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Study of avian migration patterns using stable isotope analysis in the Galite Archipelago of Tunisia

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Abstract: This research employed stable isotope analysis to investigate the migratory patterns and geographic origins of Eleonora's falcon (*Falco eleonorae*) and its associated prey species within the Galite Archipelago of Tunisia. Feathers collected from both juvenile and adult falcons along with their prey were analyzed for deuterium isotopic composition using the IsoriX package in R, which facilitated geographic assignment based on stable isotope ratios. The results demonstrated no significant difference in deuterium values (δ^2H) between adult and juvenile individuals of Eleonora's falcon, indicating a lack of geographic variation in molting locations among different age groups. However, the isotopic data for adult falcons yielded unexpected results, suggesting origins close to the sampling site, which contradicted the anticipated patterns of migration to distant wintering grounds. Furthermore, this study successfully mapped the origins of various prey species, indicating a broad geographic intake ranging from the Mediterranean to southern Scandinavia. These findings highlight the complexity of migratory behaviors in predatory birds and underscore the efficacy of stable isotope analysis as a tool for ecological research in avian migration studies.

Key words: Avian migration, deuterium, IsoriX, migratory patterns, stable isotope

1. Introduction

One of the fundamental tenets of conservation policies is the identification of breeding and wintering sites for migratory birds. Enhancing our understanding of the spatial connections between sites utilized by species during their life cycle is of paramount importance (Martin et al., 2007; Taylor and Norris, 2009). Various methodologies have been employed to gain deeper insight into seasonal movements, with the most prevalent being the use of ringing or capture and recapture. However, this method has inherent limitations, as Robertson (2004) estimated that only 0.05% of ringed birds are recaptured. An alternative method involves the use of radio or satellite transmitters placed on the backs of migratory birds, which has significantly enhanced our understanding of migration routes across Africa (Gschweng et al., 2008). This method has also been employed to study individuals of *Falco eleonorae* or Eleonora's falcon. However, according to Duxbury et al. (2019), the weight of the transmitters can cause discomfort, necessitating their use only on large individuals. Additionally, the high cost of this method limits the number of individuals that can be monitored.

Since the early work of Chamberlain et al. (1997) and Hobson and Wassenaar (1996), stable isotope analyses of feathers has been recognized as a cheaper and less invasive alternative method for describing migratory patterns and diet (Hobson et al., 2004). Building upon those studies, Hobson (2005) and Bowen et al. (2008) demonstrated a robust correlation between stable hydrogen isotope measurements in bird feathers and those found in precipitation. The stable isotope values of feathers reflect those of the prey consumed by birds during tissue synthesis, as hydrogen isotopes from ingested food and water are incorporated into growing feathers. Since feather keratin is metabolically inert after synthesis, these isotope values preserve a dietary record from the period of growth. This characteristic makes feathers valuable for ecological studies, providing stable isotopic records linked to geographic and dietary origins (Mills et al., 2021). Phillips et al. (2009) presented a comprehensive analysis of stable isotope ecology, highlighting the use of stable isotopes in studying animal diets and movement. Consequently, deuterium can be employed to map the migratory routes

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and wintering areas of diverse avian species (Hobson et al., 2015). This approach proved to be highly beneficial, particularly for species such as the flammulated owl, *Otus flammeolus*, which had limited movement data (Delong et al., 2005), and Northern Alaska duck, *Anas acuta*, for which feather δ^2H values have been used to infer the origins of breeding sites and habitat types used prior to migration (Yerkes et al., 2008).

Eleonora's falcon (*Falco eleonorae*) is a late nester with its breeding period occurring at the peak of the passage of migratory passerines, allowing adults and chicks to feed during the period of postnuptial passerine migration (Génsbøl and Cuisin, 1993). In October, Eleonora's falcon initiates its migratory journey to Madagascar and other islands along the African coast (Wink and Ristow, 2000). Its specialization in terms of prey renders the species increasingly sensitive to climatic changes, and in particular fluctuations in atmospheric pressure systems, which are considered among the main drivers of the migratory behavior of passerines (Kassara et al., 2017). It is estimated that all colonies of Eleonora's falcon consume approximately two million birds (0.02% to 0.04% of the passerine migration flow) in a single breeding season (Walter, 1979).

