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Geographic origin of migratory birds based on stable isotope analysis: the case of the greylag goose (*Anser anser*) wintering in Camargue, southern France

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Abstract

Proper delineation of flyways is a prerequisite for adequate management of migratory birds. The implementation of coordinated international management for greylag goose (*Anser anser*) is currently underway in Europe for the north-west/south-west (NW/SW) population. Some uncertainty remained as to whether greylags wintering in Camargue, Southern France, belonged to this population and bred in Norway, Sweden and Finland, or rather originated from the Central European population, especially since most neck collar observations were of birds ringed in the Czech Republic. Stable hydrogen isotope ($\delta^2\text{H}$) analyses of feathers from 147 individuals hunted or trapped during winter in Camargue provide some insight into this question and suggest north-central Europe as a more likely area of origin. This indicates that greylags wintering along the Mediterranean coast maybe largely separate from the birds of the NW/SW European population breeding in Fennoscandia, although some individuals may also come from the Polish or German regions of the NW/SW flyway, since the combined ringing and stable isotope analyses suggest these birds are mostly breeding and moulting in an isotopic area consistent with the Czech Republic, Poland and northern Germany. Earlier studies show birds wintering in other French regions rather originate from Sweden and Norway. These results should be considered for the management plan currently being developed for greylag goose in Europe. More generally, they question whether birds from two distinct populations /flyways should be applied similar or potentially different management plans within a given country.

Keywords *Anser anser*, Greylag goose, Flyway delineation, International management plans, Deuterium, Stable isotopes

Introduction

Adequate management of migratory quarry species requires precise delineation of their flyways, in order to facilitate collaboration between countries at the appropriate geographic scale (Madsen et al. 2014). Indeed, distinct flyways of the same species may show very different trends in numbers of individuals or different migration strategies, requiring contrasting management approaches (e.g. see hunting regimes for the different Taïga Bean Goose *Anser fabalis fabalis* management units in Jensen et al. 2018). A range of methods currently exist to delineate migratory bird flyways, all having their limitations under various circumstances. For example, satellite tags are expensive to deploy on a sufficient number of birds, genetic analyses do not provide much information when even limited cross breeding occurs among populations (Kraus et al. 2013), feather isotopes alone may only provide coarse-scale information in some geographic regions (Guillemain et al. 2014) and ring recoveries may be biased when ringing effort or ring recovery probability (i.e. hunting pressure) vary over time and space (Korner-Nievergelt and Liechti 2012).

Management of goose species in Europe has advanced greatly over the last couple of years, with the gradual implementation of adaptive management schemes in order to regularly revise policy for these populations (potentially including their harvest) to

current population size and knowledge about their dynamics (Madsen et al. 2017). As part of such a move, an international adaptive management plan has been adopted at the last meeting of AEWA parties for the north-west/south west (NW/SW) Europe population of greylag goose (*Anser anser*) (Powolny et al. 2018). Such a plan was required owing to the enormous growth of this population over the last decades (8.5% annual increase between 1980 and 2008; Fox and Madsen 2017) which, together with other European goose species, is causing conflict with agriculture and concern for disease transmission and air traffic safety in several countries (e.g. Bradbeer et al. 2017; Fox et al. 2017), although not in France so far (Powolny et al. 2018).

Some countries within the wintering range of greylag goose actually receive birds from both the NW/SW European and the Central European populations (Scott and Rose 1996). For instance, birds wintering or migrating along the North Sea, Channel and Atlantic coast of France are considered to belong to the former flyway, with breeding grounds mostly in Sweden and Norway (Bacon et al. 2019). Conversely, greylags observed on the French Mediterranean coast are believed to originate mostly from Central Europe (ONCFS 2014). This is by no means anecdotal since the Camargue is now the top winter quarter in the country with 2897 individuals recorded in mid January 2017, for a national total of 17,775 greylags (Gaudard et al. 2018), while very few greylags were wintering in this part of France before the 1990s (fewer than 50 geese during the 1980s on the main Camargue wintering site at Tour du Valat, Desnouhes et al. 2003). Ring recoveries and observations of neck collars in Camargue since 2005 support the assumption that despite changes in migratory behaviour following climate change (Fouquet et al. 2009; Podhrázký et al. 2017), birds present in the area mostly come from Central Europe (Fig. 1). Such data also suggest the Czech Republic is the main breeding area for birds wintering in Camargue; however, a particularly great effort has been deployed to ring and mark greylags with neck collars in that country (Podhrázký et al. 2017), which may provide a biased assessment of where most Camargue birds originate.

