

## Research Article

**Cite this article:** van der Winden J, van Horsssen PW, Deuzeman S, Piersma T (2023). Remnant Rhine delta population of Great Reed Warblers maintains high diversity in migration timing, stopping sites, and winter destinations. *Bird Conservation International*, 33, e77, 1–6  
<https://doi.org/10.1017/S0959270923000321>

Received: 22 April 2023

Revised: 24 July 2023

Accepted: 14 August 2023

### Keywords:



Geolocator; Habitat loss; Migratory plasticity; Sahara

### Corresponding author:

Jan van der Winden;

Email: [jvdwinden@hetnet.nl](mailto:jvdwinden@hetnet.nl)

# Remnant Rhine delta population of Great Reed Warblers maintains high diversity in migration timing, stopping sites, and winter destinations

Jan van der Winden<sup>1,4</sup> , Peter W. van Horsssen<sup>2</sup> , Symen Deuzeman<sup>3</sup> and Theunis Piersma<sup>4,5</sup> 

<sup>1</sup>Jan van der Winden, Ecology, Research and Consultancy, Utrecht, The Netherlands; <sup>2</sup>Greenstat, Tricht, The Netherlands; <sup>3</sup>Sovon Vogelonderzoek Nederland, Nijmegen, The Netherlands; <sup>4</sup>BirdEyes – Centre for Global Ecological Change and Conservation Ecology Group, University of Groningen, Groningen, The Netherlands and <sup>5</sup>NIOZ Royal Netherlands Institute for Sea Research, Texel, The Netherlands

## Summary

Many Afro-Palearctic songbird migrants have declined, with conservation efforts mainly focused on the restoration of breeding habitat. However, pressures outside the breeding season might play a role. This includes the possibility that local relict populations no longer maintain the original phenotypic variation in migration patterns, with a loss of flexibility. The Great Reed Warbler *Acrocephalus arundinaceus* kept stable population levels in central and eastern Europe, but was almost extinct in the western part of the breeding range. In the Rhine delta the population declined from 10,000 individuals around 1950, to fewer than 100 at present. Here we document migratory timing, routes, and destinations of members of this remnant songbird population. It turned out that the remaining adults still showed high diversity in migratory phenotypes. This is even true in each of the two last tiny subpopulations in the Netherlands (of 50 and 15 pairs). So, even very small populations maintain the possible adaptive phenotypic variation, and with hindsight this justifies the breeding habitat restoration efforts currently underway.

## Introduction

Many Afro-Palearctic songbird migrants are declining. Much conservation effort is dedicated to stop habitat loss in the breeding areas or actually restore breeding habitat. Still, threats during the non-breeding period are also suggested to cause population declines (Zwarts et al. 2009; Vickery et al. 2014). As a general pattern, songbird migrants spread to vast non-breeding areas south of the Sahara, with a substantial diversity of stopping sites *en route* (Ouwehand et al. 2016; Burgess et al. 2020). This means that populations do not concentrate at specific sites during migration, or at non-breeding destinations. Also, such songbird migrants also show weak to moderate migratory connectivity, so individuals from different breeding areas co-occur in wintering areas. Taking a conservation perspective, Gilroy et al. (2016) stress low migratory connectivity as an advantage for population resilience as long as threats are site-specific. Conversely it can be predicted that neighbouring breeding populations from populations with low connectivity, but with substantial different population trends, likely suffer bottlenecks in the breeding areas rather than in the non-breeding range.

However, what will happen if a relatively isolated songbird population becomes really small due to pressures in the breeding range? Will this lead to a “phenotype bottleneck”, and thus to a decline in the diversity of migratory itineraries and high migratory connectivity? Dolman and Sutherland (1995) illustrate how the complexity of migration patterns might be affected by habitat loss with phenotypic and genetic factors involved and influencing adaptation to varying circumstances. The question is whether remnant breeding populations become fragile from the fact that they would lose variation in migration timing and routes. In Great Reed Warblers *Acrocephalus arundinaceus* adult breeding dispersal is low (Foppen 2001; Hansson et al. 2002), and theoretically this could influence variation in migratory phenotypes. Great Reed Warblers spend the northern winter in sub-Saharan Africa. The European populations show widely different numerical trends (BirdLife International 2004). This enables us to compare the migratory patterns of a remnant local population with those from well-studied populations in Europe and Turkey (e.g. Lemke et al. 2013; Horns et al. 2016).