The aim of this study is to describe the migratory patterns and geographic origins of Eleonora's falcon and its associated prey. To this end, stable isotope analysis is used, focusing on deuterium isotopes in feathers collected from the Galite Archipelago of Tunisia. Given the keystone status of Eleonora's falcon, this research is central to understanding the broader migratory movements of passerines, which are crucial for effective ecological management and conservation strategies. The objectives of this research go beyond the simple tracking of migratory routes; it aims to deepen our understanding of migratory dynamics, thereby informing and improving bird conservation methods.

2. Materials and methods

2.1. Study site

The Galite Archipelago, located between Sardinia and northwestern Tunisia (37°31′37″N, 8°55′43″E) with six rocky islands, forms the northernmost point of Africa. Galite is the main island and the other five islands are Galiton, Fauchelle, Gallina, Pollastro, and Gallo. A first order by the Minister of Agriculture of Tunisia on 4 July 1980 declared Galite to be a marine and coastal protected area, followed by a second order on 28 September 1995 prohibiting all types of fishing within 1.5 nautical miles of the islands of Galite and Galiton (Abbes et al., 2007) (Figure 1).

2.2. Sample collection

All feathers used in this study were collected from the bottoms of nests. A total of 19 feathers from individuals of Eleonora's falcon were collected during the growth phase of juveniles, specifically between 1 September and 15 October. Of these, 10 feathers belonged to juveniles (30–35 days old) and 9 to adult individuals (>2 years old). With regard to the adults, the feathers sampled were primary remains (P8 or P9) readily distinguishable from other feathers due to their markedly larger size, which facilitated their identification. Eleonora's falcon exhibits a unique molting pattern among raptors. Unlike many bird species that molt primarily in their breeding grounds, Eleonora's falcon often initiates molting during the breeding season but completes it in their wintering grounds (Forsman, 2016). The estimated growth rate of a P8 or P9 feather for Eleonora's falcon is not available in the literature. For juveniles, sampling was random as all of their feathers had molted in Galite.

Clumps of undigested prey feathers found in Eleonora's falcon nests were sampled. A total of one feather from each prey was collected.

In order to study intrafeather variations in isotopic signatures, each feather was cut into three fragments, labeled A, B, and C starting from the rachis. All biological material was held at 4 °C until laboratory analysis. Seven prey species were identified following the morphological characterization of the feathers, as described in the relevant literature and based on an understanding of the migratory bird species observed flying above the breeding grounds of Eleonora's falcon: common nightingale *Luscinia megarhynchos*, European greenfinch *Chloris chloris*, spotted flycatcher *Muscicapa striata*, common quail *Coturnix coturnix*, hoopoe *Upupa epops*, common whitethroat *Sylvia communis*, and European storm petrel *Hydrobates pelagicus*.

2.3. Sample preparation and analysis

The thin layer of wax covering feathers is mainly composed of lipids and its presence can influence the values of isotopic ratios. Accordingly, a specific protocol was implemented that included rinsing with a solution of chloroform and methanol at 2:1 v/v, ultrasonication, drying the samples for δ^2H analyses, weighing the samples, and storing them in tin capsules (Guillemain et al., 2014). The average sample mass was approximately 1.0 ± 0.1 mg. Feather fragments were cut and placed in tin capsules of 8 × 5 mm, which were then weighed using a balance with precision of 1 µg.

The determination of δ^2H was performed using a Pyrocube Elemental Analyzer (Elementar GmbH, Langenselbold, Germany) equipped with a purge-and-trap gas separation system configured in combustion mode and connected online in continuous flow mode to an Isoprime 100 isotope ratio mass spectrometer (Elementar GmbH). The SIA technique was used as developed by Fourel et al. (2014). Stable isotope ratios were reported as deviations from a standard in parts per thousand (‰) using δ