The aim of the present study was therefore to collect feathers of greylags wintering in Camargue and assess their geographic origin by means of stable isotope and probabilistic assignment analyses. The objectives of this study were to (i) determine if they were indeed mostly originating from Central Europe, and not Fennoscandia, and (ii) assess if such analyses would confirm the ringing data suggesting most Camargue greylags originate from the Czech Republic. Such information is crucial in determining the extent to which geese wintering along the Mediterranean coast of France should be considered in the new international management plan for the NW/SW European population, which mostly considers the birds breeding in Fennoscandia and western Europe. If not, the aim of this paper was also to assess which countries should be considered for establishing coordinated management within the Central European flyway or the eastern end of the NW/SW European flyway.

Feather samples

Feathers were collected from 147 different greylag geese captured, shot or found dead within the Rhône Delta (145,000 ha) in Camargue, southern France (Supplementary Material 1) between the 2008–2009 and 2017–2018 hunting seasons. Of these, 119 were shot on the Tour du Valat estate (43°30' N 04° 40' E) between 31 January 2009 and 30 January 2017. The Tour du Valat estate comprises not only a 1845-ha Nature Reserve but also ~403 ha of hunted lands (ca. 50 ha of wetlands) where staff of the research station are allowed to hunt. Only one wing feather (remige) was collected per individual. Such feathers are grown only once per year in greylags and thus keep the isotope signature from the natal (in young birds) or moulting grounds (in adults). Information about sex and age of the individuals was generally not provided by the hunters and could hence not be considered in the analyses (see Supplementary Material 1).

Laboratory methods

Feather samples were transferred to 20-ml glass scintillation vials and soaked in 2:1 chloroform:methanol solvent overnight. They were then decanted and rinsed and allowed to dry for 24 h in a fume hood. A subsample of 0.35 mg of feather vane material was then weighed into silver capsules, crushed and loaded for stable isotope analysis.

Stable-hydrogen isotope analysis involved loading the unknowns and calibration standards in sequence on a Uni-Prep (Eurovector, Italy) carousel heated to 60 °C under vacuum. The carousel was flushed twice with dry helium, and then samples were combusted pyrolytically in a Eurovector 3000 elemental analyser using a ceramic reaction vessel with glassy carbon heated to 1350 °C. Resultant gases were separated by GC and the H₂ gas introduced via an open split to a Thermo Delta V Plus isotope ratio mass spectrometer. Calibration correcting for H exchange was accomplished using two keratin standards (CBS – 197‰; KHS – 54‰) by means of the comparative equilibration technique (Wassenaar and Hobson 2003). Based on within-run (N = 6) reproducibility of standards, we estimate measurement error to be ±2‰. All stable isotope values are reported in delta notation relative to the Vienna Standard Mean Ocean Water (VSMOW) scale.

Summary statistics and assignment method

Descriptive statistics to compare monthly and annual isotope values were conducted using analysis of variance (ANOVA) using the Statistica 10 software (Statsoft 2011). A spatially explicit likelihood assignment approach (Royle and Rubenstein 2004; Hobson et al. 2009; Hobson 2018) was then used to assign the population to potential areas of origin. To accomplish this, the amount-weighted growing-season precipitation surface from Bowen et al. (2005; $\delta^2\text{H}_p$) was converted to a feather isoscape using the calibration equation for European Mallards (*Anas platyrhynchos*) from van Dijk et al. (2014; $\delta^2\text{H}_f = -27.4 + 1.28 \times \delta^2\text{H}_p$). These calibration algorithms were developed based on the keratin standard $\delta^2\text{H}$ values (CBS and KHS) used in this study. A similar calibration is not specifically available for geese, and this species provides the only published equation for European waterfowl. That study did not publish an explicit value for the standard deviation of the residuals of their linear regression model and so the standard deviation from Lesser Scaup (*Aythya affinis*) $\delta^2\text{H}_f$ regressed against the same isoscape (SD = 12.6‰; Hobson et al. 2009) was used and incorporated into the assignments as an estimate of error. To determine the sensitivity of the probabilistic assignments to increases in the standard deviation, assignments were also conducted using a standard deviation of 25, which is greater than most of the published values (Hobson and Wassenaar 2018). The resulting calibrated feather isoscape was then clipped to a potential greylag goose natal and moulting range map based on BirdLife International and NatureServe (2011) range maps modified using published data (Scott and Rose 1996).