During the past decades breeding populations of Great Reed Warblers have been increasing in Scandinavia, remained stable in central Europe, but declining steeply in western Europe (BirdLife International 2004). The strongest decline has occurred in wetlands within the Rhine delta in the Netherlands and adjacent Germany. Formerly a stronghold, the population declined from

c. 5,000 pairs in 1950 to fewer than 100 pairs in 2020 (Sovon Vogelonderzoek Nederland 2018). In fact, Great Reed Warblers became extinct in the fragmented marsh landscape in Belgium, western Germany, and France, with an isolated Rhine delta population remaining in the Netherlands. The nearest areas with at least tens of pairs are situated more than 400 km to the south-east in France or to the east in Brandenburg, Germany (Keller *et al.* 2020).

Within the Netherlands, Great Reed Warblers nowadays are mostly limited to two wetlands 50–80 km apart, with, respectively, 50 pairs in Randmeren (40 km<sup>2</sup> of lakes with reeds along the shorelines) and fewer than 15 pairs in Vechtplassen (30 km<sup>2</sup>). Breeding success of these remaining pairs is good and declines are best explained by the loss of reedbeds growing in water as a consequence of grazing by waterbirds such as the now numerous Greylag Geese *Anser anser* (van der Winden *et al.* 2020). As a response, conservation efforts focus on habitat restoration at the breeding area. Nevertheless, we could not rule out that threats at migratory stopping sites or at wintering sites also play a role (Leisler and Schulze Hagen 2011; Vickery *et al.* 2014). For example, could the possible loss of variation in migratory phenotypes have affected this tiny population in negative ways?

Building on the studies of Great Reed Warbler migration from breeding sites across Europe (e.g. Lemke *et al.* 2013; Koleček *et al.* 2016), we tagged adults in the two remaining breeding areas in the Netherlands to answer the following questions. (1) What is the diversity in timing, migratory routes, and stopping sites? (2) Do the Netherlands-breeding Great Reed Warblers, like their European-breeding relatives, move to the western part of the Guinean zone after staging in the Sahel? (3) How large is the longitudinal migratory spread of Dutch breeders? (4) What are the differences in migratory patterns between the two remaining breeding clusters in the Netherlands, if any?

## Methods

### Study sites and tagging

We tagged Great Reed Warblers in 2016 and 2018 in Vechtplassen, Province Noord-Holland (52°11'32.31"N; 5°3'41.36"E) and Zwarte Meer, Provinces Overijssel and Flevoland (52°37'50.27"N; 5°58'11.46"E), the latter being part of the larger Randmeren wetlands. In the reedbeds bordering the two lakes, 15 and 30 territorial males respectively were present. Most of these males were paired with at least one female in the study period (van der Winden *et al.* 2020). We equipped in total 22 adult Great Reed Warblers with a light-level logger, of which 14 were tagged at the Vechtplassen, and eight were tagged at Zwarte Meer. The light-level loggers weighed between 0.75 and 0.85 g (Biotrack ML6790) with a 9-mm light stalk. They were attached using a 1.0-mm thick Teflon leg loop harness (Rappole and Tipton 1991). Together with the harness the tags weighed 0.9 g being a mean of 2.8% of body mass at capture (range 2.5–3.1%).

All tagged individuals also received a metal ring and coded colour ring which facilitated our tracing them the next season. The Dutch Great Reed Warbler population is very small and we wanted to be sure our study did not affect survival. So, we trapped Great Reed Warblers in 2016 and 2018 using 2017 to see if they would return according to the 30% return rate experienced in Sweden (Lemke *et al.* 2013). In 2016 we tagged five males and two females in Vechtplassen. In 2017 we retrieved and recaptured three males and one female (57% of the total). In 2018 we additionally tagged seven males at Vechtplassen and eight males at the other core area in