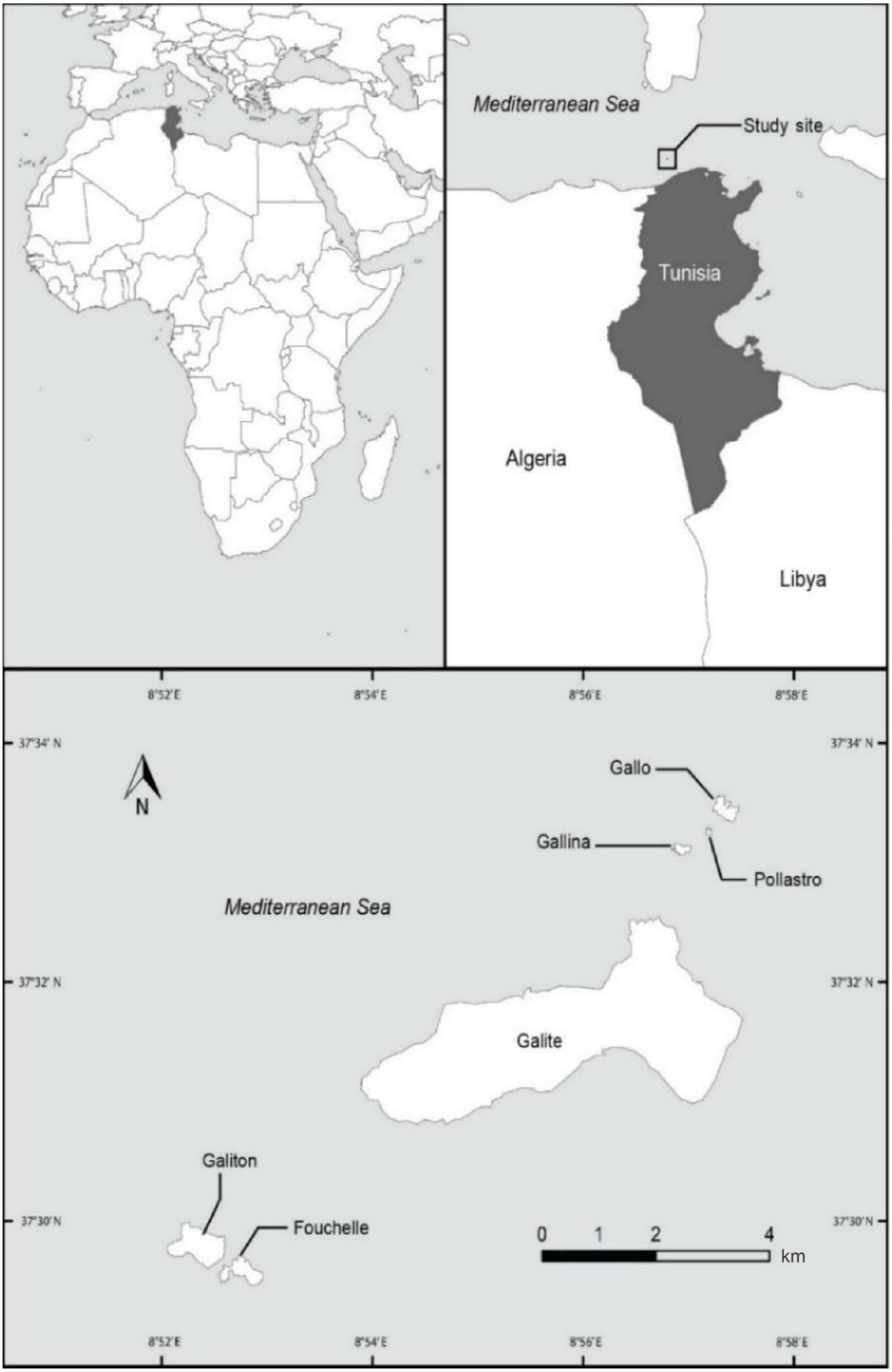

Figure 1. Map of the Galite Archipelago in northwestern Tunisia.

notation. This is defined as δX = (R_sample/R_standard − 1) × 1000, where δ is the isotopic ratio of the sample relative to a standard, and R_sample and R_standard are the proportions of heavy to light isotopes ($^2H/^1H$). The nomenclature for isotope ratios followed the guidelines of Bond and Hobson (2019), with data calibrated against international reference materials USGS KHS and USGS CBS for hydrogen. For drift correction, each series of analyses included USGS standards to monitor and correct for potential drift. Replicates of the USGS standards were used to ensure the accuracy of isotopic measurements. However, variation of 0.4‰ was observed, which can be explained by factors such as variations in laboratory conditions or differences in the standard samples used.