We then applied a normalized probability density function (Hobson et al. 2009) to estimate the probability that individual cells in the calibrated feather isoscape represented a potential origin for each bird. Individual birds were assigned to potential natal and moulting origins based on a Bayesian framework incorporating a spatially explicit isotope-based likelihood function applied at each pixel. We then applied a 2:1 odds criterion for accepting any given pixel as a potential origin and assigned pixels as either 1 or 0, accordingly. Assignment results for individual birds were subsequently 'stacked' for the sample to depict potential breeding origin for the population. Digital file manipulation and assignment to origin analyses were conducted using multiple packages including 'raster' v.2.3 (Hijmans 2015) and 'maptools' v0.8 (Bivand and Lewin-Koh 2015) in the R statistical computing environment v3.2.2 (R Core Development Team 2015).

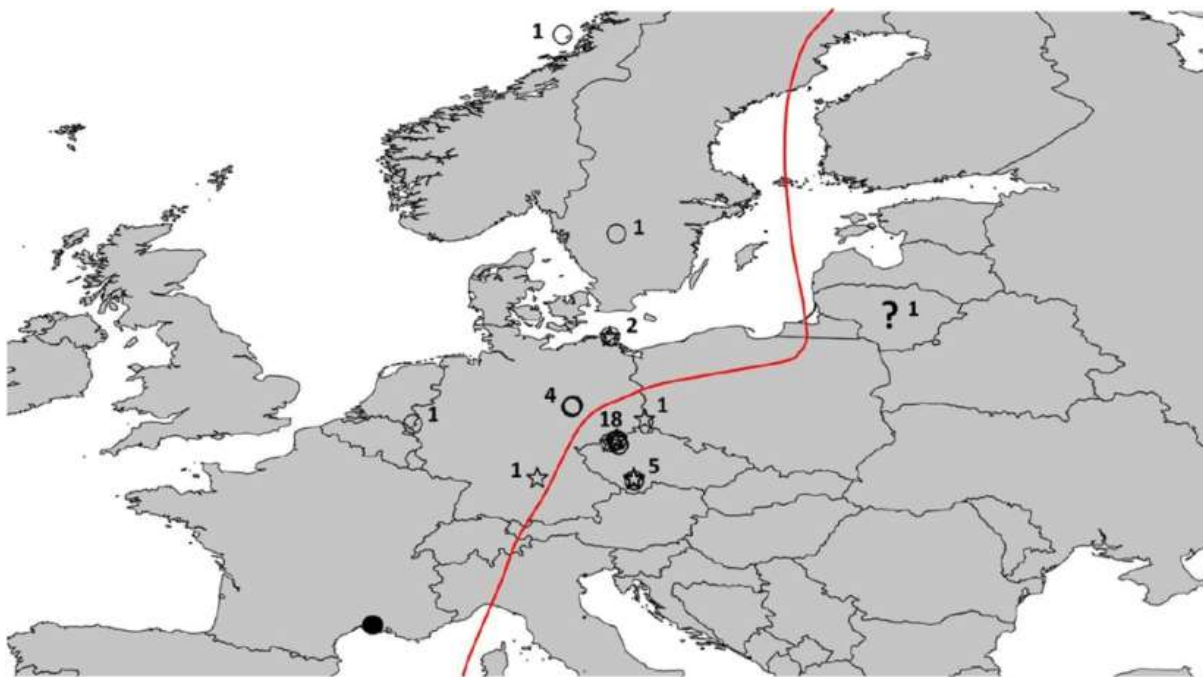


Fig. 1 Geographic origin of the 34 greylag geese observed or recovered in Camargue (black dot) since 2005. Stars represent the ringing sites of birds later recovered (i.e. hunted) in the Camargue, while circles show the origin of birds observed alive through their neck-collar. Some signs actually illustrate neighbouring ringing locations of more than one bird: numbers beside the signs indicate the number of different individuals (source of the data: www.geese.org and Dehorter & CRBPO 2018). One ring from Lithuania is indicated on the map with a question mark because the exact place of ringing could never be ascertained owing to the death of the ringer. The red curve indicates the assumed boundary between the NW/SW European and the Central European greylag goose flyways after Scott & Rose (1996)

Results

Stable H isotope values among the 147 greylag goose feathers were consistent, with 110 birds (75%) lying between -120 and -90 ‰ values (Fig. 2). Mean isotope values were similar between feathers collected in November, December or January ($F_{2,126} = 0.04$, $P = 0.96$; Fig. 2), the seven birds with a known collection date during any of the other months were discarded from the