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# Isotope record tracks changes in historical wintering ranges of a passerine in sub-Saharan Africa

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## Abstract

Billions of birds migrate from the Palaearctic to sub-Saharan Africa, yet we are unaware about where exactly they stay over winter and how consistent they have been using these wintering areas over historical times. Here, we inferred the historical wintering areas of Eurasian Golden Orioles (*Oriolus oriolus*) from stable isotope ratios of feathers. Over the past 200 years, Golden Orioles used two major wintering grounds. Between 1895 and 1971, the relative use of these areas depended on local rainfall intensities. Golden Orioles may depend strongly on humid wintering areas in sub-Saharan Africa, which may put this species at stake when the global climate continues to change.

KEYWORDS
African rainfall, bird migration, Eurasian Golden Oriole, historical feathers, Palaearctic passerines, triple stable isotope analysis

## 1 | INTRODUCTION

Each year, more than two billion birds migrate from the Palaearctic to Africa, making this route the largest of all avian migratory flyways (Hahn et al., 2009). During migration, birds depend on a sequence of suitable habitats for travelling, refuelling and overwintering, which makes long-distance migrants particularly sensitive to global changes (Sillett et al., 2000). Changes in climate, such as ambient temperature, may cause temporal shifts in arrival dates, as well as *en route* variations in the duration and number of stopovers (Gienapp et al., 2007; Lehikoinen et al., 2004; Zalakevicius et al., 2006). These observations are important to understand factors underlying the variation of migration behaviour (Gordo, 2007). However, our understanding of where Palaearctic birds stay over winter lack the historical perspective which would improve our ability to predict future changes with increasing global temperatures. Importantly, a historical perspective on bird migration may also help to evaluate why bird populations in the Palaearctic have been declining over the past decades (Sanderson et al., 2006). It has been suggested that such declines might be partly related to environmental changes in the wintering grounds (Robbins et al., 1989). However, most of our current understanding of migration is by and large built on studies limited to the summer breeding area (Busch et al., 2020; Huntley et al., 2008). Thus far, we miss comprehensive information about environmental conditions governing non-breeding habitats such as the wintering range (Dodd, 1994; Oba et al., 2001; Vickery et al., 2014), which should be considered in predicting the fate of bird populations and species in times of global change.

Bird migration research has been widely relying on ringing as a main tool to track movements and life history stages. The low probability of recapturing banded individuals and recent technological advances triggered the development of new approaches (Bächler et al., 2010;

Webster et al., 2002). Among them, stable isotopes have been applied in a growing number of migration studies (Alisauskas & Hobson, 1993; Chamberlain et al., 1997; Hobson et al., 2004; Hobson, Keith, Van Wilgenburg, Wassenaar, & Larson, 2012; Hobson, Keith, Van Wilgenburg, Wassenaar, Powell et al., 2012; Marx et al., 2020; Phillips et al., 2009). The isotopic signature of feather keratin is representative for the place of moult and it is preserved unaltered for centuries (Hobson & Wassenaar, 1997; Navarro et al., 2020). For instance, hydrogen stable isotope ratios ($\delta^2$H) are used as a major migration proxy due to their predictable distribution in meteoric water across continents (Bowen et al., 2005; Hobson et al., 1999; Hobson & Wassenaar, 2008), which varies with latitude, altitude and distance from the coast (Craig, 1961; Dansgaard, 1964). Carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) stable isotope ratios, assimilated through the diet, reflect the primary source of carbon and a bird's trophic position (Hobson & Clark, 1992a, 1992b; Marra et al., 1998; Peterson & Fry, 1987; West et al., 2010). Recently, data on vegetation coverage and plant $\delta^{15}$N variability were used to build models for the calculation of carbon and nitrogen isoscapes (Craine et al., 2009; Still & Powell, 2010a). These advances enabled the formulation of multi-isotope approaches with an improved spatial resolution and robustness for geographical assignments of migratory individuals (Hobson, Keith, Van Wilgenburg, Wassenaar, & Larson, 2012; Hobson, Keith, Van Wilgenburg, Wassenaar, Powell et al., 2012; Hobson et al., 2013).