2.4. Data analysis

Nonparametric statistical tests were employed due to the nonnormal distribution of the δ^2H data and the relatively small sample sizes. The means and standard deviations (SDs) of stable isotope values for δ^2H were calculated. Additionally, the amplitude of isotopic values for δ^2H, defined as the difference between the signatures of the A, B, and C fragments of the feathers, was evaluated. The Kruskal–Wallis test was used to investigate variation in δ^2H values across the three feather segments (A, B, and C). The Mann–Whitney U test was used to determine whether there were significant differences in the means of stable isotope δ^2H values between Eleonora's falcon and passerine prey, as well as between juvenile and adult falcons. Statistical analyses were performed using Statistica 12.0 software (StatSoft Inc., Tulsa, OK, USA).

2.5. Geographic assignments

In this section we rely on the results of isotopic analyses of deuterium, an isotope of hydrogen. The aim is to establish the provenance of adult falcons and passerines by analyzing the δ^2H values of feathers. The IsoriX 0.9.0 package, part of the R statistical computing environment, can be used to construct isoscapes and infer geographic origin based on deuterium isotopic signatures (Courtiol et al., 2019). This package uses a novel statistical framework based on generalized linear mixed models.

To obtain an isoscape, we first constructed our prediction maps using the 'prepsource ()' command, which uses data on deuterium isotope composition within the theoretical feather synthesis zone of prey and adult falcons. These data can be downloaded by creating an account with the Global Network of Isotopes in Precipitation (GNIP).

Statistical models were then fitted using the 'isofit' command and a structural raster was created using the 'prepraster' command. The maps were calibrated using the 'calibfit' command. Finally, attributions to geographic areas of origin were derived using the 'isofind' function. The confidence intervals used for the p-values in these prediction maps were 95%. The null hypothesis was based on the similarity of the sample signature and the sample collection site. Consequently, sites with p-values close to 1 were taken as indicating the most likely origin (Courtiol et al., 2019).

3. Results

3.1. Eleonora's falcon

The results of the Kruskal–Wallis test among segments A, B, and C for adult feathers ($H (2. 27) = 1.40$; $p = 0.494$) indicated that there were no statistically significant differences between the analyzed segments, suggesting consistency in the δ^2H values along the different feather segments in adults. For juveniles, similarly, the Kruskal–Wallis test for these segments ($H (2.30) = 4.48$; $p = 0.106$) indicated no statistically significant differences between the analyzed segments (Table 1).

The mean δ^2H value for the combined samples of adult and juvenile individuals of Eleonora's falcon was found to be −64.67 ± 6.6‰. For adults, the δ^2H values ranged from approximately −72.5‰ to −54.5‰, with a median value of about −65‰. In contrast, the δ^2H values for juveniles ranged from approximately −72.5‰ to −64‰, with a median value of about −68.5‰ (Table 2; Figure 2). No significant difference in deuterium ratios or amplitudes was observed between adult and juvenile feathers ($Z = 1.41$; $p = 0.157$).

The prediction maps for the sites of adult individuals of Eleonora's falcon revealed results with low p-values for both the collection site (0.10–0.20) and the theoretical wintering sites in Madagascar and the southeastern region of the African continent (Figure 3).

3.2. Prey

Mean δ^2H values for prey ranged from −85.99 ± 1.10‰ for common whitethroat to −45.76 ± 9.77‰ for common quail. The amplitude of intrafeather isotope ratios for the

Table 1. Intrafeather (segments A, B, and C) variability of δ^2H‰ in Eleonora's falcon (juveniles and adults) and their passerine preys.

		Adult (mean ± SD)	Juvenile (mean ± SD)	Both (mean ± SD)	Preys (mean ± SD)
δ^2H ‰	A	−64.41±6.98	−64.93±6.25	−64.67±6.6	−65.06±23.31
	B	−64.68±8	−68.65±3.9	−66.66±6.84	−66.54±16.09
	C	−67.56±6.41	−70.84±3.75	−69.2±5.05	−68.86±16.76
		H (2, 27) =1.40; p =0.494	H (2, 30) =4.48; p =0.106	H (2, 57) =2.38; p =0.302	H (2, 21) =0.20; p =0.9047

Table 2. Deuterium isotope signatures, means, standard deviations, and amplitudes recorded in the feathers of Eleonora's falcons.

