Toward a Deuterium Feather Isoscape for Sub-Saharan Africa: Progress, Challenges and the Path Ahead

Carlos Gutiérrez-Expósito1*, Francisco Ramírez1, Isabel Afán2, Manuela G. Forero1, Keith A. Hobson3

1 Departamento de Biología de la Conservación, Estación Biológica de Doñana (CSIC), Sevilla, Spain,
2 Laboratorio de SIG y Teledetección (LAST-EBD), Estación Biológica de Doñana (CSIC), Sevilla, Spain,
3 Environment Canada, Saskatoon, Saskatchewan, Canada

* carlines@ebd.csic.es

Abstract

A key challenge to the application of continent-wide feather isoscapes for geographic assignment of migrant birds is the lack of ground-truthed samples. This is especially true for long-distance Palearctic-Afrotropical migrants. We used spatially-explicit information on the $\delta^{2}H$ composition of archived feathers from Green-backed/Grey-backed Camaroptera, to create a feather $\delta^{2}H$ isoscape for sub-Saharan Africa. We sampled from 34 out of 41 sub-Saharan countries, totaling 205 sampling localities. Feather samples were obtained from museum collections ($n = 224$, from 1950 to 2014) for $\delta^{2}H$ assay. Region, altitude, annual rainfall and seasonal patterns in precipitation were revealed as relevant explanatory variables for spatial patterns in feather $\delta^{2}H$. Predicted feather $\delta^{2}H$ values ranged from -4.0 ‰ to -63.3 ‰, with higher values observed in the Great Rift Valley and South Africa, and lower values in central Africa. Our feather isoscape differed from that modelled previously using a precipitation $\delta^{2}H$ isoscape and an assumed feather-to-precipitation calibration, but the relatively low model goodness fit ($F_{10,213} = 5.98$, $p < 0.001$, $R^2 = 0.18$) suggests that other, non-controlled variables might be driving observed geographic patterns in feather $\delta^{2}H$ values. Additional ground-truthing studies are therefore recommended to improve the accuracy of the African feather $\delta^{2}H$ isoscape.

Introduction

In order to manage or conserve migratory birds and other wildlife, it is essential to consider the complete annual cycle by making spatial connections between key breeding, migration and wintering sites [1]. While such migratory connections are poorly known for most of the world’s migratory birds, recent development of increasingly sophisticated and light weight tracking devices are moving the field forward at a rapid rate [2]. In particular, light-sensitive geologgers have been miniaturized to now be used effectively in studies of small (~15g) passerines but require recapture, and can have significant error especially during the equinox [3, 4]. Within this scenario, the use of intrinsic markers and particularly the analysis of stable isotopes in
Feathers have emerged as a powerful contribution to the ecologist’s toolbox by providing a relatively cheap method to describe migratory patterns and population connectivity [5]. Feathers are metabolically inert following formation and their isotopic composition thus reflects isotopic values derived from foodwebs at areas of growth. Isotopic values in foodwebs, in turn, can vary spatially in a predictable fashion creating isoscapes that can be a useful means of inferring origins of birds later sampled. So, providing feather moult is well understood, isotopic approaches can be used to assign feather isotopic signals to particular geographic areas [6, 7, 8, 9, 10].

To date, geographic assignments of birds to molt origins have relied extensively on measurement of stable-hydrogen isotope values (δ²H) in feathers because they reflect amount-weighted long-term average δ²H values in precipitation and these patterns are known reasonably well at the continental or global scale [11, 12, 13, 14]. By applying rescaling functions linking precipitation and feather δ²H values [15], it is possible to model expected feather δ²H isoscapes to be used in assigning individuals or populations to molt origins. However, for Africa, the distribution of precipitation stations that collect water for isotopic measurements under the Global Network for Isotopes in Precipitation (GNIP) are generally poor and it is also unclear if rescaling algorithms used to link precipitation and feather δ²H derived for North American or European passerines can be applied to Africa [5, 16]. An alternate approach is to derive a feather δ²H isoscape directly by collecting feathers from known origins across the continent [17, 13], but little direct information exists about the stable isotope distribution in feathers along the Afrotropical areas. Feather δ²H isoscapes created using ground-truthed rescaling functions are therefore required to improve assignment accuracy in these areas [18, 19]. In Africa, widespread feather sampling is logistically extremely difficult but museum collections can be used as a source of feather samples at a continental scale. Here, we present, for the first time, a feather δ²H isoscape for sub-Saharan Africa based on museum collections. Our motive was to investigate model parameters influencing feather δ²H across Africa and to potentially provide an isoscape that could be used to assign European migratory birds to molt origins in Africa.

