most (76.0%) barn swallows from the Free State migrated to the western Palaearctic

(Supporting information Table S4, Figures 1 and 2), and the division coefficients for the other zones were similar to those for 1954–1986 (Table 1).

The 552 recovered rings included 422 recoveries of dead birds, 121 live controls (recaptures), nine sick birds, and one with unknown finding status. Of the 422 dead birds, 389 were recovered before 1987 (Supporting information Table S1b), and we estimated the ring reencounter rates and division coefficients separately for this group: ring reencounter rates, in each Palaearctic zone, were 28 reencounters in the western and eastern Palaearctic zones, and 32 in the central Palaearctic zone, per 10,000 ringed birds (Supporting information Table S5). The estimated ring reencounter rates in each Palaearctic zone thus differed when calculated using the dead recoveries and pooled birds: using the pooled data, the rate differed between zones by up to 18 birds per 10,000 ringed (Table 1), whereas using only the dead birds, this difference was reduced to

TABLE 1 Proportions of barn swallows migrating from different provinces of South Africa to each Palaearctic zone, between October and April, from 1954 to 1986 ("division coefficients"), accounting for unequal ring recovery rates in the Palaearctic. Brackets enclose 95% confidence intervals. Division coefficients sum to 100% across rows. For description of provinces and Palaearctic zones, see Figures 1a, b

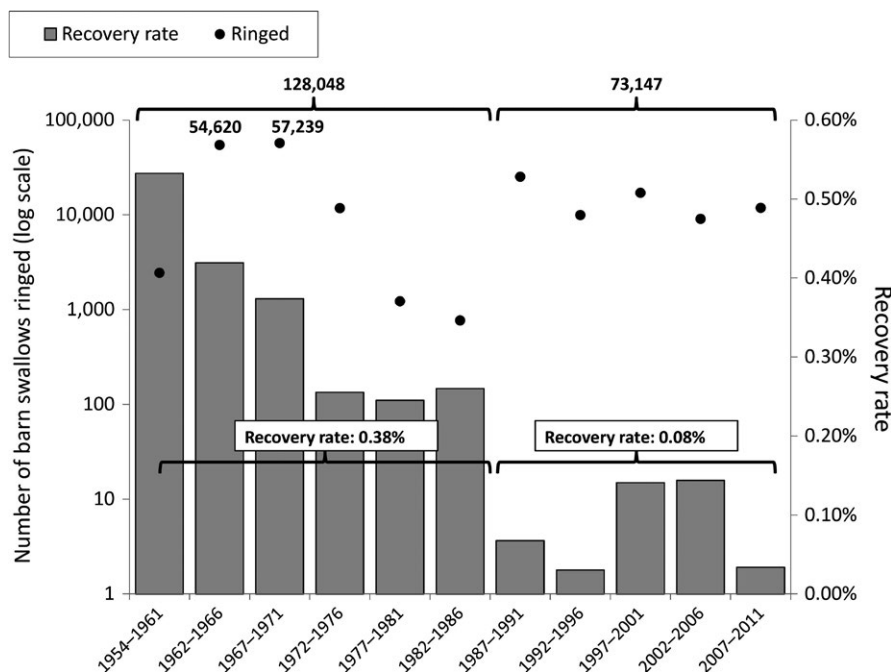| Palaearctic zone		Western (W10E)	Central (E10_W60E)	Eastern (E60E)
Ring reencounter rate (estimated reencounters per 10,000 birds ringed)		50 (30–156)	36 (30–45)	32 (20–55)
Division coefficients (expressed as percentages)	WC	33.8 (10.3–51.5)	35.4 (20.8–55.7)	30.8 (14.4–50.1)
	NC	56.3 (17.8–99.0)	43.7 (17.2–79.1)	0.0 (0.0–0.0)
	GP	15.7 (4.6–28.2)	80.5 (67.8–91.4)	3.8 (1.5–7.8)
	KZN	0.0 (0.0–0.0)	46.0 (26.8–66.2)	54.0 (34.1–73.9)

FIGURE 2 Numbers of barn swallows ringed in South Africa (filled black circles, log scale) and their recovery rates in the Palaearctic (bars), for five-year periods (except the first period) between 1954 and 2011. Ringing occurred between October and April. The totals ringed up to and after 1986 are highlighted above the graph. Further, the totals ringed in the periods 1962–1966 and 1967–1971 are included as reference values

four (Supporting information Table S5). Nevertheless, the division coefficients were similar whether obtained using the pooled recoveries or only the dead birds (Pearson's chi-squared test = 108, df = 90, p = 0.095). To reduce the possible error in our results, prior to analysis we excluded some data belonging to groups that seemed to have unrealistically high recovery rates (593 records and 14 recoveries) (Supporting information Table S6).