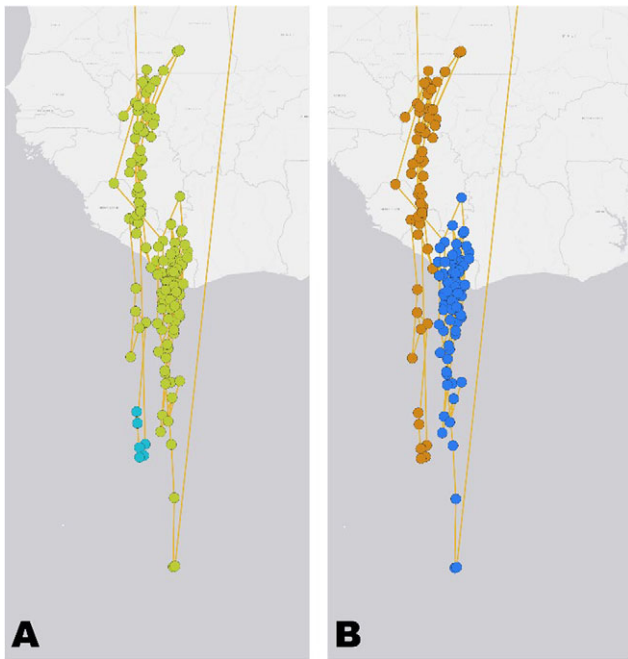
Zwarte Meer. Of these males, we recaptured four in Vechtplassen and four in Zwarte Meer in 2019. So, out of 22 tagged individuals, 12 (55%) were traced and successively recaptured in the next breeding season. As expected (Koleček *et al.* 2016; Brlik *et al.* 2020), these return rates do not indicate impacts of the tags on survival. Two tags stopped working in September–February, so the dataset includes 10 complete tracks: one of a female and nine of males. No differences were obvious, so we merged the sexes in the analyses.

### Settings, preferences, and analysing geolocator data

In the analysis of the data we closely followed the processing steps outlined by Lisovski *et al.* (2020). Our data classify as high-quality, but we stopped at step 3 referred to as *simple threshold estimates*, as we preferred to remain close to the raw data without too many assumptions in step 4 (*refinement locations*). These raw data can be used for calculations on range size and distances in conjunction with the methods presented by Burgess *et al.* (2020). The tags recorded maximum light intensity every two minutes. Light-level data were corrected for clock drift according to the Biotrack software (Fox 2018). From this point onwards we used R software to order, adjust, and analyse the data (R-version 4.0.2) (R Foundation for Statistical Computing 2020). Sunset and sunrise times were determined with the R-package *GeoLight* (Lisovski and Hahn 2012) and *TwGeos* (Lisovski *et al.* 2016) following the workflow in (Lisovski *et al.* 2020). A light-intensity threshold of two (Lisovski *et al.* 2020) was used to determine sunset and sunrise times. The resulting dark–light transition plots were used to manually check the daily sunset and sunrise moments and impossible outliers have been corrected. The dark–light transitions can be influenced by exceptional conditions causing shading. This results in clear spikes in the dark–light graph and the output was manually corrected by smoothing between previous and subsequent evenings or mornings.

Calibration of sun angle elevation is based on stationary periods of the tagged bird, these are usually in December–January. Hill–Ekstrom calibration (package *GeoLight*) was used to estimate sun angles for each tag separately. Average sun angle was  $-3.17$  (SD 0.64, range:  $-4.16$  to  $-1.88$ ,  $n = 12$ ) (see [Supplementary material](#)). This results in estimated daily (dawn and dusk averaged) light-level location points abbreviated in this paper as LLpoints. The LLpoints are uncertain during the equinox period and were deleted from the dataset between  $\pm 15$  days on both sides of the equinox periods. In the next step, stopping sites were identified by using the “changeLight” function (*GeoLight*). This function groups individual LLpoints into stopping sites and such resulting “sites” are merged with function “mergedSites” (*GeoLight*) using the estimated sun angles and the position of the centres of the densities (modes) did not differ by more than 500 km with a threshold at the 0.9-quantile of change point probability and a minimum staging time of 3 days.

The resulting merged sites were manually checked in QGIS (QGIS Development Team 2009). If we did not agree with the classification suggested by the model as it clearly separated too many stopping sites, we edited this manually (Figure 1). This was only necessary for longitudinally separated clusters south of the Sahara. After this step we calculated mean coordinates for these staging sites with spatial functions in R (package “sf” version 0.9-8) including latitudinal variation. Aggregated temporal and spatial site information was plotted in graphs and maps.