Materials and Methods

Sampling

We concentrated our analyses on potential wintering areas in Africa of European-Afrotropical migrants and so excluded the Sahara desert and all the Mediterranean areas of the Maghreb, along with all African islands in both the Indian and the Atlantic Ocean. In order to avoid taxon-specific differences in the isotopic composition of feathers and to cover the whole sub-Saharan area of the continent we chose the Green-backed/Grey-backed Camaroptera complex (Camaroptera brachyura/brevicaudata, Vieillot, 1820), hereafter Camaroptera, as a surrogate species. This small bird is a common species and thus easily found in museum holdings; widely distributed throughout the African continent, allowing the use of a single species for the whole study area. The species is also largely sedentary [20], so that we can assume that any feather analyzed was grown at the collection site. Finally, the species is mostly insectivorous and so is consistent with diets expected for most European long-distance Passerines that winter and molt in Africa. We analyzed 224 samples from museum specimens of known locations (< 10 Km accuracy), from 205 localities distributed along 34 sub-Saharan countries (Fig 1). Most specimens were on loan from American Museum of Natural History (New York, USA), Carnegie Museum of Natural History (Pittsburgh, USA), Doñana Biological Station (Sevilla, Spain), Delaware Museum of Natural History (Wilmington, USA), Field Museum (Chicago, USA), Kansas University Museum of Natural History (Lawrence, USA), Muséum National D’Histoire Naturelle (Paris, France), Naturalis Biodiversity Center (Leiden, The Netherlands), Natural History Museum of Denmark (Copenhagen, Denmark), Western Foundation for Vertebrate
Zoology (Camarillo, USA), Yale Peabody Museum of Natural History (New Haven, USA), plus two samples obtained during field expeditions by Muséum National d’Histoire Naturelle staff in Guinea Conakry, seven samples obtained by the Research Centre in Biodiversity and Genetic Resources (CIBIO, Portugal) under the collaboration protocol with the Zoological Museum and Herbarium of Lubango (ISCED-Huíla, Angola) and one found as a road kill in Windhoek (Namibia) (S1 Table—Accession numbers of museum specimens used in this study).

Isotope analysis

Feathers were cleaned with ethanol, rinsed with ultrapure water (Milli-Q from Millipore Corporation), dried in clean open vials at 45°C in a drying oven and before weighting, keratin standards (CBS, KHS and LIE-PA2) and samples are equilibrated together with lab air for at least 5 days prior to isotopic analysis in order to avoid effects of H exchange with ambient water vapor. Subsamples were weighed into silver capsules and analyzed at the Stable Isotope Laboratory at Doñana Biological Station (LIE-EBD) using a Flash HT Plus Elemental Analyzer coupled to a Delta-V Advantage Isotope Ratio Mass Spectrometer (IRMS) via a Conflo IV interface (Thermo Fisher Scientific, Bremen, Germany). A comparative equilibration approach was used based on Wassenaar and Hobson [21]; standards used were CBS (Caribou hoof: -197 ‰) and KHS (Kudu horn: -54.1 ‰) from Environment Canada and LIE-PA2 (Razorbill feathers: 20.8 ‰) from Doñana Biological Station. Based on replicate within-run measurements of standards, we estimate measurement error to be ±3‰. All δ²H values are reported relative to the Vienna Standard Mean Ocean Water (VSMOW) scale.