In this study, we analysed feathers of the Eurasian Golden Oriole (*Oriolus oriolus*; Linnaeus 1758, Oriolidae). *O. oriolus* is a long-distance migrant passerine breeding during the austral summer in the Palearctic region and wintering in sub-Saharan Africa (Mason & Allsop, 2009). Our goal was to assess the long-term responsiveness of this species to environmental changes within its wintering range. For this purpose, we applied a triple stable isotope approach ($\delta^2$H, $\delta^{13}$C, $\delta^{15}$N) on feathers collected over the past 200 years to identify the wintering areas and determine their use over time. Furthermore, we integrated the analysis with the environmental record during the corresponding time window. Based on the observation that Golden Orioles and other long-distance migratory passerines adjust their migration behaviour to weather conditions (Baumann, 1999; Herremans et al., 1992; Mason & Allsop, 2009), we hypothesized that the wintering range of Golden Orioles changes with fluctuating environmental conditions. Specifically, we predicted that the wintering range of Golden Orioles should change with precipitation intensities in Sub-Saharan Africa.

## 2 | MATERIALS AND METHODS

We analysed 87 *O. oriolus* feathers, of which 60 were from historical museum collections and 27 were from extant birds. The samples belonged to 39 females, 42 males and 6 individuals of unknown sex. All the samples analysed were collected during the breeding season and before the autumn migration, between April and late August (Table S1). Moulting in this species occurs once per year, during the wintering season (Mason & Allsop, 2009; Mead & Watmough, 1976).

From each individual, we cut a small piece of the rachis of the fifth primary counted from the centre of the wing outwards (Eck et al., 2011). Samples from extant specimens were collected during the summer of 2013 and 2015 in Hobrechtsfelde (52.665741 °N, 13.490879 °E; collection permit VSW-Beri-001/08, issued by Landesamt für Umwelt, Gesundheit und Verbraucherschutz Brandenburg). Historical specimens from 1818 to 1971 were retrieved from collections in the Natural History Museum in Berlin and the Zoological Research Museum Alexander Koenig in Bonn (Table S1).

### 2.1 | Stable isotope analyses

Stable isotope ratios were analysed at the Leibniz Institute for Zoo and Wildlife Research (Leibniz IZW). Feather material was soaked in a 2:1 chloroform: methanol solution for 24 h to remove potential surface contaminants. After being dried for 48 h, aliquots of 0.55 ± 0.05 mg from each feather were placed into tin capsules (IVA Analysentechnik) and then analysed for stable carbon and nitrogen isotope ratios using a Delta V-Advantage mass spectrometer (Thermo Fisher Scientific) connected via an interface (Conflo, Thermo Fisher Scientific) to an elemental analyser (Flash EA 1112 Series, Thermo Fisher Scientific). Samples were measured in sequences with international protein standards (tyrosine and leucine) used for offset and drift correction. Stable isotope ratios were given in the delta notation ($\delta^{13}$C and $\delta^{15}$N values) as parts per mille deviation from the international standards (Air $N_2$ for nitrogen and V-PDB for carbon). Precision of measurements was always better than 0.2‰ (1 SD).

For stable isotope ratios of non-exchangeable hydrogen in keratin, we placed aliquots of 0.35 ± 0.10 mg each into silver capsules (IVA Analysentechnik) where they dried for at least 10 days at 50°C to equilibrate exchangeable hydrogen with hydrogen of ambient moisture. We then used a high-temperature elemental analyser (HT Elementanalysator HEKAtech, GmbH), operating at 1350°C and which contained a silicon carbide (SiC) tube and a carbon/water trap. Obtained $H_2$ pulses were routed via an interface (Finnigan Conflo III, ThermoFisher Scientific) into the stable isotope ratio mass spectrometer (Delta V advantage, ThermoFisher Scientific). Feather samples were measured in sequence with three in-house keratin standards (SWE-SHE [−111.6‰], ESP-SHE [−61.5‰)] and AFR-GOA [−26.4‰]), previously calibrated against international reference materials (USGS42, CBS, KHS; Soto et al. 2017). Stable hydrogen isotope ratios were expressed as deviations from the international standard V-SMOW. Precision of $\delta^2$H measurements was always better than 1.5‰ (1 SD).