**Figure 1.** Example of manual check and adjustment of clusters after processing with mergedSites. In panel A the result of mergedSites (*Geolight*) is presented, identifying two stopping sites (green and blue). In panel B our manual correction is clarified, discriminating two stopping sites (brown and blue) each with a substantial longitudinal and time difference.

*Estimating connectivity and size of non-breeding range*

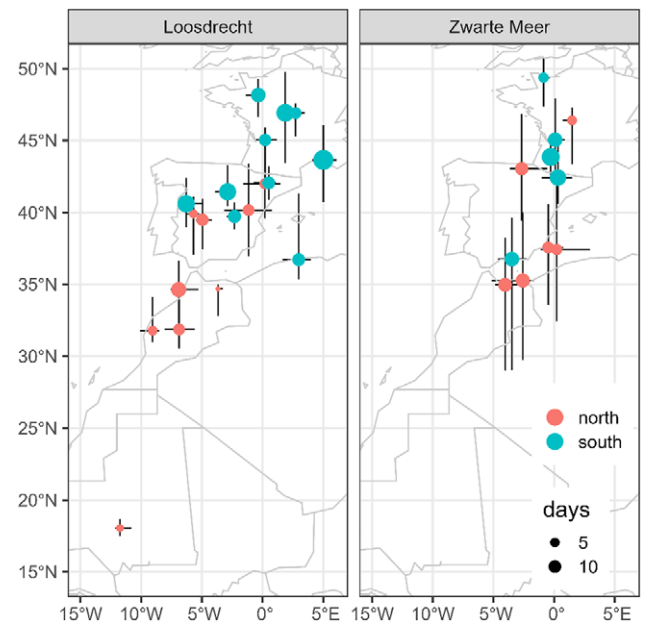
The light-level loggers do not provide accurate locations. To compare connectivity and the size of staging areas south of the Sahara with conspecifics from other European regions, we followed Burgess et al. (2020) who developed this for a songbird in the same wintering range as Great Reed Warblers. In a first step we limited the period between 1 November and 31 January to be sure no migratory movements – north of the Sahel – or equinox impacts would affect the data. This period coincides with sub-Saharan staging during the northern winter. With these selected LLpoints we calculated the 80% minimum convex polygon size for each individual with the Adehabitat R-package (Calenge 2006). The 80% threshold is visually chosen based on likelihood patterns (see *Supplementary material*). To gain an impression of the size of the total non-breeding range of all Great Reed Warblers, we calculated distances between all LLpoints of all individuals. Migration direction from the breeding range (known site) to staging areas south of the Sahara was calculated for the averaged staging area centres.

**Results**

Adult male Great Reed Warblers departed after breeding between mid-July and late August, showing a variation of 42 days (Table 1).

**Table 1.** Departure and arrival dates and migratory timing of nine male Great Reed Warblers.

	Median	Range
Departure from breeding area	3 August	20 July–30 August
Arrival in Sahel/Guinean zone	20 September	2 September–5 October
Northwards departure	7 April	21 March–13 April
Arrival in breeding area	4 May	19 April–7 May



**Figure 2.** Stopping time and sites during southward migration and the northward movements towards the breeding areas of Great Reed Warblers for the two Dutch breeding areas. All stopping sites presented sites between 17° and 50° latitude, being more or less the southern edge of the Sahara and breeding areas in the Rhine delta.