Species	δ²H ‰			Mean ‰	SD	Amplitudes
	A	B	C			
Adult 1	−63.34	−60.85	−60.56	−61.58	1.17	3.14
Adult 2	−57.48	−48.39	−58.27	−54.71	4.22	11.14
Adult 3	−71.46	−64.23	−65.16	−66.95	3.00	8.17
Adult 4	−68.81	−72.01	−75.50	−72.11	2.26	7.56
Adult 5	−72.48	−69.24	−73.05	−71.59	1.57	4.31
Adult 6	−60.80	−63.94	−65.81	−63.52	1.81	5.67
Adult 7	−54.49	−68.69	−70.50	−64.56	6.72	18.10
Adult 8	−63.36	−64.67	−68.27	−65.43	1.89	5.30
Adult 9	−67.46	−70.08	−70.92	−69.48	1.35	3.91
Elenora's falcon adults	−64.41	−64.67	−67.56	−65.54	2.67	7.47
Juvenile 1	−64.77	−73.71	−72.47	−70.32	3.70	10.10
Juvenile 2	−60.17	−70.30	−69.49	−66.66	4.32	11.45
Juvenile 3	−62.66	−61.81	−68.93	−64.46	2.97	2.14
Juvenile 4	−63.71	−62.52	−71.13	−65.79	3.56	9.73
Juvenile 5	−62.73	−70.88	−70.52	−68.04	3.54	4.12
Juvenile 6	−67.23	−78.09	−73.08	−72.80	3.71	14.99
Juvenile 7	−64.82	−66.44	−73.87	−68.37	3.66	8.39
Juvenile 8	−71.65	−68.60	−68.87	−69.71	1.30	3.00
Juvenile 9	−66.21	−72.65	−70.43	−69.76	2.37	8.24
Juvenile 10	−65.35	−63.52	−69.60	−66.16	2.30	6.87
Elenora's falcon juveniles	−64.94	−68.31	−70.65	−67.97	3.08	7.65

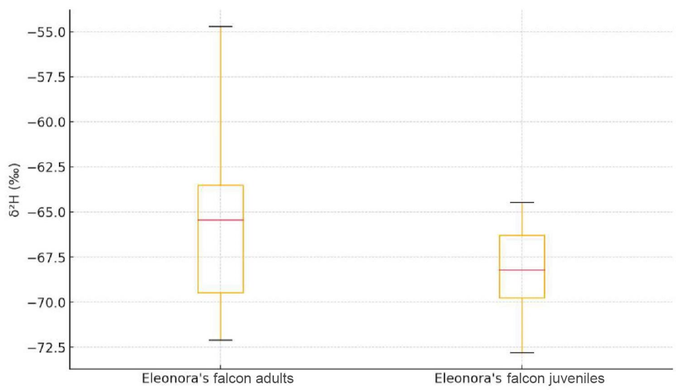

Figure 2. δ²H values in feathers of adult and juvenile individuals of Eleonora's falcon.

seven identified species varied from 2.64‰ for common whitethroat to 28.40‰ for common quail (Table 3).

The results of the area-of-origin assignments for the seven prey species showed that three of them, namely hoopoe, spotted flycatcher, and common whitethroat, originated from areas outside the collection site and even from different locations in North Africa. These species had the lowest p-values (0–0.05) in the Galite Archipelago dataset.