### 2.2 | Feather isoscape calculation

We calculated an African isoscape for each of the three elements considered in our study (Figure S1). For the hydrogen one, we used the $\delta^2$H precipitation model from IsoMAP (Bowen et al., 2021) and the GNIP database (IAEA/WMO, 2011). The model included data for the period when Golden Orioles overwinter in Africa (December to February). The environmental isoscape was then converted into a feather isoscape (Figure S1a) using the transfer function for the Eurasian reed warbler (*Acrocephalus scirpaceus*) developed by (Procházka et al., 2013) ($\delta^2H_f = -10.29 + 1.28^* \delta^2H_p$). The function was validated for *O. oriolus* using 10 extra juvenile specimens (Figure S2). These birds were born during spring 2013 and their feathers were collected in Hobrechtsfelde, Germany, in July/August of the same year. The elaboration of the European isoscapes followed the same procedure as for the African counterparts. The $\delta^2$H precipitation model from IsoMAP (Bowen et al., 2021) was based on the GNIP database (IAEA/WMO, 2011) of the period from May to July 2013. Conversion of the environmental isoscapes into feather isoscapes as well as bird assignment were performed as described above. The results indicated that Hobrechtsfelde is situated on the edge of one of the most probable surfaces (Figure S2). The validation suggests that the transfer function used as well as the rest of the assignment procedure is suitable to study the migratory behavior of this species. The observed minor geographical offset between the known birth location and the predicted one was expected due to the development stage of the 10 specimens. Being juveniles, with ecological traits differing from the adult population, may slightly affect the stable isotope discrimination in their tissues (Langin et al., 2007; Meehan et al., 2003).

The carbon isoscape was modelled for the African continent by combining data of temperature and precipitation (from WorldClim 2 [Fick & Hijmans, 2017]), distribution of C3 and C4 crops (from Global Agricultural Lands & Harvested Area and Yield for 175 Crops dataset [Ramankutty et al., 2008]) and woodland (from Modis MOD44B Vegetation Continuous Fields [DiMiceli et al., 2015]). To produce the environmental isoscapes, we used the R package *grassmapr* (Still & Powell, 2010b). We calculated the corresponding feather isoscape applying a discrimination factor of +2‰ (Hobson, Keith, Van Wilgenburg, Wassenaar, & Larson, 2012; Hobson, Keith, Van Wilgenburg, Wassenaar, Powell et al., 2012; Figure S1b). The nitrogen isoscape was modelled based on the relationship of $\delta^{15}$N geographic foliar distribution with temperature and rainfall compiled by Craine et al., (2018). The atmospheric datasets used were the same ones as those used for the carbon isoscape (from WorldClim 2). For the nitrogen feather isoscape, we applied a discrimination factor of +5‰ (Hobson, Keith, Van Wilgenburg, Wassenaar, & Larson, 2012; Hobson, Keith, Van Wilgenburg, Wassenaar, Powell et al., 2012; Figure S1c).

## 2.3 | Suess correction and clustering

We applied a correction to control for the Suess effect to directly compare extant feather material with historical samples. Specifically, we corrected stable carbon isotope values of historical feather material using Equation (4) in Verburg (2007). The individual isotope data were clustered using the algorithm “clara” from the R package *cluster* (Maechler et al., 2019) based on the partitioning around medoids (PAM), to detect natural groupings in the multivariate space (Hobson, Keith, Van Wilgenburg, Wassenaar, & Larson, 2012; Hobson, Keith, Van Wilgenburg, Wassenaar, Powell et al., 2012). Prediction of clustering strength was computed using the R package *fpc* by constraining the number of clusters between two and ten. The suitable number of clusters was assessed to be two, following the criterion of “prediction strength” by Tibshirani and Walther (2005). Firstly, we standardized the dataset by transforming each value of the three variables into *z*-score. Subsequently, to calculate the prediction strength, we subdivided the dataset into training and test sets 50 times. Then, we measured how well the training set centroids predicted the co-membership in the validation set. For this, we evaluated whether each pair of test observations assigned to a specific test cluster were also assigned to the same cluster using the training set centroids. For each test cluster, we calculated the proportion of observations assigned to the same cluster in the two sets. The minimum of these proportions was representing the prediction strength. The metric used by the clustering algorithm to calculate dissimilarities between observations was the Euclidean distance.

