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RESEARCH

Broad geographic variation in age- and sex-dependent origin of harvested eurasian wigeon (*Mareca penelope*) revealed by stable-hydrogen (δ^2H) isotope analyses of feathers

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Abstract

Migratory waterfowl are a harvested resource shared among multiple European countries, exposing them to potential overexploitation. Management of take is challenging since the life cycle of migratory waterfowl consists of several stages distributed among several locations, with possible spatio-temporal overlap among populations with differing population trends. Successful harvest management in such situations requires knowledge about the connections between breeding and non-breeding locations, and where birds are harvested. Breeding populations of Eurasian wigeon (*Mareca penelope*) are declining in Finland, underlining the need for more effective harvest management. Relative proportions and temporal distribution of local breeding birds and migrants from a larger Russian breeding population within the Finnish hunting bag has been unknown to date. We studied spatio-temporal origins of Finnish harvested wigeon by measuring stable-hydrogen (δ^2H) isotope values from legally harvested birds. We modelled the changes in δ^2H values of the feather samples within the hunting season using Gaussian processes and found that the origin of harvested wigeon in Finland changed during the hunting season and differed by age and sex. In juveniles and adult females but not in adult males, origin of harvested birds shifted from local and possibly western Russian birds to more long-distance migratory birds during the harvest season. These patterns likely reflected sex- and age-specific differences in migratory behaviour of Eurasian wigeon in the East Atlantic flyway, which can be used to guide future management and conservation of this species through the implementation of spatio-temporal harvest regulation.

Keywords Flyway management · Harvest · Migration · Waterfowl · Deuterium · Assignment

Introduction

While migratory animals move between their breeding and non-breeding areas, they utilize multiple habitats possibly thousands of kilometres apart (Newton 2018). A migratory strategy exposes animals to several habitats during the annual cycle and subsequently to varying anthropogenic threats (Greenberg and Marra 2005). In addition, many migratory populations are also exploited by humans through commercial or recreational harvest. This exposes them to potential overexploitation through a phenomenon known as the “tragedy of the commons”, which predicts that any public resource shared by many is under a threat of overexploitation (Hardin 1968).

Waterfowl management provides an excellent example of the challenges faced by wildlife managers (Elmberg et

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al. 2006; Johnson et al. 2015). During migration, waterfowl move through multiple countries and are often exploited by humans through recreational, subsistence or commercial hunting. Thus, they are a natural resource shared among multiple countries and are subject to country-specific harvest and management frameworks (e.g. Madsen et al. 2015). In Europe, many waterfowl populations are declining, underlining the need for more effective means to conserve their habitats and manage harvest sustainably (Holopainen et al. 2018a). Article 7 of the European Birds Directive (79/409/EEC) and Article III of the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) demand wise use of migratory gamebird populations. However, European waterfowl management typically lacks details on species- and population-specific structures and information for flyway-level management (Elmberg et al. 2006; Madsen et al. 2015; Holopainen et al. 2018a).

Sustainable harvest management of migratory resources such as waterfowl requires detailed knowledge regarding the harvested populations and monitoring of both the population and the harvest bag size (Elmberg et al. 2006; Cooch et al. 2014; Holopainen et al. 2018a). More specifically, it requires also spatio-temporal knowledge about population distributions and the origin of harvested individuals. It is crucial for successful harvest management to understand the connections between the breeding or natal origin of birds and the non-breeding locations; a concept known as migratory connectivity (Webster et al. 2002). Unravelling both spatial and temporal connectivity is particularly important in cases where different subpopulations of the same species show diverging status and/or trends (Knight et al. 2021), as it allows for spatial and/or temporal protection of declining populations while maintaining harvest of the subpopulations with favourable status and trend (Piironen et al. 2022). Similarly, spatio-temporal management could also be used to regulate or promote sex-specific or age-specific harvest pressure, as suggested by Christensen et al. (2017).

Traditionally, mark-recapture analyses based on bird ringing data have been used to provide information on large-scale movements of waterfowl (Scott and Rose 1996; Thorup et al. 2014). However, without extensive ringing programs, establishing connections between breeding and non-breeding sites is hampered by low recovery rates (Guillemain et al. 2014). In addition, ring-recovery data are usually biased due to incomplete marking coverage on breeding grounds and variation in recovery due to differential hunting pressure and reporting probabilities (Thorup et al. 2014; Guillemain et al. 2023). An alternative approach to establishing origins of harvested waterfowl is to analyse isotopic composition of wing feathers. The stable-hydrogen isotope ratios of amount-weighted precipitation (δ^2H_p) vary in a spatially predictable fashion across continents (Bowen et al. 2005). These patterns are transferred to foraging animals through food chains and incorporated, for example, into tissues like feathers (δ^2H_f) that are metabolically inert following growth. Stable-hydrogen isotope analyses can thus be used to map migration and movement of a wide range of animals (Hobson 1999; Hobson and Wassenaar 2019). Waterfowl moult all their flight feathers simultaneously following breeding, making them flightless for a few weeks (Cramp et al. 1986). Flight feathers thus enable the isotope approach to delineate approximate geographic locations of moulting sites of adult birds and natal sites of juveniles as they grow their first feathers (Hobson et al. 2004). However, assignment of origin based on stable isotopes usually benefits from prior framing of possible origins using other data especially through Bayesian assignment approaches (e.g. Gunnarsson et al. 2012). In practice, this means eliminating isotopically similar areas that are unlikely origins using prior knowledge such as data from individually marked birds or knowledge of spatial distributions of origin based on other tools (e.g. Guillemain et al. 2014; Hobson and Wassenaar 2019).