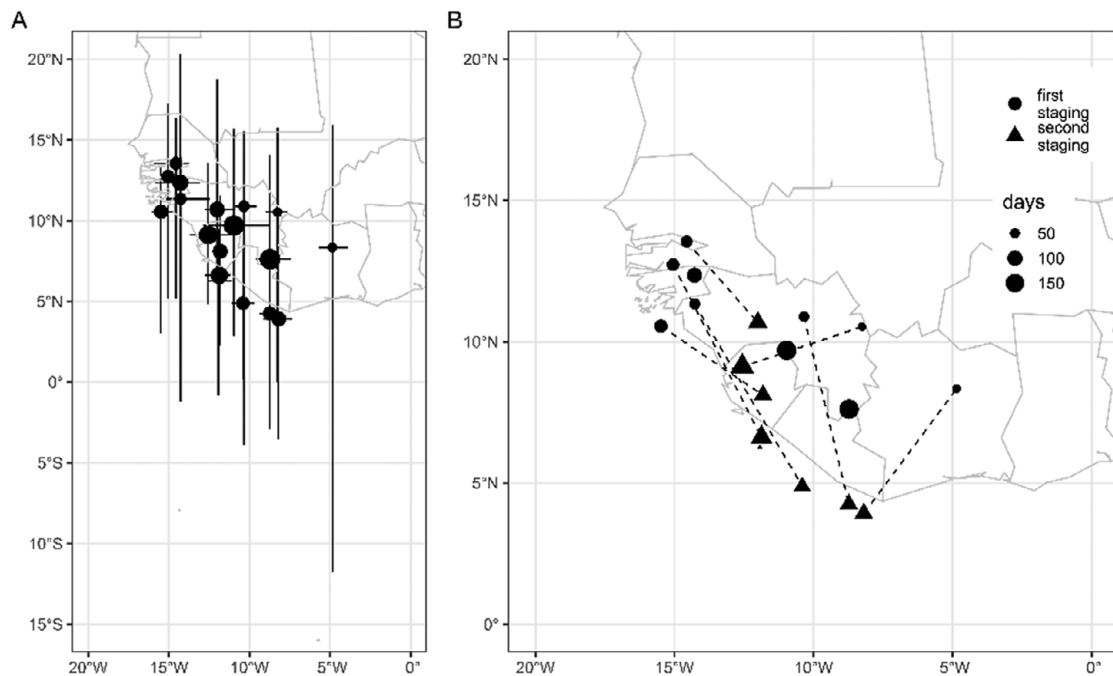
The arrival dates in the Sahel also varied by about a month. The timing of northward migration varied less, but for males still ranged between 25 days and 19 days for arrival. During southward migration, Great Reed Warblers stopped first in France and Spain and sometimes briefly in North Africa or even the Sahara (Figure 2). The locations of the stopping sites varied over a substantial range in south-western Europe.

After crossing the Sahara, Great Reed Warblers spent their first period of the non-breeding season from Gambia–Senegal in the west up to central Ivory Coast in the east (Figure 3A). Eight of the 10 individuals moved further southwards to the Guinean zone after an initial staging period of 47–114 days in the Sahel (Figure 3B). This area is smaller as western individuals move south-east and eastern ones move south-west. They stayed in this region until they started northward migration to the breeding areas.

The migration directions to staging areas in the Sahel varied among the 10 Great Reed Warblers, resulting in a migratory spread of directions of 15.24° upon arrival (Table 2), matching approximately 1,300 km distance west–east. The total calculated surface of all LLpoint polygons in West Africa for these Great Reed Warblers was more than 1 million km<sup>2</sup> (80% minimum convex polygon area [MCPA]) overlapping substantially (Figure 4). Most LLpoints were within a range of 100–1,200 km apart up to more than 2,000 km. There was no difference in LLpoint distances between Great Reed Warblers originating from Loosdrecht and Zwarte Meer (Figure 4 and *supplementary material*).

**Discussion**

The individual Great Reed Warblers from the tiny remnant Rhine delta breeding populations, even in a small sample of 10 tagged adults, showed substantial diversity in routes stopover and staging as well as migratory spread south of the Sahara. These migratory patterns fit very well into those from the non-breeding range



**Figure 3.** Averaged centre of non-breeding staging areas of Rhine delta Great Reed Warblers (including staging time) south of the Sahara. All sites and its variation (A) and intra-African movements after early September (B) are expressed as first staging in the Sahel and southward movement to the Guinean zone.

comparable to conspecifics from neighbouring strong increasing or stable European breeding populations (Figure 5). The Rhine delta individuals move to the west and overlap mostly with warblers breeding in Spain, partly with Swedish birds, and not or hardly with more eastern breeders (Lemke *et al.* 2013; Horns *et al.* 2016; Sjöberg *et al.* 2021).