## 2.4 | Assignment to wintering grounds

To assign individual feathers based on their isotopic compositions ($\delta^2$H, $\delta^{13}$C, $\delta^{15}$N) to a potential wintering ground, we calculated the likelihood at each georeferenced location of the raster (cell with size of 0.5° × 0.5°) using a multivariate normal probability density function implemented in the *mvtnorm* R package (Seifert et al., 2018; Veen et al., 2014). The variance-covariance matrix for the multi-isotope values of the single feathers was calculated using the *mvnmle* R package (Gross & Bates, 2018). To identify the most probable wintering grounds, the resulting spatially-explicit probability surfaces were binarized by assigning value 1 (“likely location”) to the raster cells with the upper 25% probability values (i.e., 3:1 odds ratio), and 0 (“unlikely location”) to the rest (Veen et al., 2014) (Figure 2). In addition, we used the coarse geographical distribution of Golden Orioles in Africa to exclude north-Saharan areas from the assignments. Seasonal observations data from eBird were extracted using the *auk* R package (Strimas-Mackey et al., 2018), rasterized and used as masks on the binary probability surfaces. In each cluster, the joint assignment probability was calculated as product of the individual probabilities using the *assignR* R package (Ma et al., 2020). The assignment procedure was then applied to shuffled isotope data and 50 randomization runs were performed. *Schoener's D* index was used as measure of the similarity between the wintering ground probability surfaces calculated from the original dataset and the ones generated by permutation. The index ranges between 0 (complete divergence) and 1 (complete overlap).

## 2.5 | Environmental conditions at wintering grounds

We evaluated the relationship between ambient conditions and wintering grounds (WG1 and WG2) of Golden Orioles through time using the historical record of ambient temperature and rainfall. To our knowledge, these variables represent the longest period over which gridded instrumental data is available for Africa. For air temperature, we used the dataset from CRU TS 04.03 (Climatic Research Unit, University of East Anglia [Mitchell & Jones, 2005]) with starting point in year 1901 and with a spatial resolution of 0.5° × 0.5°. For rainfall, we used the GPCC V2018 dataset with a starting point in year 1891 and with a spatial resolution of 0.5° × 0.5° (Schneider et al., 2011). Gridded data (December to February) were averaged for each wintering ground area. To reduce the effect of high-frequency noises, we calculated time series based on 5-year moving averages. Ambient temperatures fluctuated between 19 and 21°C in WG1 and between 19 and 20˚C in WG2. The extremely limited temperature variability challenged further interpretation of the results and therefore only rainfall data were considered for further discussion.

## 2.6 | Quantification and statistical analysis

For data analysis we used the RStudio environment (version 1.3.959) for R software (version 4.0.1; R Core Team). We performed two-way ANOVAs followed by Tukey post hoc tests to assess the isotopic composition among *O. oriolus* clusters and sexes (significance $p < 0.05$; Table S2). We used Pearson correlation analysis to test whether wintering ground preferences were significantly correlated to rainfall patterns (significance $p < 0.05$).

# 3 | RESULTS

## 3.1 | Feather stable isotope ratios

We identified two clusters of Golden Orioles with respect to the stable isotope composition of the fifth primary feather from historical and extant specimens using a PAM algorithm (Table S1). Feathers of individuals from cluster 1 ($n = 54$) averaged −28.0 ± 12.2‰ for $\delta^2$H (Figure 1a), −22.1 ± 1.2‰ for $\delta^{13}$C (Figure 1b) and 8.3 ±1.1‰ for $\delta^{15}$N values (Figure 1c). Feathers of cluster 2 individuals ($n = 33$) averaged −7.6 ± 9.5‰ for $\delta^2$H, −20.9 ± 1.2‰ for $\delta^{13}$C and 10.5 ± 2.1‰ for $\delta^{15}$N (Figure 1). The isotopic composition was different between clusters but similar between the sexes (Table S2). Only in the case of $\delta^2$H values, there was a difference between the means of the sex grouping levels, with females being characterized by more positive $\delta^2$H values than males.

## 3.2 | Geographic assignment to wintering grounds

Based on stable isotope feather composition and African isoscape distribution (Figure S1), birds of cluster 1 were assigned to southeastern Africa (WG1; Figure 2a). Individuals of cluster 2 were assigned to wintering grounds in central Africa (WG2) mainly located in central Democratic Republic of Congo (DRC), central Republic of Congo, central Angola, northern Zambia, western Tanzania as well as in some areas of western Ethiopia (Figure 2b). Most of WG1 (95% of the 0.5° × 0.5°grid cells) was included in WG2 (Figure 2c). This overlap consisted of 272 grid cells, representing 26% of the area occupied by both WGs. Because possibly related to overlying diets, WG1 overlap over WG2 was preventively excluded from being part of WG2. The spatial similarity between the original wintering probability surfaces ground and the counterparts obtained from permutation, expressed as *Schoener's D* index averaged 0.41 ± 0.09 and 0.67 ± 0.09, for WG1 and WG2 respectively.