The two main flyways in Europe are partly overlapping, with the East Atlantic flyway covering northern and western Europe and the Black Sea/Mediterranean flyway covering southern Europe, also reaching east- and northwards. While the two flyways are thought to divide Europe into a northern and a southern part, they overlap in Russia as well as in Africa (Scott and Rose 1996). Waterfowls using the East Atlantic flyway breed mainly in Fennoscandia and northern Russia, and winter from the Baltic Sea to France and Britain, even reaching Africa (Scott and Rose 1996). This flyway is used also by Eurasian wigeon (*Mareca penelope*, hereafter wigeon), which is a common waterfowl species in Europe (categorized as Least Concern on the IUCN Global and European Red Lists) with estimated 225,000–367,000 breeding pairs (BirdLife International 2015; Keller et al. 2020; Mitchell 2022). The largest breeding population of wigeon in Europe is found in Russia with a possibly increasing trend (Mitchell 2022). However, this increasing trend does not hold for the whole breeding area and in Finland the national Red List classification for wigeon is Vulnerable due to decreasing breeding population trends (Lehikoinen et al. 2019).

Wigeon are commonly hunted in European countries with an annual harvest estimate of 400,000 to 500,000 individuals (Mitchell 2022; see also Guillemain et al. 2016; Solokha and Gorokhovsky 2017). In Finland, the annual harvest estimate is 3,000–30,000 birds (years 2010–2022: bag reporting was made mandatory in 2020 and showed a drop in bag estimates; Natural Resource Institute Finland 2023). Importantly, Finnish harvest can consist of birds which breed in Finland or elsewhere, but the proportion of Finnish wigeon harvested in Finland as well as the spatial and temporal variation in this proportion is unknown. Unravelling the origins of harvested wigeon might assist in conserving the declining Finnish breeding population while still maintaining some harvest of the abundant migrating population from Russia. As such, wigeon is potentially a good model species for the application of adaptive flyway-level management of dabbling duck populations in Europe (Holopainen et al. 2018a), highlighting the importance of unravelling the connections between breeding and non-breeding sites.

Here we utilized feather samples from wigeon harvested in Finland and measured their stable-hydrogen (δ^2H_f) isotope values to determine moult sites or natal origin. We hypothesize that there is a shift in the geographical origin of hunted birds during the hunting season with resident Finnish birds harvested first and migrants of Russian origin later, as was found by Gunnarsson et al. (2012) with mallard (*Anas platyrhynchos*) hunted in Sweden. However, we hypothesize that these patterns are sex-dependent. We expected that early in the season harvest bag includes locally breeding females and juvenile birds, and that a clear gradient in isotope values along the course of the harvest season would be found. Since adult males do not typically moult at the breeding sites (Salomonsen 1968), we expected that, due to moult migration, temporal patterns of feather δ^2H values in adult males could be vague and without clear trends.

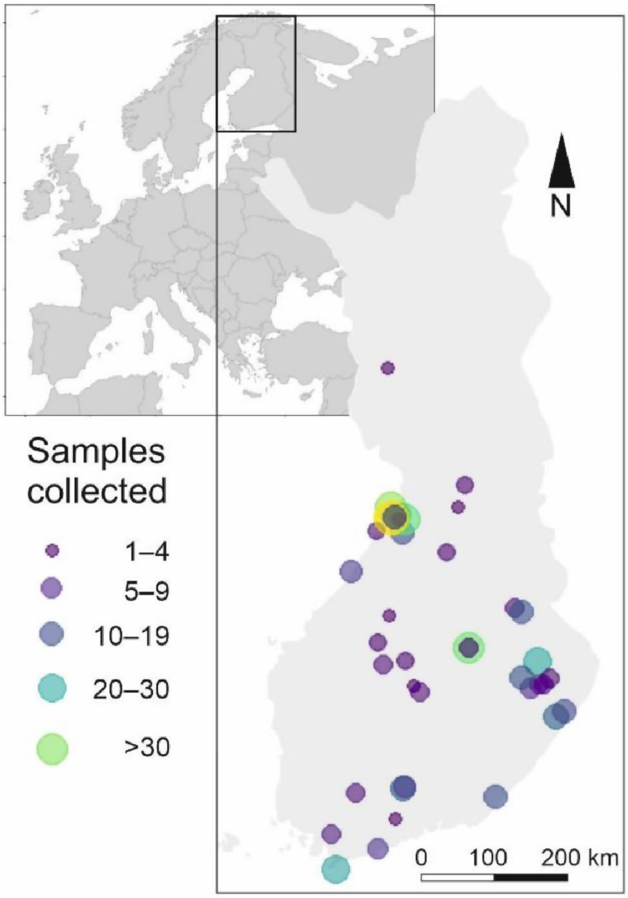

Fig. 1 Location of Finland in Europe and locations of 383 wing samples collected during the 2021 harvest season. The size of the circle indicates the number of wings gathered at site-level (e.g. lake or a bay) and colours are used to indicate the number of wings collected, but also to separate close locations

Materials and methods

Study species

In the northern hemisphere, wigeon breed following ice melt in spring (Mitchell 2022). Females moult from late June to early September on brood-rearing (breeding) sites or make only short moult migrations (Hochbaum 1956; Salomonsen 1968). Males moult between late May and July, typically migrating to moulting sites in Russia, Estonia, Sweden, Denmark and the Netherlands (Salomonsen 1968; Mitchell 2022). Autumn migration typically starts in September and birds arrive at their wintering sites in western and central Europe in October and November (Mitchell 2022).