analyses. Similarly, the mean isotope value was similar among the years of collection, those with a known collection date before the 2010–2011 hunting season ($n = 7$ birds) being excluded from the analysis ($F_{6,129} = 0.29$, $P = 0.94$; Fig. 3). In general, these discarded individuals had isotope values within the main range of the other birds, but there were also considerable outliers (e.g. bird no. 95 or 115 in the Electronic Supplementary Material), which could also indicate different origins and could have included some locally born birds.

Based on feather isotopes from each individual, the results of the probabilistic assignment exercise for the breeding/ moulting origin of greylag geese wintering in Camargue are shown in Fig. 4. This depiction illustrates that the isotope values in wing feathers were consistent with a geographic origin across a band of latitude extending from the UK across north-central Europe, particularly consistent with Poland and north-eastern Germany. The assignment to origin analysis using a higher standard deviation showed very similar regions of origin (not shown), indicating that the analysis was robust to an increased standard deviation.

Discussion

Feather $\delta^2\text{H}$ values from our sample are consistent with a geographic origin either in the UK or in north-central Europe, reflecting the nature of the underlying feather isoscape and the ambiguity often associated with bands of latitude. Greylags breeding in the UK are, however, mostly resident feral birds, and the UK is not known as a major moulting area for greylags breeding elsewhere (Mitchell and Fox 1999). It is therefore reasonable to conclude that the feathers of greylag geese wintering in Camargue mostly originate from northern central Europe. Although a Danish or even Dutch origin cannot be completely ruled out (see the few blue dots on map in Fig. 4), the core of the region of origin after the isotope analyses lies in Poland and northeastern Germany.

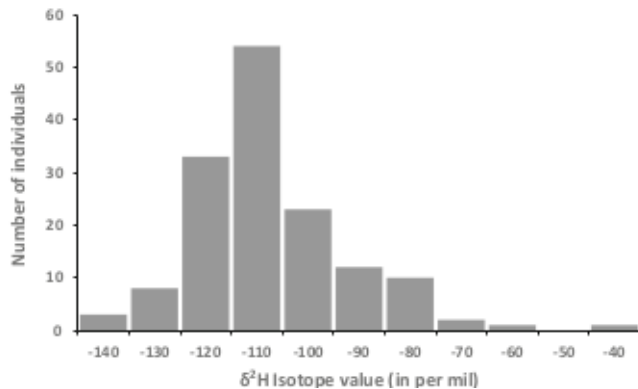


Fig. 2 Number of Camargue greylag goose feathers per category of $\delta^2\text{H}$ isotope values (expressed in per mil). -120 stands for the interval from -120 to -110.1