The majority of birds (63%) collected at central European longitudes between 1818 and 1971 (in Italy, Germany, Poland and Greece) migrated to WG1, and 37% to WG2. Most birds (70%) collected in Eastern European between 1887 and 1953 (Russia, Estonia, Ukraine and Belarus) or Middle East countries between 1922 and 1930 (Turkey and Iran) migrated to WG1 and 30% to WG2. All three birds sampled in Western Europe (Spain) migrated to WG2. Two specimens (8009 and 157990) captured in 2013 and 2015 were assigned to WG1 in both years, suggesting an individual consistency in the use of wintering grounds, at least for the two birds.

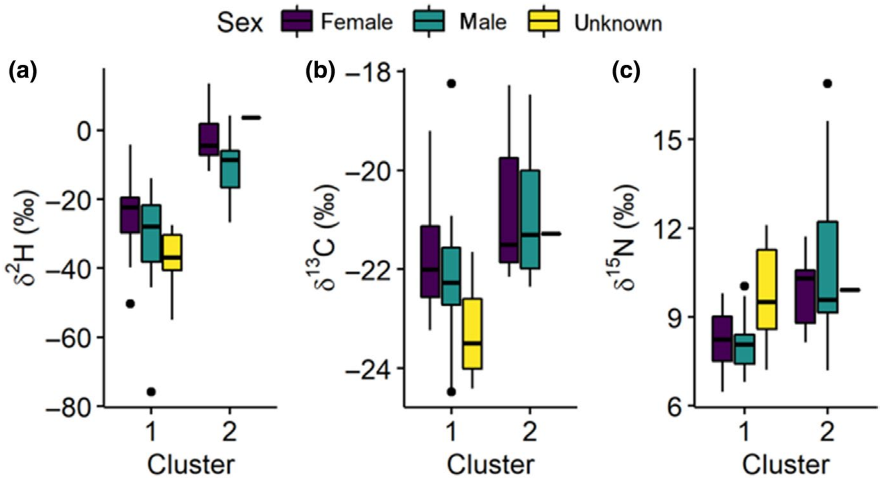

**FIGURE 1** Boxplots of (a) hydrogen, (b) carbon and (c) nitrogen stable isotope ratios in Golden Orioles projected for the two clusters corresponding to the groups heading to different wintering grounds (cluster 1: $n = 54$; cluster 2: $n = 33$) and classified according to sex. Boxes show the interquartile range around the median, 25 and 75 percentiles, solid horizontal lines the median, whiskers the 95 percentiles and solid circles the outliers

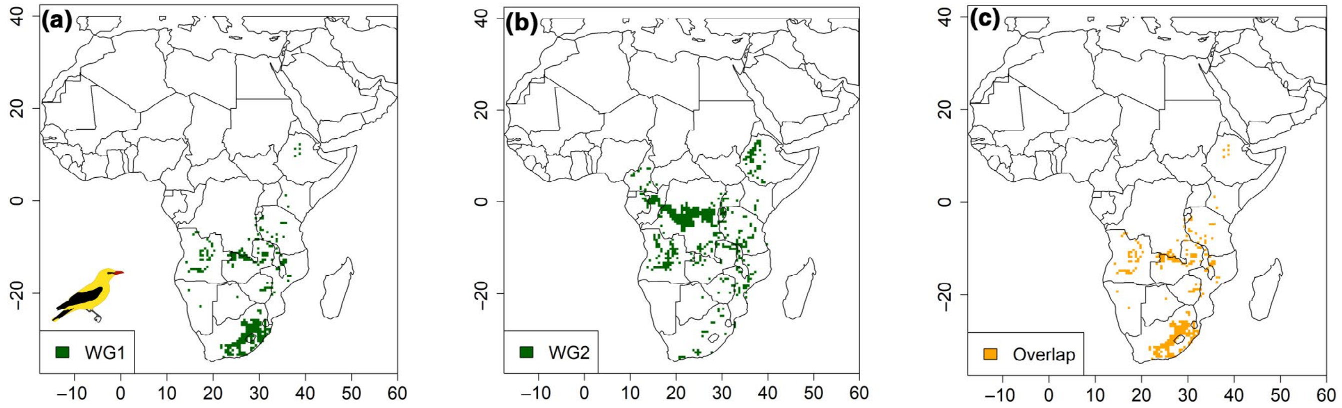

FIGURE 2 Maps locating Golden Orioles African wintering ground (a) WG1, (b) WG2 and (c) their overlap. The coloured areas represent the most probable locations based on the multi-isotope feather assignment (*O. oriolus* in inset)