Model construction

We first compared our measured feather δ²H values with those predicted from the theoretical African feather isoscape raster map created by Hobson et al. [14]. That isoscape was based on
an amount-weighted mean annual grid map of δ²H values in precipitation at a 16.5 km spatial resolution as sourced online primarily from the Global Network of Isotopes in Precipitation (GNIP) database from IAEA/WMO [http://www-naweb.iaea.org] [22]. In a second step, values from this database were also used to examine whether the observed variability between measured and predicted feather δ²H values could be explained by the effect of phenological differences in the moult period for the different Camaroptera populations sampled. Finally, we examined if additional covariates other than latitude and altitude [23] may have contributed to the observed variability in feather δ²H values. We extracted all environmental variables associated with each sampling location that could have an important role in influencing precipitation δ²H values [11]. Monthly precipitation (mm) rasters were obtained from WorldClim [24] (http://www.worldclim.org) at 1 km spatial resolution. Altitude, was extracted from the GLOBE Project at 1 km spatial resolution [25] (http://www.ngdc.noaa.gov/mgg/topo/globe.html), and compared with data provided by specimen label when altitude was available, in the very few cases of discordance, we used label data.

One of the challenges with creating a feather isoscape is determining over which period precipitation should be averaged to reflect the major H signal in the foodweb leading to birds at the time of moult [26]. Vegetation growth is highly correlated with the photosynthetically active radiation absorbed by the plant canopy, and thus with the Normalized Difference Vegetation Index (NDVI), accounting for the study of phenological changes in vegetation [27] and thus deduce the most likely mouling season for each considered pixel. Mean and standard deviation of monthly NDVI (extracted from satellite NOAA-AVHRR images) computed over an 18-year period (from 1982 to 2000, excluding 1994 data from calculation) were downloaded from EDIT Geoplatform at 10 km spatial resolution [28] (http://edit.csic.es/Soil-Vegetation-LandCover.html). Global evapotranspiration from the MODIS sensor (MOD16 product, 1 km spatial resolution) was downloaded from the University of Montana [29], ftp.ntsg.umt.edu. Monthly mean values for the 2000–2010 time period were used.

From monthly precipitation data, we reconstructed intra-annual rainfall patterns for each sample location. Assuming that reproduction takes place during the rainy season, and that moult is performed mostly after breeding [30, 31, 32], we assigned a moult period for each sampled bird based on seasonal patterns. We assigned the most likely month for mouling body feathers as two months after the maximum rain peak (hereafter moult month). We also considered the moult period as the four months after the maximum rain peak (hereafter moult season) and before the beginning of the dry season. Predicted precipitation δ²H values for moult month and moult period were weighted by the monthly rain amount. Regionalized cluster-based water isotope prediction (RCWIP) from the International Atomic Energy Agency [33, 34] was used to group feather samples into six climatic cluster domains, hereafter regions. The RCWIP allowed us to assign to all pixels in the study area a relative weight of belonging to each of the considered regions (S1 Fig—African regionalization by using climatic regression models). Because rain is the main source of water δ²H, monsoonal and Atlantic fronts undoubtedly play an important role in the distribution pattern of precipitation δ²H values across the continent. Thus, minimum distance from each sampled locality to the coast was also included as a covariate. Finally, we calculated a rain seasonality index following Walsh & Lawler [35] with values under 0.19 denoting precipitation spread throughout the year, and with values over 1.2 indicating extreme seasonality with almost all precipitation occurring in one or two months.

We considered up to seven explanatory variables: absolute latitude (ABS_LAT), annual precipitation (PREC-TOT), distance to the coast (DIST_SEA), Walsh Lawler seasonality index (SI), altitude (ALT), Normalized Difference Vegetation Index (NDVI) and Evapotranspiration (ET); bioclimatic region (REGION), with six levels [34] as a factor. Correlations among
continuous variables were explored through a Pearson correlation matrix. Both NDVI and ET showed a high correlation (Pearson’s $r = 0.62$), and were also significantly correlated with PREC_TOT (Person’s $r = 0.434$ and $r = 0.57$, respectively). Additionally, DIST_SEA was highly correlated with ALT (Pearson’s $r = 0.54$). Accordingly, these three variables were excluded from further analyses. A set of competing models was built by considering: PREC_TOT, SI, ALT as well as ABS_LAT and its quadratic term, REGION as factor. PREC_TOT was selected instead of precipitation during moult month or moult season, since our feather $\delta^2$H values showed a better correlation with annual-averaged rainfall $\delta^2$H values than period-specific rainfall $\delta^2$H values (see results). Model selection was done using the Akaike information criteria corrected for small sample sizes (AICC) and the corresponding AICC increments ($\Delta$AICC < 2) and weights (AICC Wgt). Geographical information were treated by using ArcGis 10.0 software (ESRI, Redland, USA), whereas statistical analyses were performed using R statistical environment 3.0.2., and the MuMIn [36], lme4 [37] and arm [38] packages.