Sample collection and stable isotope analyses

We collected wings from legally harvested wigeon during the 2021 hunting season (Fig. 1). To collect wings effectively around Finland, we advertised our survey in the Finnish hunters' magazine (Piironen et al. 2021), by messaging through the mobile application Oma riista, and using our personal contacts with hunters. Oma riista is an application made for Finnish hunters to report their harvest and observations. In 2021, the application had c. 200,000 users (Metsästäjä 2021). Hunters provided one wing of each shot wigeon with date and location. We determined age and sex for the samples from the characteristics of the wing feathers following Mouronval et al. (2019). During the 2021 hunting season, we collected 383 wing samples, of which 354 had a known harvest date and 29 were missing the harvest date. Out of the 383 wings, 51 (13%) were adult females, 118 (31%) juvenile females, 69 (18%) adult males and 145 (38%) juvenile males. Samples were distributed around southern and central Finland, while northern parts were poorly covered (Fig. 1). The first wigeon were harvested at the onset of duck hunting season in Finland (20 August) and the last ones were shot on 13 November, spanning a total of 86 days. Most of the wings were collected later in the season (Supplementary Fig. A1).

We removed one primary flight feather from each wing for stable-isotope analyses. Feathers were soaked overnight in 2:1 chloroform: methanol, decanted, rinsed, and dried under a fume hood for 24 h. Samples were then analyzed for stable-hydrogen isotope abundance by weighing subsamples (0.35 mg) into silver capsules using exclusively the feather barbs (not rachis). Capsules were crushed and trays of samples and standards were analysed by KAH at the LSIS-AFAR Stable Isotope Laboratory, University of Western Ontario for δ^2H analysis. There, samples were loaded in a UNI-prep (Eurovector, Milan, Italy) heated carousel (60 °C) coupled with a Eurovector elemental analyser and combusted under helium flow on a glassy carbon reactor at 1350 °C. The resultant H_2 gas was analyzed using a coupled Thermo Delta V Plus (Thermo Scientific®, Bremen, DEU) isotope-ratio mass spectrometer in continuous-flow mode via a Conflo interface.

Pre-calibrated in-house keratin standards (CBS; -197‰; KHS: -54.1‰) were used to derive the δ^2H value of the non-exchangeable H fraction, according to the comparative equilibration technique described by Wassenaar and Hobson (2003). Results were expressed in the standard delta (δ) notation in parts per thousand (‰) deviation from the Vienna Standard Mean Ocean Water (VSMOW, Table A2). Based on replicate measurements ($n=5$ for 38 unknowns) of each keratin standard, analytical error (SD) was estimated to be ± 2‰.

Modelling temporal changes in feather δ^2H values

We modelled changes in feather δ^2H values within the Finnish hunting season using Gaussian processes (hereafter GP), which is a flexible, non-parametric method for modelling non-linear data (see Piironen et al. 2022; Piironen and Laaksonen 2023 and references therein). In our case, the essential benefit of GPs is that no assumptions of the form of dependency (linear, polynomial etc.) between the variables of interest are needed. This suits our analyses well as the behaviour of δ^2H_f values through time (reflecting the change in the origin of samples) was difficult to assess a priori.

Our preliminary analysis indicated that there were no differences in δ^2H_f values between wigeon harvested in different parts of Finland, so we pooled all samples together. For the modelling, we divided the data into three different groups: adult females ($n=49$), adult males ($n=62$) and juveniles ($n=243$). We had no reason to expect any differences in the origin between juvenile males and juvenile females, so we pooled them to the same group (Fig. A2). We fitted the model to each of these groups separately. We standardized the values y (δ^2H_f) to the mean of zero and standard deviation of one and assumed the observations of standardized values (y') followed the Gaussian observation model, i.e. $y'_i \mid \mu_i, \sigma \sim N(\mu_i, \sigma^2)$. We modelled the expected value of y' as a function of time (t) by introducing a latent function $\mu(t)$, to which we gave a zero-mean GP prior so that $\mu(t) \sim \mathrm{GP}(0, k(t, t'))$. The heart of the model is the covariance function $k(t, t')$, which specifies the covariance between any t and t'. Here, we used a neural network covariance function (Williams 1998), which produces non-stationary functions (i.e. values of $\mu(t)$ can vary at different speeds at different values of t) and thus matches our prior beliefs regarding the behaviour of $\mu(t)$ (for the formulation of the covariance function, see Williams 1998). For model fitting, we have two hyperparameters for the covariance function (τ and τ_0) and one hyperparameter (σ) for the likelihood to be estimated. We gave half-Student's-t prior distributions for τ and τ_0 and a log-uniform prior to σ. We estimated hyperparameters by optimizing them to their marginal maximum *a posteriori* values.