Adult Great Reed Warblers leave the European breeding areas between mid-July and early September and return between mid-April in the southern part of the range and late May in Sweden (Koleček *et al.* 2016). Arrival dates for Great Reed Warblers in the Netherlands were intermediate, from late April to early May. Bijlsma *et al.* (2001) suggested a progressively later arrival in the period 1941–1983 as the species became scarcer. Our data do not suggest a narrowing arrival window. We propose that the later arrival dates might be an observer effect, caused by the lower encounter probability of early arrivers as the population is so small. If 10% of the Rhine delta population arrives early it means only 10 males are present in April, so quite a challenge to detect one.

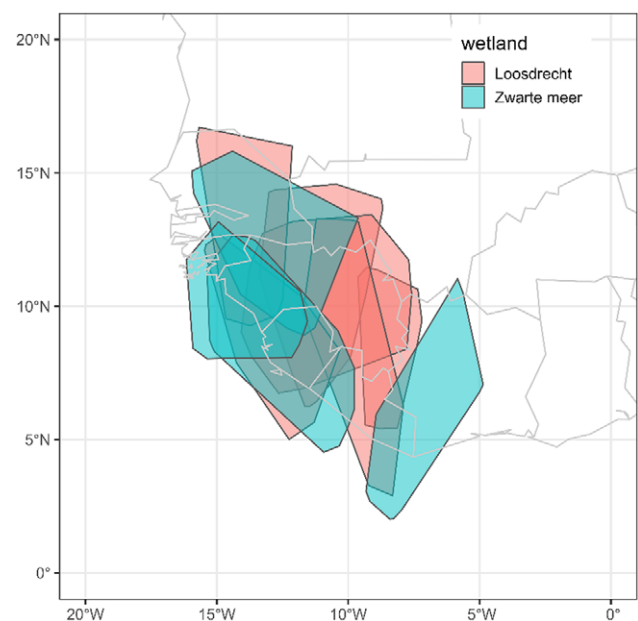
The stopping sites for Eurasian Great Reed Warblers are mostly situated in southern Europe during southward migration and in North Africa during northward migration. The variety in stopping sites does not suggest specific wetlands to be key, indicating that pressures on the population will be geographically diffuse.

After an initial staging period in the Sahel, most adults moved further south, concentrating in a smaller second wintering region.

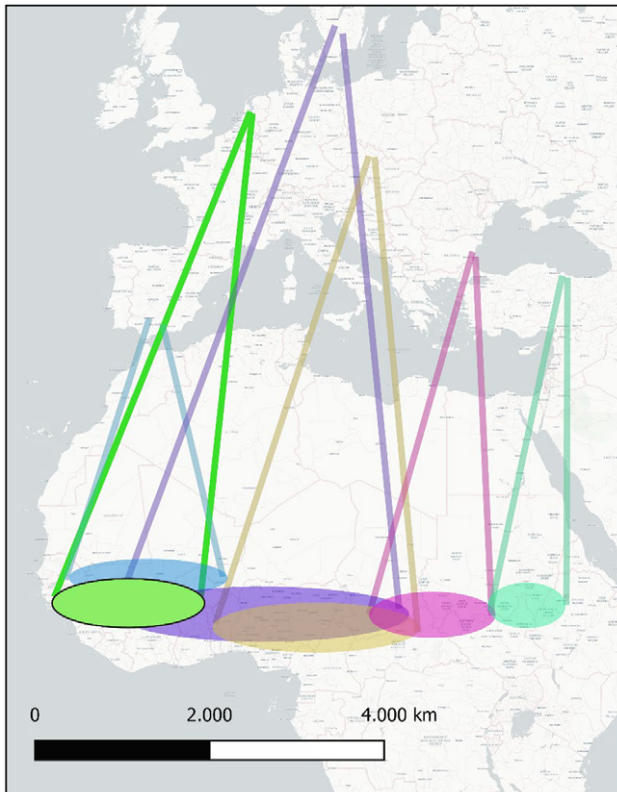
**Table 2.** Migration directions of 10 Great Reed Warblers tagged in the Rhine delta. Direction between breeding site and first staging site south of the Sahara and between the staging area in January–March and the breeding area. Southward migration south =  $-180^\circ$  and northward migration north =  $0^\circ$ .