Results

Linear regression between estimates of feather $\delta^2$H based on Hobson et al. [14] and our Camaroptera feather $\delta^2$H results yielded a significant relationship but with a relatively low explanatory power ($F_{1,222} = 16.68$, $p<0.001$, $R^2 = 0.07$) (Fig 2). The same analysis was done comparing $\delta^2$H in Camaroptera feathers with mean annual precipitation $\delta^2$H values ($F_{1,222} = 25.71$, $p<0.001$, $R^2 = 0.09$) and those for the moult month ($F_{1,222} = 4.16$, $p = 0.04$, $R^2 = 0.02$) and the moult season ($F_{1,222} = 12.9$, $p<0.001$, $R^2 = 0.05$). Higher correlation was obtained when relating...
Camaroptera feather δ²H values against total precipitation δ²H values than those based on moulting periods and so we considered only annual rainfall as covariate. Following Bowen & Revenaugh [23] and Bowen [39], we made a Linear Model, using as covariates altitude, absolute latitude and lat². Although both altitude and latitude affected δ²H in Camaroptera feathers, the model was not significant (F₃,₂₂₀ = 3.54, p = 0.015, R² = 0.03). Our top ranked model included all variables and had a weight of 0.73. That Linear Model was highly significant (F₁₀,₂₁₃ = 5.98, p < 0.001, R² = 0.18). Covariates coefficients, confidence intervals and relative importance of covariates of this model are shown in Table 1 and were used, together with the covariates grids and probability of each pixel to belong to a region, to build a Camaroptera feather isoscape. The resulting map is shown in Fig 3.

In order to compare our results with those predicted by Hobson et al [14], we resampled our high spatial resolution δ²H feather map to match the spatial resolution of previously published feather isoscapes (0.33 degrees cell size). Once both maps were resampled, we calculated the standard deviation of both values for each pixel in order to explore the spatial distribution of mismatches (Fig 4).

**Discussion**

We provide for the first time, a high resolution ground-truthed feather δ²H isoscape for African insectivorous passerines based on a model that considered latitude, altitude, annual precipitation, a seasonality index and geographical region as covariates. We expected a better correlation among our Camaroptera feather δ²H values and the theoretical δ²H isoscapes model derived by Hobson et al. [14] but high dispersion in our data suggested that we were unable to control for all influential variables and greater refinement of our model is now needed. We suspect that variation in timing of moult for Camaroptera and uncertainties and assumptions inherent in museum collections of feathers collected over many decades, together with inherent complexities in modeling precipitation and foodweb δ²H for Africa, all contributed to total model variance. However, and owing to the low signal to noise ratio in the isotopic composition of feathers, the small isotopic variance of the whole suite of samples with respect expected isotopic variance based on individuals of known moult origin [39], our model could be still doing a reasonable job of describing the component of that variance attributable to large-scale environmental factors.

Differences among the predicted mean annual precipitation δ²H values and those for actual mean δ²H in precipitation contributing H to the foodweb leading to Camaroptera feathers is

| Estimate | Std. Error | t value | Pr(|t|) |
|----------|------------|---------|--------|
| (Intercept) 4.785867 | 13.429 | 0.36 | 0.722 |
| ABS_LAT² 0.024396 | 0.019 | 1.30 | 0.200 |
| ABS_LAT -0.481181 | 0.549 | -0.88 | 0.382 |
| ALT 0.003328 | 0.001 | 2.25 | 0.025 |
| PREC_TOT -0.008978 | 0.002 | -4.78 | < 0.001 |
| SI -14.578157 | 6.076 | -2.40 | 0.017 |
| RegV11 -14.103769 | 13.260 | -1.06 | 0.289 |
| RegV13 -25.349481 | 12.900 | -1.97 | 0.051 |
| RegV14 -17.133694 | 13.092 | -1.31 | 0.192 |
| RegV15 -27.852456 | 13.446 | -2.07 | 0.040 |
| RegV26 -25.3549 | 14.320 | -1.77 | 0.078 |