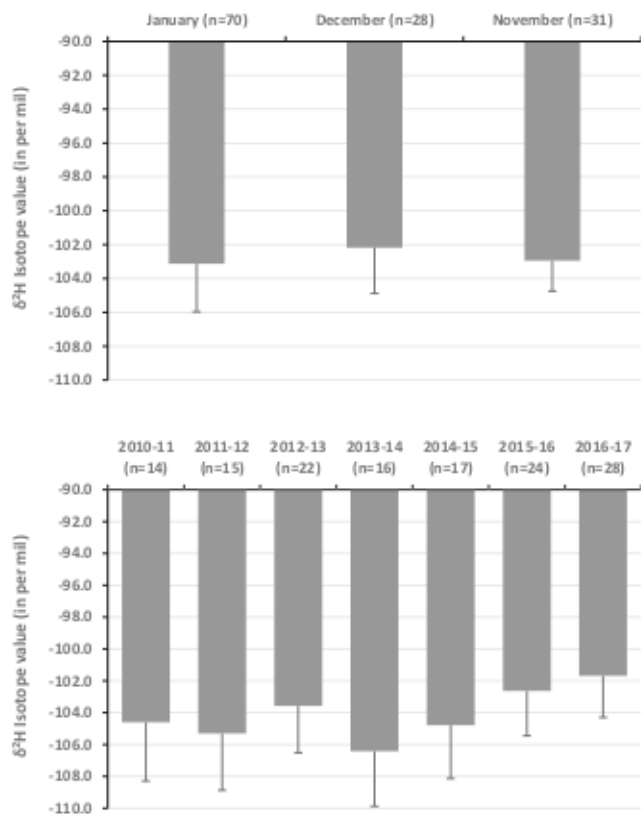


Fig. 3 Mean Camargue greylag goose feather $\delta^2\text{H}$ isotope values expressed in per mil per month (top) and hunting season (bottom). Vertical bars show standard errors. No significant difference was found between months or between hunting seasons (see text)