Assignment to the origin

To probabilistically assign harvested wigeon to their geographic origins, we first calibrated geospatial models of amount-weighted growing-season average δ^2H of precipitation (δ^2H_p) to predicted values δ^2H_f of wigeon wings. To do this, we used known-origin samples from mallards provided by van Dijk et al. (2014) and estimated the relationship between δ^2H_f and δ^2H_p using a linear model (see Kusack et al. 2023a). The fitted calibration equation was $\delta^2H_f = -31.77 + 1.26 * \delta^2H_p$, which we further used to create an expected feather isoscape for the samples (R^2 for the calibration model was 0.65, see also Fig. A3 illustrating the model fit).

We assigned the moult origins for sampled wigeon based on δ^2H_f using a likelihood-based assignment method (see Hobson et al. 2009; van Wilgenburg and Hobson et al. 2011; Kusack et al. 2023b), which estimates the probability that a sample originates from a given (pixel) location. Importantly, the method provides a possibility to include prior information to the assignment, and thus to refine the geographic assignments a priori.

For the geographic assignment, we defined potential and expected breeding and moulting distributions for Finnish harvested wigeon (Fig. 2). We first framed broad potential areas from several subsidiary sources (Scott and Rose 1996; Ottosson et al. 2012; BirdLife International 2015; 2023; Fig. 2). We excluded Iceland and the British Isles since Finnish harvested wigeon are not expected to breed there (Scott and Rose 1996). As wigeon harvested in Finland likely originate from a smaller area than the potential Eurasian breeding and moulting distribution, we formed an expected distribution map to further restrict the possible origin of wigeon harvested in Finland. The delineation was drawn based on the potential map and the constricted framing using all available ring-recoveries (Spina et al. 2022), GPS-tracking data by van Toor et al. (2021) and our own GPS-data (unpublished).

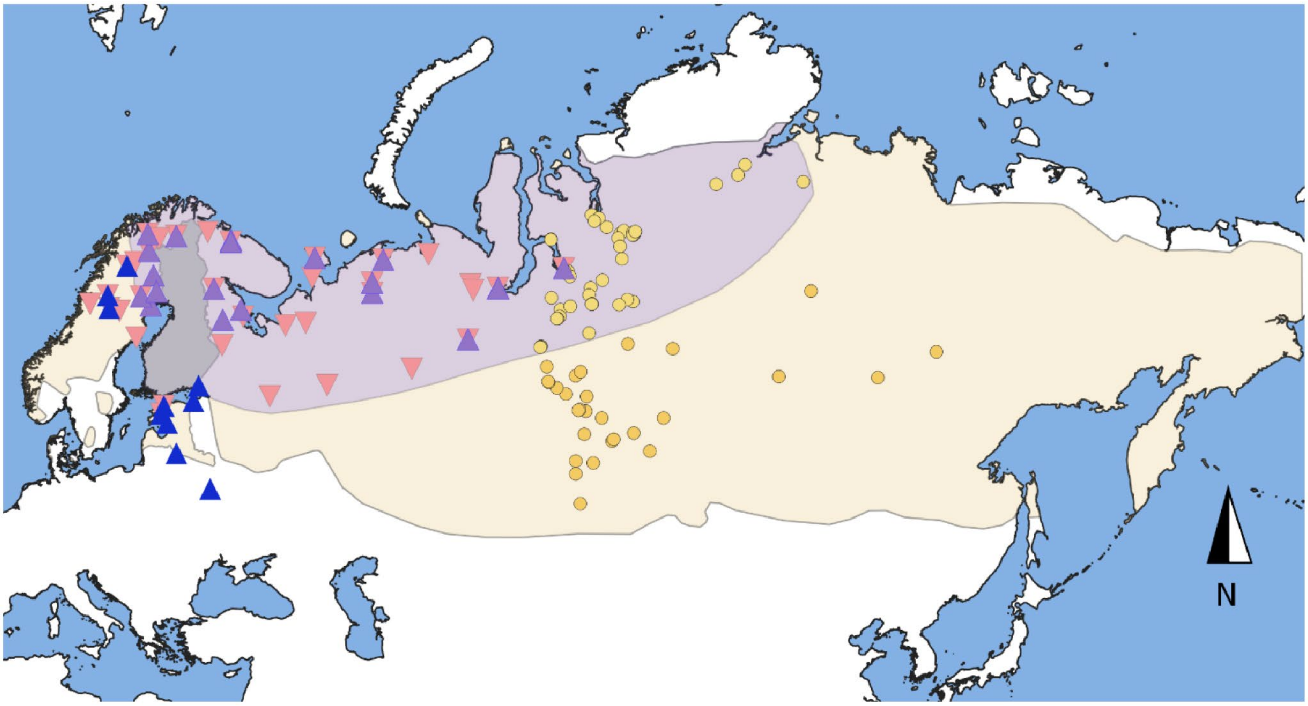

Fig. 2 Potential breeding distribution for all Eurasian wigeon (yellow) and on the top of that expected breeding/moulting distribution for wigeon harvested in Finland (purple). The delineation was drawn following Scott and Rose (1996), Ottosson et al. (2012), BirdLife International (2015, 2023), Spina et al. (2022) and van Toor et al. (2021), and the constricted framing using all available ring-recovery and GPS-tracking data (see Methods). Triangles indicate possible moulting sites of our own GPS-tracked wigeon outside Finland: birds that migrated through Finland during the Finnish harvest season (violet ▲), birds that did not autumn migrate through Finland (blue ▲) and birds without known autumn migration routes (pink ▼). Yellow circles indicate wigeon ring recovery sites east from the Pur-river