doi:10.1371/journal.pone.0135938.t001
likely a primary source of error in our feather isoscape. Values of $\delta^2$H in meteoric water can vary greatly from the rainy season through the dry period, with enrichment of water available to plants also due to evapotranspiration [40]. In many regions of Africa, we suspect that local foodweb $\delta^2$H can differ considerably from that predicted by models that assume periods of plant water integration leading to birds. Unfortunately, knowledge about timing of moult in Afrotropical birds is poor with few studies [41, 42, 43] and only a few researchers have examined Camaroptera in particular [30, 32, 31]. We predicted a moult season and a moult month
Fig 4. Standard deviation map resulting from the comparison between the Camaroptera feather δ²H isoscape (present work) and the feather δ²H isoscape predicted by Hobson et al. (2012) [14].

doi:10.1371/journal.pone.0135938.g004
for the sampled Camaropteras, but narrowing periods of H integration into the foodweb for these periods generally resulted in poorer model fit than those based on annual rainfall. This may be due to the assumption that Camaropteras only moult after the breeding season and that reproduction takes place at the beginning of the rainy season. Although this must be true in broad sense, local adaptations to more than one breeding season or to different habitats within the same site, a greater mismatch between rains and reproduction and thus moult process, all can occur and indeed an unexpected variation in deuterium values within the same locality [44]. Stations in Africa contributing to the GNIP database are also relatively few (20 are found within the study area boundaries) [23] and so a more refined precipitation δ²H basemap is clearly needed for this continent. Similarly, the rescaling function used by Hobson et al. [14] to transform the African precipitation δ²H isoscapes into a δ²H feather isoscape was based on a calibration using known-origin Eurasian Reed Warbler (Acrocephalus scirpaceus) in Europe [16] and we do not know how well this function applies to African-grown Camaroptera feathers.

Most differences between the feather δ²H values predicted by Hobson et al. [14] and those predicted by our Camaroptera model were found in the northeast of our study area, corresponding mostly to the Ethiopian highlands, north and south of the Great Rift Valley and the Horn of Africa. Here, expected feather δ²H values were much more positive than those obtained in the Camaroptera sampled by us. Camaroptera sampled in Sudan, Ethiopia and Somalia had feather δ²H values ranging between -61.6‰ and 1.5‰, while the predicted values from Hobson et al. [14] were all positive. This region has a complex isotope hydrology. Precipitation patterns are dominated by monsoonal seasonality, where most of the rains occur at high altitude (i.e. Bale Mountains) and so are expected to be less enriched in δ²H compared with precipitation in the dryer and lower surrounding areas. Foodwebs can also be fed by rivers flowing from the mountains to the Nile basin and to the Indian Ocean lowlands. Camaropteras may moult in cooler or shaded habitats with corresponding foodweb δ²H values lower than those based solely on larger scale averages. Although the only positive feather δ²H value (+ 1.5 ‰) we measured for the whole continent was obtained in Ethiopia, the δ²H predicted value for that location was much more positive (i.e. 35.8‰)

Our study indicates that much more on-the-ground sampling and isotopic measurement of feathers of known moult origin are required for Africa. Efforts to increase our ability to predict rainfall δ²H through an increase in GNIP stations will also be crucial together with refinement of our understanding of moult in targeted species. Africa is a complex continent isotopically and much effort will be required to improve our feather isoscapes to permit key studies on migratory connectivity between African wintering grounds and European breeding grounds for a variety of species. Nonetheless, previous studies in Africa and North America indicate that the rewards for this effort can be considerable [14, 45, 46]. We especially encourage those researchers engaged in the use of light-sensitive geolocators and/or gps tags [47] to track Eurasian-Afrotropical migrants to sample feathers of birds of known trajectory in order to assist in elucidating patterns of feather isotopes for Africa.