Conversely, the p-values closest to 1 generated by our prediction maps indicated that the hoopoe originated from the British Isles, western France, and Germany to the south of the Scandinavian countries, with similar regions identified for the spotted flycatcher, albeit showing a higher concentration in the Scandinavian countries. The common whitethroat is concentrated in the southeastern regions of France and extends as far as northern Italy, but mainly in the eastern region of Europe. For the common

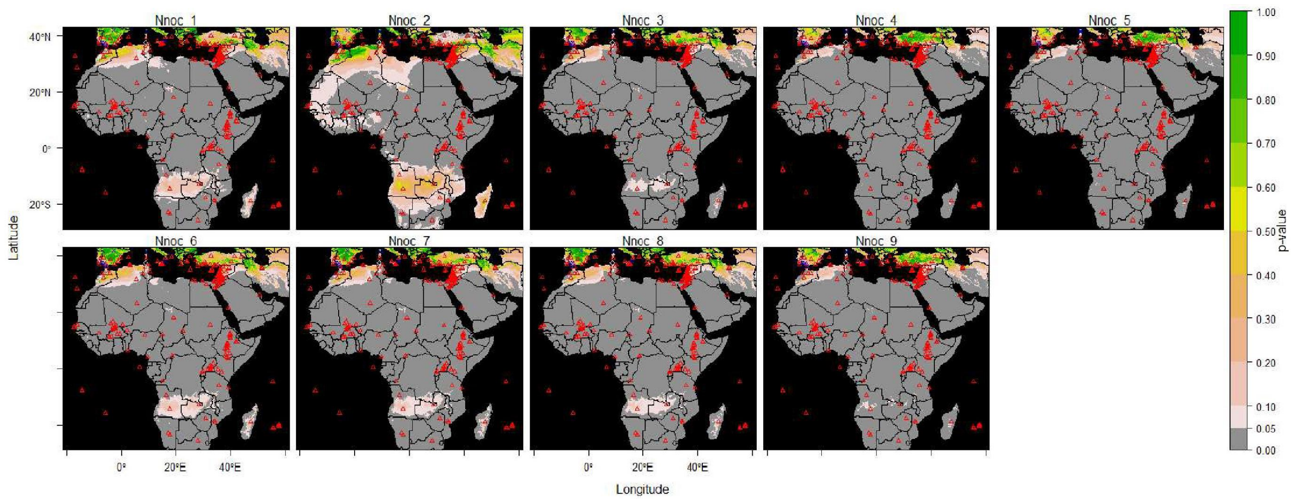

Figure 3. Prediction maps of wintering grounds for nine adult individuals of Eleonora's falcon: Nnoc_1 = Eleonora's falcon adult 1…. Nnoc _9 = Eleonora's falcon adult 9. Even if a location presents a perfect match (i.e., with a p-value close to 1), it does not mean that the location is the true place of origin. Red triangles represent the sites of stations of the Global Network of Isotopes in Precipitation (GNIP).

Table 3. Deuterium isotope signatures, means, standard deviations, and amplitudes recorded in the feathers of prey of Eleonora's falcons.

Species	δ^2H ‰			Mean ‰	SD	Amplitudes
	A	B	C			
Common nightingale	–82.66	–76.71	–76.84	–78.74	2.62	6.73
Spotted flycatcher	–81.51	–76.13	–83.93	–80.52	2.93	8.81
Hoopoe	–67.65	–68.63	–70.37	–68.89	0.99	3.08
Common whitethroat	–86.59	–84.53	–86.86	–85.99	0.98	2.64
European storm petrel	–44.17	–49.62	–46.62	–46.80	1.88	6.16
Common quail	–32.79	–46.57	–57.92	–45.76	8.65	28.40
European greenfinch	–60.08	–63.61	–59.48	–61.06	1.70	4.65

nightingale a very low p-value (0.10–0.20) was also observed in the direction of the feather collection site. The prediction map for this species identified potential areas of origin including the Iberian Peninsula, France, some regions of northern Italy, the British Isles, and even some regions of Morocco. In contrast, for the other three species, higher p-values were recorded in areas closer to the collection site. Both the storm petrel and common quail exhibited p-values that were nearly identical to 1 in areas encompassing the southern Mediterranean coasts, with some occurrences in the Mediterranean. Similarly, the European greenfinch had elevated p-values in western regions of France, the Iberian Peninsula, and southern Italy (Figure 4).

4. Discussion

The results of this study demonstrated no significant difference between the P8 and P9 feathers from adult individuals of Eleonora's falcon and those of juveniles, suggesting that the diets and geographic origins of feather synthesis were similar. This leads to the conclusion that the P8 and P9 feathers of the adults were synthesized in the breeding area of Galite.