In 2021–2023 we trapped 89 wigeon (42 males, from which one produced data from two consecutive years, and 47 females) in Finland during their spring migration and equipped them with OrniTrack-10 solar powered transmitters by Ornitela, attached with individually fitted backpack harnesses (see methods in van Toor et al. 2021). To measure the expected breeding and moulting distribution outside Finland, we took a conservative approach and included all possible breeding/moulting sites of our GPS-tracked wigeon from June to September (females) or May to July (males). We considered all sites where birds stayed for ca. a week or longer, as some birds never spent more than one week at any site. Note that several sites may have been included for each individual, since we cannot for certain identify moulting sites. To form the expected distribution area for the origin of harvested birds (in addition to Finland), we considered possible breeding/moulting areas outside Finland from our GPS-tracked wigeon that (1) migrated through Finland during autumn (some were shot in Finland) or (2) had started migration, but Finland was not on the route. The first class was included inside the expected distribution area and the latter one outside. In 2021 there were 11 wigeon with these classifications, in 2022 six wigeon and in 2023 seven wigeon. In addition, while we did not know the final migration routes of the wigeon we lost contact with during summer, we expect that some of these birds, especially those breeding in Russia, migrate through Finland in autumn. We thus also used their potential moulting sites during migration to delineate the expected moulting distribution area (Fig. 2).

To add ring-recovery information to our expected map delineation, we used the EURING database and filtered recoveries by using the following ringing regions: North-west, West, Central and North (Spina et al. 2022; see also Kharitonov et al. 2024). In total these data included 7,881 wigeon encounters, from which most of the recoveries were of birds ringed in North-west ($N=4{,}517$) and West ($N=2{,}024$) (i.e. most birds were ringed in the British Isles or in the Netherlands). Ringing recoveries revealed that European-ringed wigeon can potentially migrate as far as the eastern parts of Taimyr, Russia. None of our GPS-tracked wigeon migrated that far, but stayed at the Taz- and Pur-rivers. Therefore, the eastern border of the expected breeding and moulting area was defined with ringing data, since we consider it possible that ringed birds observed in the north-eastern parts of Siberia might migrate through Finland in autumn. Since our GPS-tracks end at the Pur-river, we only considered ring recoveries east of that river. We defined the expected map border to include ring recovery sites from where birds might be expected to migrate through Finland and south of this border, we expected the birds might have migrated using more southern routes. The resulting map (Fig. 2) outlines the area we believe the Finnish harvested wigeon to have bred or moulted in (i.e. they may exhibit the isotope values of such areas). Note however, that we did not expect that the wigeon moulted evenly across the area.

Using the expected distribution map, we masked and clipped the calibrated δ^2H_f isoscape to only represent the region of expected origin. We then estimated the probability of origin for each sample using a normal probability density function:

$f\ (y|\mu_c,\ \sigma_c) = \frac{1}{\sigma_c\sqrt{2\pi}}e^{-\frac{1}{2}\left(\frac{y-\mu_c}{\sigma_c}\right)^2}$, where $f(y|\mu_c,\sigma_c)$ is the probability that location c within the feather isoscape (δ^2H_f) represents a potential origin for a sample of unknown origin (y), given the expected mean δ^2H_f for the cell (μ_c) from the calibrated δ^2H_f isoscape, and the expected error for that cell (σ_c). This error takes into account both the standard deviation of residuals from the calibration relationship (10.02‰), the expected isoscape error, and their covariance (Ma et al. 2020).

To illustrate the origins of wigeon, we classified the data as follows. After estimating the probability of origin for each bird, we divided them into six categories based on their age, sex and time of season they were harvested. We divided the harvest season into two parts based on the preliminary analyses: early (20 Aug – 8 Sep) and late (9 Sep – 13 Nov) (see Supplementary material A1 for the reasoning). The age-sex categories were adult females harvested in early ($n=10$) and late season ($n=39$), adult males harvested in early ($n=21$) and late ($n=41$) seasons, and juveniles of both sexes harvested in early ($n=60$) and late ($n=183$) season. We followed Hobson et al. (2009) and Chabot et al. (2012) and assessed the probability of origin of all samples within the categories as follows: we assigned individuals to the feather isoscape one-by-one and selected the spatial area consistent with an odds ratio for probability of origin of 2:1 (i.e. equal to the highest 67% of the probability density of origin of each bird). We set the probability of origin for these areas as 1, and outside these areas as 0. This resulted in individual binary maps, which were summed within the six categories, resulting in one map per category depicting the spatial distribution of likely origins for all birds within each category.