Supporting Information

S1 Fig. African regionalization using climatic regression models, obtained from Terzer et al. [34].
(TIF)

S1 Table. Accession number of the specimens used on this study, with reference to coordinates, location and country of origin as well as scientific collection origin. Raw δ²H values
Acknowledgments

Support was provided by a National Science and Engineering Council of Canada (NSERC) grant 103367 to CGE and an Environment Canada operating grant to KAH. Sampling costs were supported by the Spanish Ministry of Economy and Competitiveness, through the Severo Ochoa Programme for Centres of Excellence in R&D&I (SEV-2012-0262). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. Invaluable technical assistance was provided by LIE-EBD (Ricardo Álvarez & Susana Carrasco). Thanks to the staff of all institutions that supplied with Camaroptera samples: Teresa Garcia and José Cabot (Estación Biológica de Doñana, Sevilla), Ben Marks (The Field Museum, Chicago), Paul R. Sweet and Lydia Garetano (American Museum of Natural History, New York), Steve Rogers and José Manuel Padial (Carnegie Museum of Natural History, Pittsburgh), Jean L. Woods (Delaware Museum of Natural History, Wilmington), Mark B. Robbins (Kansas University Natural History Museum, Lawrence), Scott Edwards and Jeremiah Trimble (Harvard University Museum of Comparative Zoology, Cambridge), Jerôme Fuchs (Muséum National d’Histoire Naturelle, Paris), Steven van der Mije (Naturalis Biodiversity Center, Leiden), Jon Feldsá (Natural History Museum of Denmark, Copenhagen), Martim Melo (CIBIO, Vairão), Rene Corado (Western Foundation of Vertebrate Zoology, Camarillo) and Kristof Zyskowski (Yale Peabody Museum of Natural History, New Haven). Also thanks to Hanjo Böhme. This work would not have been possible without the help of Jaime Potti. Gabriel Bowen and two anonymous reviewers made valuable comments on an earlier draft of this manuscript.

Author Contributions

Conceived and designed the experiments: CGE FR IA MGF KAH. Performed the experiments: CGE FR MGF. Analyzed the data: CGE FR IA MGF KAH. Contributed reagents/materials/analysis tools: CGE FR IA MGF KAH. Wrote the paper: CGE FR IA MGF KAH.

References

1. Webster MS, Marra PP, Haig SM, Bensch S and Holmes RT. Links between worlds: unraveling migratory connectivity. Trends Ecol Evol. 2002; 17: 76–83.
2. Bridge ES, Thorup K, Bowlin MS, Chilson PB, Diehl RH, Fléron RW et al. Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. BioScience. 2011; 61: 689–698. doi: 10.1525/bio.2011.61.9.7
3. Hebblewhite M and Haydon DT. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philos Trans R Soc Lond B Biol Sci. 2010; 365(1550): 2303–2312. doi: 10.1098/rstb.2010.0087 PMID: 20566506
4. Bridge ES, Kelly JF, Contina A, Gabrielson RM, MacCurdy RB and Winkler DW. Advances in tracking small migratory birds: a technical review of light-level geolocation. J Field Ornithol. 2013; 84(2): 121–137.
5. Hobson KA, Møller A and Van Wilgenburg SL. A multi-isotope (δ¹³C, δ¹⁵N, δ²H) approach to connecting European breeding and African wintering populations of barn swallow (Hirundo rustica). Animal Migration. 2012; 1: 8–22. doi: 10.2478/am-2012-0002
6. Gunnarsson G, Latorre-Margalef N, Hobson KA, Van Wilgenburg SL, Elmberg J, Olsen B et al. Disease dynamics and bird migration. Linking Mallards Anas platyrhynchos and influenza A virus in time and space. PLoS ONE. 2012; 7(4): e35679. doi: 10.1371/journal.pone.0035679 PMID: 22536424
7. Hobson KA, Van Wilgenburg SL, Piersma T and Wassenaar LI. Solving a migration riddle using isoscapes: house martins from a Dutch village winter over West Africa. PLoS ONE 2012; 7(9): e45005. doi: 10.1371/journal.pone.0045005 PMID: 23028734
8. Mazerolle DF, Hobson KA and Wassenaar LI. Stable isotope and band-encounter analyses delineate migratory patterns and catchment areas of white-throated sparrows at a migration monitoring station. Oecologia. 2005; 144: 541–549. PMID: 15900746

9. Pain DJ, Green RE, Giessing B, Kozulin A, Poluda A, Ottoisson U et al. Using stable isotopes to investigate migratory connectivity of the globally threatened aquatic warbler Acrocephalus paludicola. Oecologia. 2004; 138: 168–174. PMID: 14595555