The use of stable isotopes to assign the geographic origins of natural species has numerous advantages, but it may also have limitations at various levels (Hyland et al., 2022). Local variability in isotopic signatures in rainwater from one season to another, as well as global warming and groundwater pollution, can distort the results of geographic assignment work (Hobson and Wassenaar, 2018; Courtiol et al., 2019). In our study of the assignment of adult individuals of Eleonora's falcon to their wintering grounds, we found results that differed significantly from those described in the literature. The wintering grounds of falcons are frequently located in southeastern African regions or even on the island of Madagascar, with the island of Reunion also being a potential destination (Walter, 1979; Ristow, 1999). The results of this study

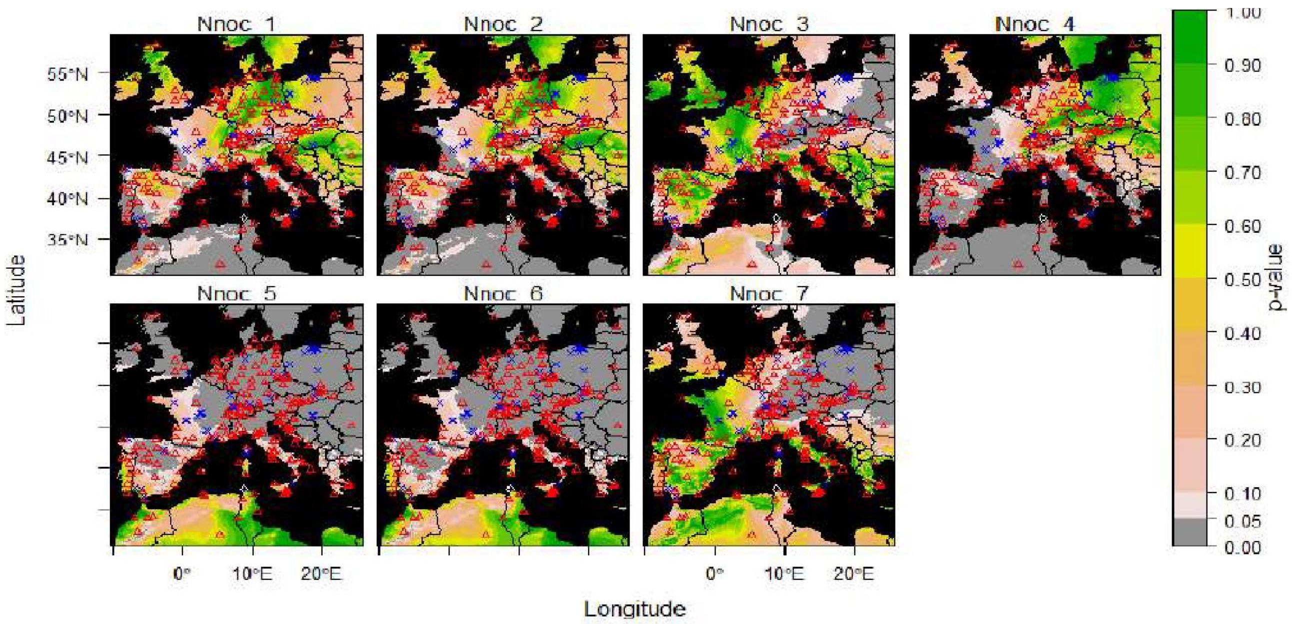

Figure 4. Prediction maps for the prey of Eleonora's falcon: Nnoc_1 = hoopoe, Nnoc_2 = spotted flycatcher, Nnoc_3 = common nightingale, Nnoc_4 = common whitethroat, Nnoc_5 = European storm petrel, Nnoc_6 = common quail, and Nnoc_7 = European greenfinch. Even if a location presents a perfect match (i.e., with a p-value close to 1), it does not mean that the location is the true place of origin. Red triangles represent the sites of stations of the Global Network of Isotopes in Precipitation (GNIP).

indicate that the average feather values of adult falcons exhibit signatures of δ^2H that are below the levels expected for individuals in the theoretical wintering areas.