### 3.3 | Historical use of wintering grounds and relative environmental conditions

The proportions of Golden Orioles assigned to either WG varied over time (Figure 3). The highest percentages in WG1 were recorded from 1842 to 1854 (100% of the individuals), from 1887 to 1927 (on average 65% of the individuals), from 1940 to 1948 (54% of the individuals) and from 1953 to 1957 (100% of the individuals; Figure 3a). In contrast, the highest proportions of Golden Orioles migrating to WG2 were identified between 1920 and 1948 (on average 73% of the individuals), from 1834 to 1838 and from 1877 to 1911 (on average 46% of the individuals; Figure 3b).

Systematic rainfall records for sub-Saharan Africa, starting from 1895, showed that during Golden Oriole wintering season (December to February) the average rainfall was 103 mm/month in WG1 and 192 mm/month in WG2. The wettest years in WG1 were recorded between 1895 and 1902, between 1907 and 1923, between 1936 and 1948 and from 1954 to 1962 (Figure 4a,d). In WG2, the wettest years were clustered between 1933 and 1944 (Figure 4b,c).

We observed, in each WG between 1895 and 1971, a positive correlation between rainfall intensity and the proportion of birds overwintering there (WG1: $r = 0.24$, $p = 0.04$; WG2: $r = 0.23$, $p = 0.01$; Figure 4a,b). Furthermore, we noted a stronger relationship between rainfall in WG2 and proportion of birds in WG1. The correlation was negative, showing that drier conditions in WG2 corresponded to more birds wintering in WG1 ($r = -0.39$, $p = 0.01$; Figure 4c). In contrast, we did not find a relationship between rainfall in WG1 and birds in WG2 ($r = 0.01$, $p = 0.9$; Figure 4d).

## 4 | DISCUSSION

We studied the wintering ranges of Golden Orioles in sub-Saharan Africa using the isotopic record preserved in feathers collected from 1818 onwards and deposited in museum collections. Our results show that the most probable wintering grounds for this passerine were located in south-eastern (WG1) and central (WG2) Africa. These areas are situated within the broader non-breeding range established by previous observational studies (Fry & Keith, 2000).

Feathers of birds from WG1 were characterized by more negative $\delta^2$H values compared to feathers grown in WG2. This distribution is consistent with the large-scale circulation governing rainfall patterns in sub-Saharan Africa (Levin et al., 2009). Specifically, the Congo Air Boundary, located over Namibia and Zambia during austral summers, is considered to be a major isotopic demarcation front. It divides easterly heavy isotope depleted moisture from the Indian Ocean and westerly enriched moisture from the Atlantic Ocean. The

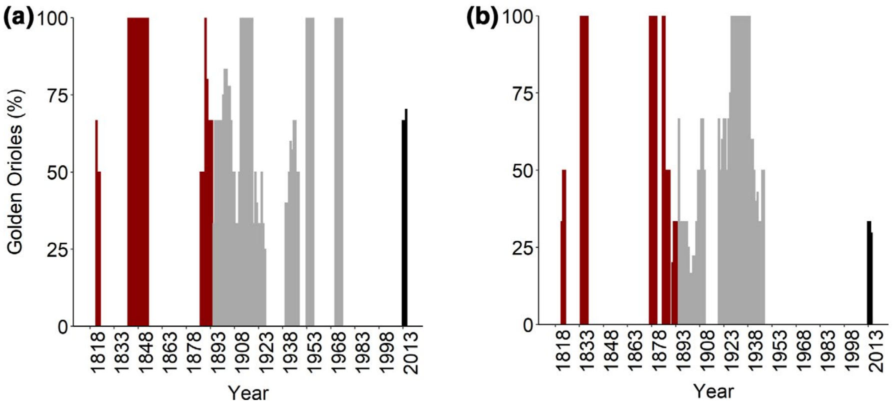

FIGURE 3 Proportions of birds migrating to WG1 (a) and to WG2 (b). Historical specimens collected before the start of the instrumental record in Africa (1818–1984) are marked red, all other historical specimens (1895–1971) in grey and extant birds (2013–2015) in black