We performed the analysis using packages gplite (model fitting, Piironen 2021), assignR (assignment to origin, Ma et al. 2020) and related packages in R software v.4.3.1 (R Core Team 2023). The script used in the analysis is included in the electronic supplementary material.

Results

Among juveniles and adult females, δ^2H_f values of the collected feathers were significantly higher in the beginning of the season, but decreased after mid-September, showing a change in putative origin (Fig. 3). However, we note that no adult females were harvested in the very end of the season (Fig. 3, Supplementary Fig. A2), which increased the uncertainty of model predictions for the late season. There was no change in the δ^2H_f values of adult males during the season, indicating the same putative moulting sites for the adult males harvested throughout the hunting season (Fig. 3).

Geographic distribution of assigned sites of origin for harvested wigeon indicates that in the early season, the expected area for harvest origin of adult females and all juveniles is non-specific potentially due to a broad isoscape, while later in the season the probability of origin shifts clearly to the eastern parts of the range (Fig. 4). While assignment of the sites was necessarily vague, the change in putative origin indicates that birds shot in the early season were likely of local or possibly western Russian origin, but in the late season, the hunting bag included birds of more distant Russian origin. Among adult males, the geographic distribution of assigned sites was similar between the two periods, indicating moulting sites either far in the east or in the north, but with no clear differences in origin (Fig. 4). Results of the assignment of the origins to the entire wigeon breeding range (i.e. without using information from satellite tracking data or bird ringing) are shown in Fig. A4 in supplementary material. The calibrated δ^2H_f isoscape is included as supplementary material (Fig. A5).

Discussion

Origin of harvested wigeon in Finland showed some changes during the hunting season, but, as we hypothesized, patterns were age- and sex-dependent. The origin of juveniles and adult females shifted from local and potentially western Russian to birds migrating from further east or north, while in adult males the pattern suggested an eastern or northern moulting site origin throughout the hunting season. This pattern likely reflects sex- and age-specific differences in locations where feathers were grown and the general migratory behaviour of wigeon in the East Atlantic flyway. Since possibilities for adjusting sustainable harvest levels within a migratory species emerge from spatio-temporal limitations, we suggest that the differences in temporal migratory patterns of wigeon can be used to guide management and conservation of the species within the flyway.

Origins of the harvested ducks in Europe are poorly known (see Guillemain et al. 2014). Most breeding areas in

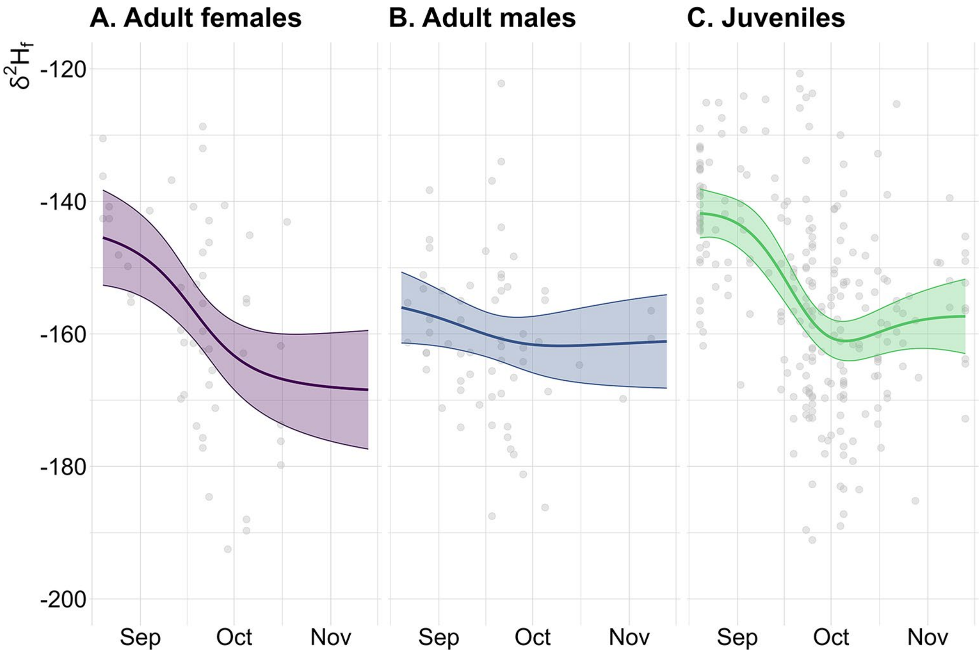

Fig. 3 Data and model predictions for the relationship between putative origin (as indicated by δ^2H_f values of flight feathers) for wigeon harvested in Finland during autumn 2021. Subplots **A**, **B** and **C** show the results for adult females ($n = 49$), adult males ($n = 62$) and all juveniles ($n = 243$), respectively. In all subplots, grey dots denote the data, and the lines and shaded areas denote the posterior mean and 95% credible intervals for $\mu(t)$, i.e. the expected δ^2H_f values for birds in each group as a function of time. All values are scaled to the VSMOW scale. Timeline in the horizontal axis reaches from the beginning of duck hunting season in Finland (20 Aug 2021) to the date when the latest sampled birds were harvested (13 Nov 2021). Note that in all plots, the credible intervals describe the uncertainty related to the underlying function $\mu(t)$, but do not include the observation noise