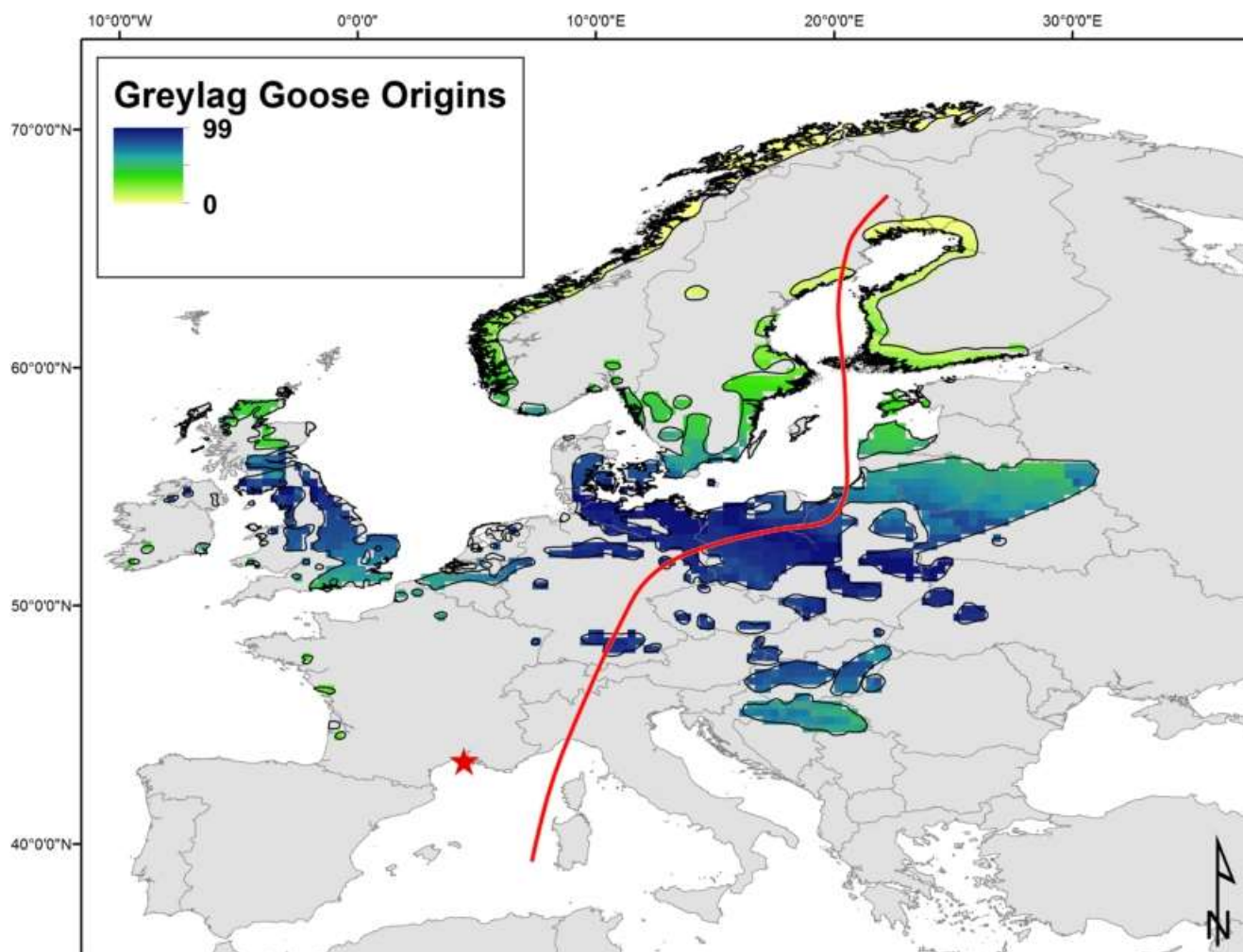


Fig. 4 Depiction of the origins of the sample of Camargue greylag goose feathers, based on stable isotope analyses. The bluer the area, the higher the number of birds that potentially originated from that area. See 'Methods' for an explanation of the procedure used. The red curve indicates the assumed boundary between the NW/SW European and the Central European greylag goose flyways after Scott & Rose (1996). The red star shows the Camargue

The $\delta^2\text{H}_f$ values were consistent across years and among months of feather collection, indicating the Camargue greylag geese likely originated from the same general breeding/ moulting areas. A parsimonious consideration of the range in error in $\delta^2\text{H}_f$ to be expected from any given location is of the order of 12‰ which was propagated in our Bayesian based assignment, incorporating that error still distinguished areas north of the Czech Republic, Poland and northern Germany as being likely origins. Other sources of error involve potential year-to-year variation in the IAEA-GNIPbased precipitation $\delta^2\text{H}$ data for Europe, but the long-term database appears consistent with little advantage to considering year-specific variation (Vander Zanden et al. 2015). Based on a long-term $\delta^2\text{H}$ and $\delta^{18}\text{O}$ analysis of river waters in Germany, Reckerth et al. (2017) found that rivers can serve as a proxy for long-term average precipitation. Those authors demonstrated long-term stability in the northern German river water isotopic dataset (2002–2013) and, by extension, the

GNIP data record for this region. Thus, it is unlikely that the years corresponding to moult in our greylag feather sample were not in any way anomalous compared to the expected growing season precipitation used in our model. Although other stable isotopes (e.g. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) can be useful in increasing the precision of probabilistic assignments (Hobson and Wassenaar 2018), there is little spatial variation in $\delta^{13}\text{C}$ across Europe and there are issues with anthropogenic inputs altering local $\delta^{15}\text{N}$ values, which potentially skews results.

Our isotope results do not preclude the Czech Republic but rate that area as generally of lower probability of origin given our odds ratio. It should also be noted that the nature of the largely east-west isoclines in predicted feather $\delta^2\text{H}$ values means that we cannot easily distinguish between northern Germany and Poland using isotope data alone. Another source of error in our assignments was the use of an assumed calibration relationship derived from mallards in Europe. While this calibration was the

most appropriate available, we encourage further refinement of calibrations between goose feathers grown and known sites and the long-term GNIP data at those sites (Hobson 2018).