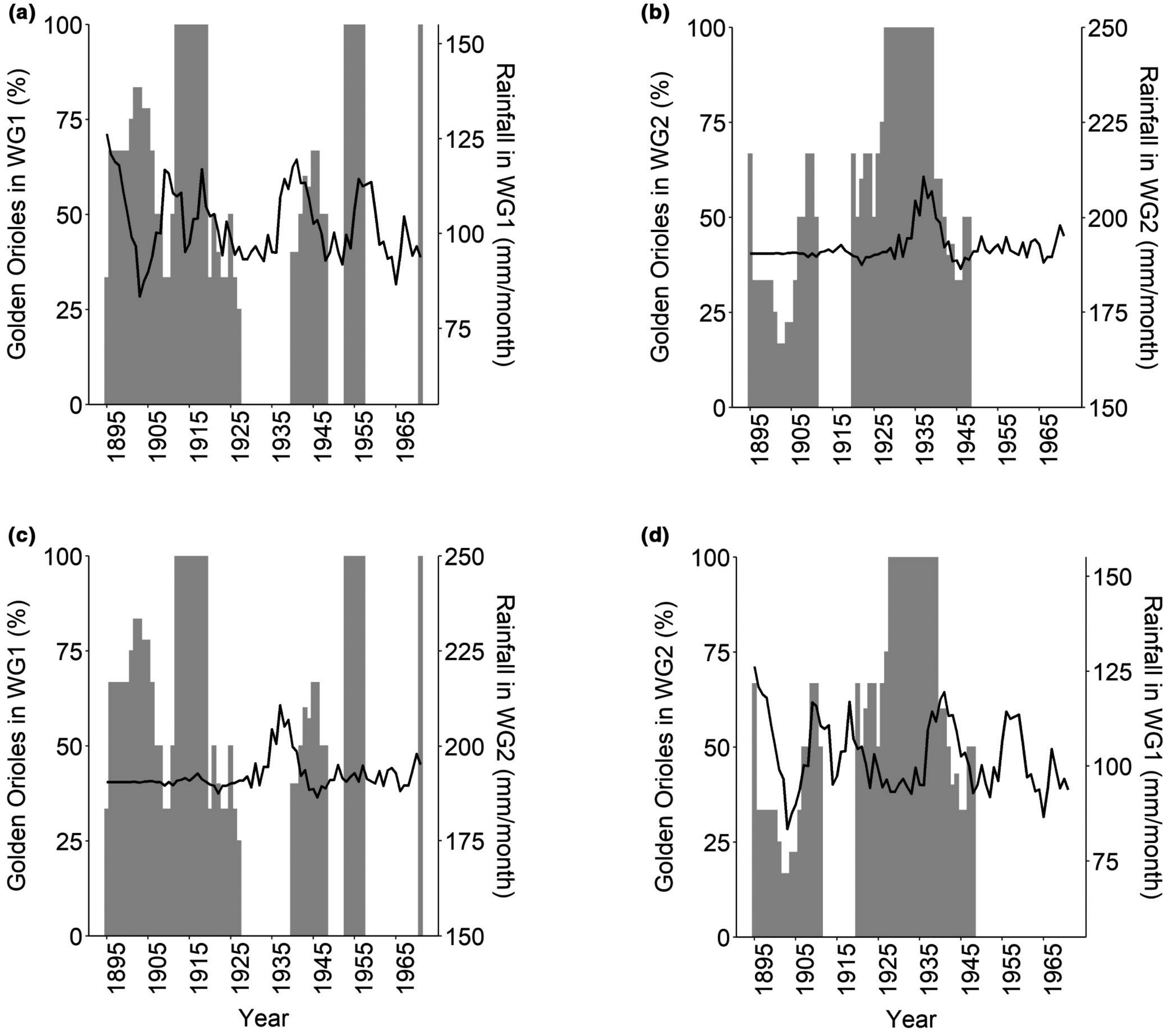

**FIGURE 4** Use of sub-Saharan wintering grounds by historical Golden Orioles (grey bars) in relation to local rainfall records from 1895 to 1971 (black lines). (a) Proportions of birds migrating to WG1 and rainfall in WG1. (b) Proportions of birds migrating to WG2 and rainfall in WG2. (c) Proportions of birds migrating to WG1 and rainfall in WG2. (d) Proportions of birds migrating to WG2 and rainfall in WG1. Precipitation axes are differently scaled among graphs

vapour from the latter is then recycled in the central African rainforests, where evapotranspiration dominates the water cycle. Here, plants return most of the water to the atmosphere, without large changes in stable isotope ratios (Brubaker et al., 1993; Gat & Matsui, 1991; Levin et al., 2009). In addition to this geographical distribution, feather $\delta^2H$ values are different between males and females, which might result from sex-specific dietary habits (Langin et al., 2007).