Fennoscandia and Siberia are remote with ducks breeding at a low density (Keller et al. 2020; Mitchell 2022). Thus, the number of ducks ringed in these areas are low, leading also to low numbers of harvest recoveries (Thorup et al. 2014; Kharitonov et al. 2024). Isotope assignment from the harvest bag is an effective method to collect data about the origin of birds, but the geographical accuracy of this method in Eurasia is only approximate as it is dictated by the structure of the underlying precipitation isoscape. However, precision can be improved as we have done here with GPS-tracking of target populations, since it allows the boundaries of expected origin to be defined, narrowing down the general assignment area in question.

Our results indicated that for adult females and all juveniles, there was a shift in δ^2H values between early and later season. Based on the Finnish ring-recoveries, juveniles are often hunted at the beginning of the season near areas they were hatched (Väänänen 1996), but our data suggest that even early harvested birds might be from broad origins. However, we assume that juveniles and adult females (that moult close to breeding sites) shot early in the season were mainly local, but unfortunately due to a broad isoscape this method cannot distinguish between local and western Russian birds. However, we observed a clear change in δ^2H_f values in juveniles and adult females after mid-September, indicating that late season harvest was focused primarily on northern and eastern birds from Russia.

For adult males, δ^2H_f values indicated that the harvest consisted of more birds from eastern or northern areas throughout the season. Adult males undergo moult migration away from breeding sites and these appeared to be over a broad area. Important male moulting sites are known to be located for example in Russia, Estonia, Sweden and Denmark (Mitchell 2022) and males might return to the same sites year after year (Hochbaum 1956). Based on data produced by our GPS-tracked birds, some of the males indeed migrated to the Baltic countries south of Finland to moult and did not enter Finland during their autumn migration. On the other hand, some males that bred in northern parts of the Scandinavian mountains migrated to Finland in summer and therefore were huntable during the Finnish hunting season. Furthermore, some Finnish breeding males migrated east into Russia during the summer. Our results for isotope assignments for harvested wigeon support these observed patterns of males dispersing widely to their moulting areas from their breeding sites.