It is surprising that the isotope results point to Poland and NE Germany as the main regions of origin for the greylags wintering in Camargue, while most ring recoveries and observations of neck collars rather suggest a Czech origin (it should be noted, though, that 2 Polish collared greylags were observed very recently in the Tour du Valat, after the present analyses were run). However, rings are often fitted to birds on the hatching area and/or the breeding grounds, when the young are still flightless, while the isotopes are related to where the feathers were grown (in juveniles, that is, on the natal sites) or moulted (in adult birds). It is therefore possible that some of the birds observed in Camargue during winter actually bred in the Czech Republic but then moulted in Poland or NE Germany during later years or post-breeding for adults; hence, the ring/collar and the isotope data would not be contradictory to each other. There are no records of individual geese caught on a Czech breeding site and recorded moulting in another country during the same year. However, the Czech ringing database contains records of

28 individuals collared in the Czech Republic as yearlings and 7 individuals marked as older birds (> 1 year old), which were observed moulting in Germany or Poland during subsequent years (M. Podhrázký, unpub. data). Recoveries of Czech greylag goose rings are also common in Poland and especially Germany, demonstrating frequent movements of individuals between these countries (Hudec 2008; Podhrázký et al. 2017).

A non-mutually exclusive hypothesis is that some of the Camargue birds were not only moulting in Poland and NE Germany but actually also originating from these countries as their breeding grounds as well. Both countries do host major breeding sites for greylag geese (Nilsson et al. 1999; Dick et al. 1999). It is possible that a disproportionate ringing effort in the Czech Republic compared to, for instance, Poland, simply led to the over-representation of Czech birds among the rings recovered or the neck collars observed during winter in Camargue. The total number of greylags fitted with a neck collar between 2000 and 2017 was 702 and 601 in the Czech Republic and Poland, respectively, while the numbers of birds ringed in the two countries were 1076 and 849 (Podhrázký and Mokwa, unpub. data). Such very similar figures in the Czech Republic and Poland allow ruling out the hypothesis of disproportionate marking effort leading to a biased evaluation of the geographic origin of greylags wintering in the Camargue. It is therefore reasonable to say that the ringing and isotope data, given their associated margins of error, collectively point to central Europe (Czech Republic, Poland and Eastern Germany) as the most likely region of origin for the birds wintering along the Mediterranean coast of France. One future improvement of this research program will be to train the local hunters to determine the age of the shot birds, which will help separate feathers from breeding (juvenile birds) and moulting sites (adult birds) in the sample. Interestingly, no link could be demonstrated between the birds shot during winter on the Tour du Valat estate and the very small local breeding population in Marais du Vigueirat, 10 km to the east (which hosts ca. 25 pairs; Massez 2009). Fitting satellite tags to the wintering greylags to better understand their movements and place of origin is also an obvious research need for the near future.

Some earlier studies have considered the Camargue greylag geese to belong to the NW/SW European flyway and the boundary between this and the Central European flyway to lie somewhere within Poland and the Czech Republic (Scott and Rose 1996; Dick et al. 1999; Podhrázký et al. 2017). The present isotope results, although they do not allow completely ruling out a geographic origin in Denmark or NW Germany, do point to NE Germany and Poland as a more likely region of origin for the birds wintering in Camargue (Fig. 4). It is a fact that the currently accepted boundary between the NW/SW European flyway and the Central European flyway runs across northern Poland and the core region of origin suggested by the isotope analyses. However, recent kernel analyses of neck collar data at the European scale actually found very few of the NW/SW European breeding greylags to wander into these countries (Bacon et al. 2019), so that Poland and the Czech Republic are not considered in the International Single Species Management Plan for the NW/SW European population (Powolny et al. 2018). It could be that future research (e.g. based on satellite tag or new analyses of ringing data) leads to a redefinition of the exact flyway boundaries, as done recently for Common Teal *Anas crecca*, for example (Guillemain et al. 2017). In any case, the present results suggest the Camargue wintering greylags do not originate from Norwegian or Swedish breeding grounds in the NW/SW flyway as do the birds wintering in north-east France or along the Atlantic Coast but come from northern Central Europe with a much greater likelihood. This outcome appears essential to discern management interests at the regional scale. Indeed, it is envisioned that an adaptive management scheme will be set up for greylags in NW Europe (Madsen et al. 2017), which may lead to a change in hunting legislation in some countries of the wintering range such as Spain and France. While this would be highly relevant for geese wintering on the French North Sea, Channel and Atlantic coasts, the present results suggest it would be irrelevant to include the birds wintering in the Camargue. These should rather be included in a separate management plan for the birds originating from Central Europe, which remains to be written. Such results also question the extent to which birds from

the same species but originating from different flyways/populations shall be applied similar management procedures within a given country.

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