The peculiarity of Eleonora's falcon as a late spawning species that stalls its breeding period to feed on migratory passerines (Walter, 1979) may explain the results observed. During this period, passerines constitute a significant component of the diet of Eleonora's falcon. Deuterium signatures are transferred across food webs through the consumption of drinking water and food from land as a result of precipitation (Hoefs and Hoefs, 1997). The prey passerines of Eleonora's falcon, which feeds in their geographic areas of origin, will bring with them different deuterium signatures specific to their areas of origin.

Consequently, the deuterium signatures observed in the feathers of Eleonora's falcon during this period of its life cycle will be strongly influenced by the signatures provided by the passerines in question rather than by those of the falcon's synthesis sites. These findings provide further support for the hypothesis that the feathers of the adult individuals of Eleonora's falcon molted in Galite. The lack of precise information in the literature regarding the molting of Eleonora's falcon prevented further information from being obtained about its wintering sites, although the present results indicated that the P8 and P9 feathers were synthesized in Galite.

In contrast to the allocation of falcon prey, this method has proven to be highly effective, yielding results that are in close alignment with those documented in the literature. The common nightingale, the hoopoe, the common whitethroat, and the spotted flycatcher are well-documented migratory species (Moreau, 1972; Shirihai et al., 2001; Dubois and Cézilly, 2002). These findings are consistent with the results predicted by our maps. For the common nightingale captured by falcons, the individual may have originated in metropolitan France; it occupies most of the country during the breeding season (Dubois and Cézilly, 2002). The hoopoe is present during the breeding season in a range extending from the south of the British Isles to northeastern Germany and into some regions of French territory (Hagemeijer and Blair, 1997), which aligns perfectly with the areas indicated on our maps. The breeding range of the common whitethroat encompasses the entirety of Europe and extends eastward to include Mongolia (Voous and Thomson, 1960). Consequently, the individual captured by the falcons may have originated from the northern regions of Italy or the extreme southeast of France, potentially even from an East European country. The spotted flycatcher breeds from northern North Africa to Lake Baikal in Russia and northern Norway (Drôme, 2003). Given the very low isotopic signature of δ^2H recorded in the feathers of this species and the results revealed by our prediction maps, it is possible that the individual captured by the falcons may have been the bird that traveled the greatest distance during its migration and may have had the most northerly breeding grounds.

It can be argued that the storm petrel is the only species among the analyzed prey that can be considered sedentary. This assertion is supported by an analysis of the data presented in the literature, which was then compared with the findings of our own prediction maps. Among the few studies conducted on the avifauna of the Galite Archipelago, Abbes et al. (2007) considered the storm petrel to be nesting on the island, a conclusion corroborated by our prediction maps. With regard to the European greenfinch caught by the falcons, it can be reasonably assumed that it was either a migratory or sedentary individual. Both possibilities are indicated by the literature data and our prediction maps (Shirihai et al., 2001; Dubois and Cézilly, 2002).

In the case of the common quail, the greatest intrafeather amplitude was observed at 25.13‰ for δ^2H between zone A (δ^2H: −37.79‰, N = 3) and zone C (δ^2H: −57.92‰, N = 3) of the feather. The common quail is renowned for its highly variable behaviors and migratory routes (Rodríguez-Teijeiro et al., 1992). In the majority of cases, the flight feathers of the common quail are synthesized during postnuptial molting, which typically lasts for an average of 4.5 to 5 months (Guyomarc'h, 1996). Molting is divided into two phases, with the first phase occurring during a period of significant fattening and migration (Guyomarc'h, 1996). The results of the analysis indicated that the feathers in question were synthesized in different habitats. The hypothesis that molting was initiated on the breeding grounds is supported by evidence indicating that it occurred during or after the migratory period. The maps indicated a high p-value for the Mediterranean shores, thereby confirming that the species is migratory to regions around the Mediterranean.

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Authorship contributions

Hsan BEN JEMAA: Conceptualization of ideas; formulation of research questions; hypothesis development; design and implementation of computer programs and algorithms; application of statistical methods; data/evidence collection; writing of the initial draft.

Said NOUIRA: Writing of the initial draft; research supervision.

François FOUREL: Isotopic analyses using isotopic ratio mass spectrometry.

Ilham BENTALEB: Conceptualization of ideas; formulation of research questions; hypothesis development; design and implementation of computer programs; research supervision; writing of the initial draft.

Conflict of interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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