Heading to	Mean $^\circ$	SD $^\circ$	Minimum $^\circ$	Maximum $^\circ$
Staging Sahel	-155.21	5.58	-164.71	-149.48
Breeding area	-157.45	2.79	-161.64	-154.19

This is also found for other European subpopulations suggesting that the spread of the first staging region might be influenced by wind direction and force over the Sahara (Lemke *et al.* 2013; Koleček *et al.* 2016). Although the spread in the second staging regions is smaller, it is still large, i.e. from southern Guinea to south-eastern Liberia. This is about 160 times larger than the breeding range in the Rhine delta and comparable to the wintering range of other European populations. Also, the timing of migration does not point to a bottleneck situation. The variation in stopping sites



**Figure 4.** Non-breeding spread in West Africa, presented as convex hull polygons (80%) during the period 1 November to 31 January of 10 Great Reed Warblers tagged with light-level loggers at two wetlands in the Netherlands.



**Figure 5.** Migratory spread and schematic sub-Saharan staging range of Great Reed Warbler populations from the Netherlands, Spain, Sweden, Hungary, Bulgaria, and Turkey (after Koleček et al. 2016 and our results).

during southward and northward migration is also comparable to conspecifics for other European populations (Lemke et al. 2013; Koleček et al. 2016), not indicating loss of migratory variation.

The two separate Dutch populations showed no obvious differences in their migratory patterns. Even birds of the Loosdrecht breeding site, with fewer than 15 territorial males (van der Winden et al. 2020), retained strong variation in migratory phenotypes. So, the pressure in the breeding area, resulting in a population decrease, did not lead to loss of phenotypic variation. The observed lack of bottlenecks in the time away from the breeding grounds supports previous findings and resulting conservation recommendations (van der Winden et al. 2020) that the decline of the Rhine delta Great Reed Warblers has to do with factors during the breeding season. This study then can be seen as an encouragement of efforts to restore breeding habitat.

**Acknowledgements.** This study was funded by Vogelbescherming Nederland. Especially Nico Korpelaar, Andrea Kuiper-Vos, and Sandra Peters are thanked for their efforts to organise this. Several owners of nature reserves and wetlands gave us permission to trap Great Reed Warblers: Natuurmonumenten, Staatsbosbeheer, Recreatieschap Vechtplassen, Waternet, and Rijkswaterstaat. All geolocators were deployed by ornithologists with a permit (Animal Welfare Law, WoD) and ringing licence (Vogeltrekstation). The Provinces of Noord-Holland, Flevoland, and Overijssel gave us permission to trap Great Reed Warblers in Natura 2000 sites. We especially thank Sonja Weeda, Yvonne Verkuil, Ruud Foppen, Erik Kleyheeg, Martin Poot, Nico Bouwman, Vincent van der Spek, Tim Kreetz, and Eric van der Velde for support with logistics or fieldwork. The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional guides on the care and use of animals. Author contributions: data collection was carried out by J.W. and S.D.; P.H. and J.W. analysed the data; J.W. wrote the manuscript under the supervision of T.P.; all authors provided feedback on manuscript drafts and approved publication.

**Supplementary material.** The supplementary material for this article can be found at <http://doi.org/10.1017/S0959270923000321>.