4 | DISCUSSION

These estimates quantify barn swallow migratory connectivity across the Palaearctic breeding grounds, accounting for the observation process in terms of spatially variable ring reencounter rates. These results provide quantitative confirmation of the intuitive hypotheses about uneven rates of barn swallow mixing in South Africa (Oatley, 2000; Rowan, 1968) that were based on the raw recovery data. Although our study incorporated the data used to formulate those hypotheses (Oatley, 2000; Rowan, 1968), this consistency was not a foregone conclusion, because accounting for the observation process can produce results that are quite different to the raw recovery distribution (Busse & Kania, 1977; Kania & Busse, 1987). Our results are consistent with the finding that long-distance migrant land birds tend to have high levels of mixing at their nonbreeding grounds (Finch, Butler, Franco, & Cresswell, 2017).

Barn swallows migrate into and out of Europe in a broad east–west front, rather than along narrow routes (Turner, 2006). Even in southern Africa, barn swallows partially maintain the south–north migratory axis—we found a greater proportion of barn swallows from the central and eastern Palaearctic in eastern South Africa, and more from the western Palaearctic in western South Africa. The south–north axis is similarly revealed from patterns of recoveries in Africa of barn swallows ringed in Europe (Thorup, Korner-Nievergelt, Cohen, & Baillie, 2014). Our findings support the hypothesis (Rowan, 1968) that barn swallows from east of the Urals migrate to the eastern and southern coastal regions of South Africa (KwaZulu-Natal and Western Cape) and therefore likely also to the Eastern Cape (which was not included in our analysis due to paucity of data). The division coefficients reveal that most barn swallows in Gauteng, the Free State and Northern Cape breed west of the Ural Mountains. On the contrary, those inhabiting eastern South Africa, and to a lesser extent those from the south-western coastal plain, breed east of the Ural Mountains. This pattern suggests that barn swallows from the eastern Palaearctic arrive in South Africa along an eastern African coastal route, with some eventually reaching the Western Cape—this is a known migration route for intra-African migrants (Berruti, Harrison, & Navarro, 1994) and probably also for long-distance Palaearctic migrants. For birds using this migratory route, the Great Escarpment (the mountain range separating the central South African plateau from the coast) could act as a migratory barrier, constraining most of the eastern Palaearctic barn swallows to the coastal plain of South Africa.

The first descriptions of barn swallow connectivity between the 1950s and 1990s were anecdotal, and until the late 1960s were based on small sample sizes (de Bont, 1970; Davis, 1965; Loske, 1986; Mead, 1970; Moreau, 1952, 1972; Oatley, 2000; Rowan, 1968; Zink, 1970). The earliest studies of recovery distributions suggested that birds from the United Kingdom spent the nonbreeding season in South Africa but not further north, whereas those from continental Europe stayed mostly near the equator, where birds from different parts of Europe mixed (Drost & Schüz, 1952; Moreau, 1952). Evidence from Africa confirmed this mixing, with birds ringed in the Congo in the 1950s recovered across a wide range in Europe and into the former USSR (de Bont, 1970), and those recovered in Namibia and Botswana coming from England and other northern European countries (Loske, 1986; van den Brink et al., 1997). Our work could not address these suggestions, because ringing data for further north in Africa is relatively sparse, and birds ringed north of South Africa could be on migration. Therefore, the latitudinal separation in Africa of Palaearctic breeding populations must be addressed using other methods. The migratory connectivity of this subspecies north of South Africa has been estimated using cluster detection (Ambrosini, Møller, & Saino, 2009) and analysis of stable-isotope profiles and phenotypic and demographic characteristics in breeding populations (Møller & Hobson, 2004). Those studies cannot be compared directly with ours, because of the different objectives, methods and resolution of the results.

The European subspecies of the barn swallow experienced spatially diverse phenological changes, over a period during which its abundance in Europe west of Russia also declined (Vickery et al., 2014): in the United Kingdom from 1950–2005 barn swallows arrived on average nine days earlier in spring (Sparks & Tryjanowski, 2007); in the Baltic region, from 1973–1990, barn swallows arrived several days earlier (Sokolov et al., 1998); in Denmark, from 1984–2003, arrival of male barn swallows advanced 4.4 days, whereas arrival was unchanged for females (Møller, 2004); from 1960–2000, in the Slovak Republic barn swallow arrival shifted later by 2.5 days, and departure earlier by 1.5 days, per decade (Sparks & Braslavská, 2001). Barn swallow migratory phenology in South Africa changed between the 1980s and the 2000s, and the directions of changes varied regionally (Altwegg et al., 2012): in the Western Cape (south-west) migratory arrival was unchanged but departure shifted six days later; in Gauteng (north-east), arrival was unchanged but departure shifted six days earlier. In KwaZulu-Natal (east coast), the changes were unclear (Altwegg et al., 2012), and a different method suggested earlier arrival and later departure (Møller et al., 2011). Further, moult shifted later in the Free State (central highlands) (Møller et al., 2011). It has been suggested that these changes in different hemispheres are the carry-over effects of Palaearctic climate change (Altwegg et al., 2012; Møller et al., 2011).