10. Reichlin TS, Hobson KA, Van Wilgenburg SL, Schaub M, Wassenaar LI, Martín-Vivaldi M et al. Conservation through connectivity: can isotopic-gradients in Africa reveal winter quarters of a migratory bird? Oecologia. 2013; 171(2): 591–600. doi: 10.1007/s00442-012-2418-5 PMID: 23011847

11. Bowen GJ, Wassenaar LI and Hobson KA. Global application of stable hydrogen and oxygen isotopes to wildlife forensics. Oecologia. 2005; 143: 337–348. doi: 10.1007/s00442-004-1813-y PMID: 15726429

12. Hobson KA and Wassenaar LI. Tracking Animal Migration Using Stable Isotopes. Academic Press, London. 2008.

13. Hobson KA, Van Wilgenburg SL, Larson K and Wassenaar LI. A feather hydrogen isotope for Mexico. J Geochem Explor. 2009; 102(3): 167–174. doi: 10.1016/j.gexplo.2009.02.007

14. Hobson KA, Van Wilgenburg SL, Wassenaar LI, Powell RL, Still CJ and Craine JM. A multi-isotope (δ13C, δ15N, δ2H) feather isoscape to assign Afro-tropical migrant birds to origins. Ecosphere. 2012; 3:5, art44. doi.org/10.1890/ES12-00018.1.

15. Wunder MB. Using isoscapes to model probability surfaces for determining geographic origins in: West JB, Bowen GJ, Dawson TE and Tu KP. Isoscapes. Understanding movement, pattern, and process on Earth through isotope mapping. Springer; 2010. pp 251–270.

16. Procházká P, Van Wilgenburg SL, Neto JM, Yosef R and Hobson KA. Using stable hydrogen isotopes (δ2H) and ring recoveries to trace natal origins in a Eurasian passerine with a migratory divide. Journal of Avian Biology. 2013; 44: 541–550.

17. Hobson KA, Bowen GJ, Wassenaar LI, Ferrand Y and Lormee H. Using stable hydrogen and oxygen isotope measurements of feathers to infer geographical origins of migrating European birds. Oecologia. 2004; 141: 177–488. doi: 10.1007/s00442-004-1671-7

18. Hobson KA, Van Wilgenburg SL, Wassenaar LI and Larson K. Linking Hydrogen (δ2H) Isotopes in Feathers and Precipitation: Sources of Variance and Consequences for Assignment to Isoscapes. PLoS ONE. 2012; 7(4): e35137. doi: 10.1371/journal.pone.0035137 PMID: 22509393

19. Bridge ES, Kelly JF, Xiao X, Takekawa JY, Hill NJ, Yamage M et al. Bird migration and avian influenza: A comparison of hydrogen stable isotopes and satellite tracking methods. Ecol Indic. 2014; 45: 266–273. PMID: 25045322

20. Del Hoyo J, Elliott A and Christie D Handbook of the Birds of the World. Vol. 11 Old World Flycatchers. Barcelona. Lynx Edicions. 2006.

21. Wassenaar LI and Hobson KA. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. Isotopes Environ Health Stud. 2003; 39: 1–7.

22. IAEA. Statistical treatment of data on environmental isotopes in precipitation. Technical report series N ° 331. International Atomic Energy Agency, 1992. Vienna.

23. Bowen GJ and Revenaugh J. Interpolating the isotopic composition of modern meteoric precipitation. Water Resour Res. 2003; 39(10), 1299, doi:10.1029/2003WR002086

24. Hijmans RJ, Cameron SE, Parra JL, Jones PG and Jarvis A. Very high resolution interpolated climate surfaces for global land areas. Int J of Clim. 2005; 25: 1965–1978.

25. Hastings DA, Dunbar PK, Elphingstone GM, Bootz M, Murakami H, Maruyama H et al. The Global Land One-kilometer Base Elevation (GLOBE) Digital Elevation Model, Version 1.0. National Oceanic and Atmospheric Administration, National Geophysical Data Center. 1999. Available: http://www.ngdc.noaa.gov/mgg/topo/globe.html.