The observed small overlap of $\delta^{13}C$ and $\delta^{15}N$ values between the two clusters, as well as the limited variability of $\delta^{13}C$ values may indicate that the studied Golden Orioles are members of similar food webs, feeding on similar proportions of C3 and C4 plants and insect species. Analogous dietary habits across the geographical range of the wintering grounds may have a homogenising effect on the bulk feather isotope ratios translating into the observed overlap between the two WGs. Due to the unavailability of the stable isotope ratios of consumed resources, this study cannot provide a sufficiently robust diet analysis to quantify a potential bias. Therefore, the WG1 overlap over WG2 was preventively excluded from being part of WG2.

Previous ringing campaigns in Europe suggested the existence of three major migration routes for Golden Orioles. Birds breeding in central Europe pass over the Mediterranean Sea and continue across Egypt (Mason & Allsop, 2009). Birds from the Balkan regions fly over Saudi Arabia and Yemen (Mason & Allsop, 2009), and those from Iberian, Moroccan and Algerian areas move south rounding the Western Sahara into northern Nigeria (Mason & Allsop, 2009). Our results indicate that this longitudinal partitioning in the breeding areas may not necessarily translate into a corresponding spatial separation in the WGs. Most of the birds migrated to WG1, regardless of whether they had bred in central or eastern European countries. Given that only three specimens were collected in Spain, we cannot draw larger inferences about Western European populations. Generally, the absence of a clear subdivision agrees with observations of Golden Oriole merging into mixed flocks of various geographic origins over the Rift Valley before continuing their journey to their final destinations (Archer & Godman, 1961).

Our results show that humidity levels in sub-Saharan wintering grounds are particularly relevant for Golden Orioles, and potentially also for other long-distance migrants of the Palaearctic/African pathway. Following the classification by Kottek et al. (2006), both WGs are located in humid subtropical climate zones. Here, one of the major controls over the rainfall is the seasonal north-south displacement of the Intertropical Convergence Zone (ITCZ) which separates northeast from southeast air masses. During the austral summer, the ITCZ front crosses over the equator in western Africa and over DRC and Mozambique in the east. As a result, the wintering localities are characterized by dry winters and warm/wet summers with forest transitions, woodlands and mosaics as main vegetation cover types (Geiger, 1961; Kottek et al., 2006; White, 1981). According to the observations by Herremans (1998), the arrival of Golden Orioles is accurately coordinated with the ITCZ southward movement and consequent start of local heavy rainfalls.

Our data indicated that areas in south-eastern Africa are the preferred WGs of the studied Golden Orioles. Yet, when rainfall in central Africa is sufficiently intense, birds may stop and settle here without moving further south, as they would do during drier summers. Therefore, along with targeting moist habitats and wet seasonal cycles, Golden Orioles show further environmental responsiveness by actively relocating to WG1 when rainfall is scarce in WG2. Our interpretation is consistent with previous studies observing that passerines follow moving storm fronts and wet weather patterns (Baumann, 1999; Herremans et al., 1992; Mason & Allsop, 2009). Yet we acknowledge that although rainfall seems to be a major driver of the migratory movements, other ambient conditions such as photoperiod and vegetation cover, may be involved too.

To conclude, through a multi stable isotope analysis on historical feathers we studied long-term changes in wintering ranges of the Eurasian Golden Orioles. The combination with the rainfall record allowed us to understand the influence of weather on migratory phenology of this species. Climate projections in (sub)-tropical Africa describe a range of drier to wetter scenarios, according to the different scales and models considered (Dunning et al., 2018; Fotso-Nguemo et al., 2017). The dependency of Golden Orioles on rainfall patterns suggests that any of these weather variations will likely alter this species' spatial use of WGs. An altered wintering behaviour of Golden Orioles in sub-Saharan Africa may cascade into population changes and shifts within its Palaeartic breeding range.

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## CONFLICT OF INTEREST

The authors declare no competing interests.

## AUTHOR CONTRIBUTIONS

Conceptualization, C.C.V.; Methodology, S.M. and C.C.V.; Resources, S.F., A.H., T.T., F.W.; Writing—Original Draft, S.M. and C.C.V.; Writing—Review & Editing, S.M. S.F., A.H., T.T., F.W., C.C.V.; Funding Acquisition, C.C.V.

## DATA AVAILABILITY STATEMENT:

The data that supports the findings of this study are available in the supplementary material of this article.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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