## References

- Bijlsma R.G., Hustings F. and Camphuysen C.J. (2001). *Algemene en Schaarze Vogels van Nederland*. Avifauna van Nederland 2. Haarlem: GMB Uitgeverij/ Utrecht: KNNV Uitgeverij.
- BirdLife International (2004). *Acrocephalus arundinaceus* Great Reed Warbler. In *Birds in Europe: Population Estimates, Trends and Conservation Status*. Cambridge: BirdLife International, p. 223.
- Brlik V., Koleček J., Burgess M., Hahn S., Humple D., Krist M. et al. (2020). Weak effects of geolocators on small birds: a meta-analysis controlled for phylogeny and publication bias. *Journal of Animal Ecology* **89**, 207–220.
- Burgess M.D., Finch T., Border J.A., Castello J., Conway G., Ketcher M. et al. (2020). Weak migratory connectivity, loop migration and multiple non-breeding site use in British breeding Whinchats *Saxicola rubetra*. *Ibis* **162**, 1292–1302. <https://doi.org/10.1111/ibi.12825>.
- Calenge C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**, 516–519.
- Dolman P.M. and Sutherland W.J. (1995). The response of bird populations to habitat loss. *Ibis* **137**, 38–46.
- Foppen R. (2001). *Bridging Gaps in Fragmented Landscapes*. Dissertation, Wageningen University, Wageningen.
- Fox J.W. (2018). *Intigeo® Geolocator Manual*. Cambridge: Migrate Technology.
- Gilroy J.J., Gill J.A., Butchart S.H.M., Jones V.R. and Franco A.M.A. (2016). Migratory diversity predicts population declines in birds. *Ecology Letters* **19**, 308–317.
- Hansson B., Bensch S., Hasselquist D. and Nielsen B. (2002). Restricted dispersal in a long-distance migrant bird with patchy distribution, the great reed warbler. *Oecologia* **130**, 536–542.
- Horns J.J., Buechley E., Chynoweth M., Aktay L., Coban E., Kirpik M.A. et al. (2016). Geolocator tracking of Great Reed-Warblers (*Acrocephalus arundinaceus*) identifies key regions for migratory wetland specialists in the Middle East and sub-Saharan East Africa. *The Condor* **118**, 835–849.
- Keller V., Herrando S., Voříšek P., Franch M., Kipson M., Milanese P. et al. (2020). *European Breeding Bird Atlas 2: Distribution, Abundance and Change*. Barcelona: European Bird Census Council/Lynx Edicions.
- Koleček J., Procházka P., El-Arabany N., Tarka M., Ilieva M., Hahn S. et al. (2016). Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. *Journal of Avian Biology* **47**, 756–767.
- Leisler B. and Schulze-Hagen K. (2011). *The Reed Warblers. Diversity in a Uniform Bird Family*. Zeist: KNNV Uitgeverij.
- Lemke H.W., Tarka M., Klaassen R.H.G., Akesson M., Bensch S., Hasselquist D. et al. (2013). Annual cycle and migration strategies of a trans-Saharan migratory songbird: A geolocator study in the Great Reed Warbler. *PLOS One* **8**, e79209.
- Lisovski S., Bauer S., Briedis M., Davidson S.C., Dhanjal-Adams K.L., Hallworth M.T. et al. (2020). Light-level geolocator analyses: A user's guide. *Journal of Animal Ecology* **89**, 221–236.
- Lisovski S. and Hahn S. (2012). GeoLight – Processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution* **3**, 1055–1059.
- Lisovski S., Wotherspoon S. and Sumner M.D. (2016). TwGeos: Basic Data Processing for Light-level Geolocation Archival Tags. R package version 0.1.2.
- Ouwehand J., Ahola M.P., Aulsems A.N.M.A., Bridge E.S., Burgess M., Hahn S. et al. (2016). Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*. *Journal of Avian Biology* **47**, 69–83.
- QGIS Development Team (2009). QGIS Geographic Information System. Manual.
- R Foundation for Statistical Computing (2020). R: A Language and Environment for Statistical Computing. <https://www.R-project.org/>.
- Rappole J.H. and Tipton A.R. (1991). New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* **62**, 335–337.
- Sjöberg S., Malmiga G., Nord A., Andersson A., Bäckman J., Tarka M. et al. (2021). Extreme altitudes during diurnal flights in a nocturnal songbird migrant. *Science* **372**, 646–648.

- Sovon Vogelonderzoek Nederland (2018). In *Vogelatlas van Nederland*. Utrecht: Kosmos Publishers, pp. 450–451.
- Van der Winden J., Deuzeman S., Weeda S., Foppen R., van Horssen P. and Poot M. (2020). Broedsucces en nesthabitat van de Grote Karekiet in begraasde rietkragen in de kerngebieden. *Limosa* **93**, 153–164.
- Vickery J.A., Ewing S.R., Smith K.W., Pain D.J., Bairlein F., Skorpilova J. et al. (2014). The decline of Afro-Palaeartic migrants and an assessment of potential causes. *Ibis* **156**, 1–22.
- Zwarts L., Bijlsma R.G., van der Kamp J. and Wymenga E. (2009). *Living on the Edge. Wetlands and Birds in a Changing Sahel*. Zeist: KNNV Uitgeverij.