Southern Hemisphere phenological changes in long-distance migratory birds are partly caused by Northern Hemisphere climate change (Bussière, Underhill, & Altwegg, 2015; Ockendon, Leech, & Pearce-Higgins, 2013). However, climatic drivers in the Southern Hemisphere, such as changes in temperature or precipitation, can also affect the phenology of migratory birds

(Barshep, Underhill, Balachandran, & Pearson, 2013) and other taxa (Chambers et al., 2013), as can conditions experienced during migration (Finch, Leech, Pearce-Higgins, & Evans, 2014; Robson & Barriocanal, 2011). Multi-year climatic cycles such as the Southern Oscillation can influence phenology (Chambers et al., 2013). Phenological changes can arise from nonclimatic phenomena, such as lead and mercury poisoning (Provencher et al., 2016), and can be influenced by urbanization (Tryjanowski, Sparks, Kuzniak, Czechowski, & Jerzak, 2013). Cause and effect in phenological change can be difficult to separate. For example, the reported northward shift of the barn swallow nonbreeding range in Africa could be a carry-over effect of phenological responses to climate change in the Palaearctic, but it would also facilitate earlier arrival at the breeding grounds (Ambrosini et al., 2011). To disentangle these complex causes and effects, which can operate at any time in the annual life cycle, one must know the source and destination of migratory populations.

There are many methods for estimating connectivity, each with their own data requirements, strengths and limitations (Webster et al., 2002). The division coefficient method has a set of requirements and assumptions which can be difficult to fulfil, therefore it should be used in conjunction with other evidence wherever possible (Kania & Busse, 1987). For our data, we found the assumptions and requirements to be reasonably well supported (Supporting information Appendix C). Nonetheless, methods that combine multiple kinds of data are valuable because they can reduce bias associated with, for example, sampling and location error, the *a priori* choice of locations, and large differences in abundance or human population (Cohen et al., 2017; Procházka et al., 2017). For our study, the data did not support a more spatially detailed or multifactor analysis, and there was no other appropriate method. The division coefficient method (Busse & Kania, 1977; Kania & Busse, 1987) solves a nontrivial problem, that of accounting for unequal observation rates when estimating migratory mixing from simple ringing and recovery data, using simple mathematics (or linear modelling, in our study). This represents a milestone in the study of migratory connectivity, and it has not been superseded by better methods of similar simplicity, to the best of our knowledge.

Light-level geolocator tracking is a promising way of studying long-distance migrations of small birds (e.g., Hobson et al., 2015). Retrieval of these expensive devices is relatively easy at the breeding grounds, for species such as the barn swallow with high nest-site fidelity (Turner, 2006). At the nonbreeding grounds, however, communal roosts can number many thousands of birds, so the chance of reencountering an individual is low. For example, geolocators fitted at the breeding grounds to barn swallows in North American had a retrieval rate of 27% (Hobson et al., 2015). For barn swallows fitted with geolocators in Switzerland, 40% were retrieved, and of these, most had nonbreeding grounds in central and west Africa (Liechti et al., 2015). Geolocators fitted at the breeding grounds will certainly clarify the routes and migratory connections of migratory populations, and their use will increase as the devices become cheaper. Fitting devices at the

nonbreeding grounds is, however, unlikely to result in enough retrievals, because the chance of retrieving an individual from a roost of thousands or millions of birds is low. Thus, to detect the origin and destination of many individuals, the simplest mark and recapture method, ringing and recovery, is appropriate and affordable because it uses large long-term data sets which are available at little or no cost to researchers. We suggest therefore that the division coefficient (Busse & Kania, 1977; Kania & Busse, 1987) applied to large databases of ringing recoveries provides a simple, cheap, and powerful tool in studies of migratory connectivity, where other data are not available.

The barn swallow is capable of surviving under diverse conditions and feeds on a broad range flying insects (Roselaar, 1988); hence, it should be resilient to such change. Therefore, its decline of 18% in abundance in parts of Europe (Vickery et al., 2014) is all the more concerning. Our work provides a preliminary geographic framework to begin exploring the complex relationships between phenological changes in barn swallow life stages in two hemispheres. Specifically, our results can help in describing how the patterns of phenological change could be related to climate change at the breeding or nonbreeding grounds. The barn swallow is one of many species in which patterns of migratory mixing vary between regions. Understanding the pattern of mixing is the first step in assessing the capacity of a migratory species to cope with global change.

DATA ACCESSIBILITY

The data are freely available, on request, from the South African Bird Ringing Unit, FitzPatrick Institute of African Ornithology, University of Cape Town. Email: safring@adu.org.za.

CONFLICT OF INTERESTS

The authors declare no conflict of interests.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.