26. Vander Zanden H, Wunder M, Hobson KA, Van Wilgenburg SL, Wassenaar LI, Welker J et al. Contrast-mapping of migratory organisms to geographic origins using long-term versus year-specific precipitation isotope maps. Methods in Ecology and Evolution. 2014; 5: 891–900.

27. Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jędrzejewska B, Lima M et al. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research. 2011; 46: 15–27.

28. Lobo JM. European Distributed Institute of Taxonomy Geoplatform. MNCN–CSIC. 2007. Available: http://edit.csic.es/Soil-Vegetation-LandCover.html.

29. Mu Q, Zhao M and Running SW. Improvements to a MODIS global terrestrial evapotranspiration algorithm. Remote Sensing of Environment. 2011; 115: 1781–1800.
30. Craig AFJK. Moul in southern African passerine birds: a review. Ostrich. 1983; 54: 220–237.
31. Payne RB. Overlap of breeding and molting schedules in a collection of African birds. The Condor. 1969; 71: 140–145.
32. Fogden MPL and Fogden PM. The role of fat and protein reserves in the annual cycle of the Grey-backed Camaroptera in Uganda (Aves: Syrphidae). Journal of Zoology. 1979; 189 (2): 233–258.
33. IAEA/WMO. Global Network of Isotopes in Precipitation. The GNIP Database. 2014. Available: http://www.iaea.org/water.
34. Terzer S, Wasenaar LJ, Araguás-Araguás LJ and Aggarwal PK. Global Isoscapes for δ¹⁸O and δ²H in precipitation: improved prediction using regionalized climatic regression models. Hydrology and Earth System Sciences. 2013; 17: 1–16
35. Walsh RPD and Lawler DM. Rainfall seasonality: description, spatial patterns and change through time. Weather. 1981; 36: 201–208.
36. Barton K. MuMIn: Multi-model inference. Model selection and model averaging based on information criteria (AICc and alike). R package version 10.0.0. 2014. Available: http://cran.r-project.org/web/packages/MuMIn/index.html.
37. Bates D, Maechler M, Bolker B and Walker S. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1–7. 2014. Available: https://github.com/lme4/lme4/.
38. Gelman A and Su Y. arm: data analysis using regression and multilevel/hierarchical models. R package version 1.7–03. 2014. Available: http://CRAN.R-project.org/package = arm.
39. Bowen GJ Isoscapes: Spatial Pattern in Isotopic Biogeochemistry. Annu Rev Earth Planet Sci. 2010; Vol. 38: 161–187
40. Clark I and Fritz P. Environmental Isotopes in Hydrogeology. London. CRC Press. 1997.
41. Bannerman DA. The birds of tropical west Africa. With special reference to those of The Gambia, Sierra Leone, The Gold Coast and Nigeria. London. The Crown Agents for the Colonies. 1939.
42. Mackworth-Praed CW and Grant CHB. Africa Handbook of Birds. Series 1. Volume 2. Birds of Eastern and North Eastern Africa. Longmans. 1960.
43. Urban EK, Fry CH and Keith S. The Birds of Africa. Volume V. Academic Press. 1997.
44. Oppel S, Pain DJ, Lindsell JA, Lachmann L, Diop I, Tegetmeyer C et al. High variation reduces the value of feather stable isotope ratios in identifying new wintering areas for aquatic warblers Acrocephalus paludicola in West Biol. 2011 42(4): 342–354.
45. Hobson KA, Van Wilgenburg SL, Wesolowski T, Maziarz M, Blijsem RG, Gredelmeier A et al. A multi-isotope (δ⁶H, δ¹³C, δ¹⁵N) approach to establishing migratory connectivity in Palearctic-Afrotropical migrants: An example using Wood Warblers Phylloscopus sibilatrix. Acta Ornithologica. 2014; 49:57–69.
46. Hobson KA, Van Wilgenburg SL, Faaborg J, Toms JD, Rengifo C, Llanes Sosa A et al. Connecting breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopes: a call for an isotopic atlas of migratory connectivity. J Field Ornithol 2014a; 85: 237–257.
47. Hallworth TH and Marra PP. Miniaturized GPS Tags Identify Non-breeding Territories of a Small Breeding Migratory Songbird. Scientific Reports. 2015. 5. doi:10.1038/srep11069