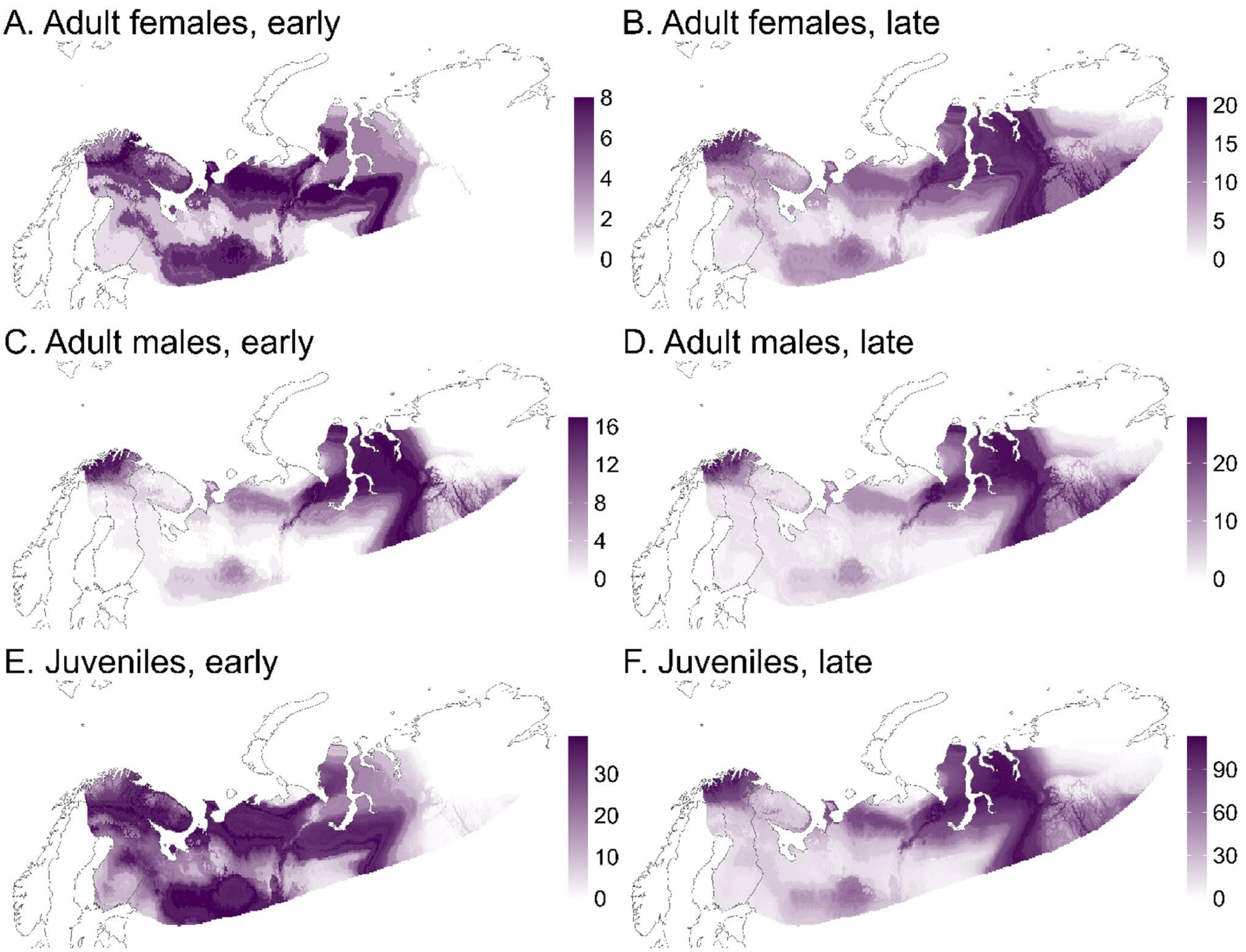

Fig. 4 Geographic distribution of assigned sites of origin for adult female (**A-B**), adult male (**C-D**) and juvenile (**E-F**) wigeon harvested in Finland in 2021. Left and right panels show the putative origin for birds harvested in early (20 Aug – 8 Sep) and late (9 Sep – 13 Nov) hunting season respectively. Sample sizes in each subplot are A (*n* = 10), B (*n* = 39), C (*n* = 21), D (*n* = 41), E (*n* = 60) and F (*n* = 183). The darker the colour purple, the more individuals assigned to that pixel (indicated in the legend bar for each figure), under a 2:1 odds ratio

Management implications

Our results underline the challenges for harvest management caused by different migration patterns of female and male wigeon. Ducks pair in the wintering areas and while female ducks are philopatric to their breeding grounds, males are assumed to follow their partners to the breeding grounds (Cramp et al. 1986; Baldassarre 2014). Therefore, between-year migratory connectivity can be inherently weaker among males than among females, if males pair with different females in consecutive years. Males may furthermore execute moult migration which reduces their migratory connectivity within the annual cycle (i.e. males from different breeding areas may mix at the moulting sites). It is therefore easier to conduct targeted spatio-temporal management of females at the breeding areas, as management can target continuously the same locally breeding individuals. In ducks, females are typically the limiting part of the population's productivity (i.e. a male-biased sex ratio is common among dabbling ducks; Bellrose et al. 1961). Furthermore, a decline in the proportions of females has been observed in many duck species and therefore management efforts especially targeting females could have high benefits (Devineau et al. 2010; Christensen and Hounisen 2014; Fox and Christensen 2018; Ellis et al. 2022). The methods used in this study can be used to reveal sex-dependent migratory behaviour and optimize harvest strategies for structured populations by minimizing the loss of demographically valuable individuals (Kokko and Lindström 1998; Cooch et al. 2014). Accordingly, our results suggest that concerning the threatened Finnish breeding wigeon population, temporal restrictions of the hunting season could reduce the hunting pressure on reproductively valuable local wigeon females (see also Christensen et al. 2017).

While our study provides arguments for how to implement a regulation in Finland, flyway-level actions and their spatio-temporal implementation to protect declining waterfowl species, like wigeon, remain to be studied. Managing migratory waterfowl would benefit from better knowledge of population dynamics and the origin of the harvest bag at European scale (Elmberg et al. 2006; Holopainen et al. 2018a). However, the data we utilized in this study are rare in Europe. European waterfowl population measures are often based on wintering surveys (the International Waterbird Census) providing approximate numbers of ducks and their distribution within the wintering range, but this approach suffers from possible gaps in coverage in time and space, especially in the light of climate change (Johnson 1998, Elmberg et al. 2006; Guillemain et al. 2013). In addition, surveys of large aggregations mask local changes in population distribution and abundance; for example, long-term declines in Finnish-breeding wigeon (Pöysä et al. 2013; Lehikoinen et al. 2016) contrast overall stable European wintering numbers (BirdLife International 2015; but see Fox et al. 2016), likely because Finnish breeders are outnumbered in winter by the far greater numbers of Russian breeding individuals. Therefore, even though Finland could regulate harvest to decrease pressure on the national breeding population, to be more effective, coordinated spatio-temporal regulation should apply to all its non-breeding areas in Western and Central Europe.

The declining Finnish wigeon population could furthermore benefit from flyway-level spatio-temporal management that is adjusted to annual production, that would optimally also decrease the harvest focusing on productive females. Currently wigeon harvest bag size along the flyway in Finland and Denmark does not mirror the annual production of young based on Finnish reproduction data, although the wigeon harvest in Denmark increases with increasing juvenile ratio there (Holopainen et al. 2018b; see also Mitchell et al. 2008). While the Finnish birds only represent a fraction of the total population, to be able to justify whether or not a given level of annual harvest from a population is sustainable, we need to not only monitor annual population size and reproductive output, but also harvest rates at larger geographical scale (Sutherland 2001; Madsen et al. 2015). Ideally, a population-level adaptive harvest management plan could be established to measure the overall harvest sustainability and to provide tools to give guidance to hunting restrictions where needed (e.g. driven by the European Commission, see NADEG Task Force on the Recovery of Birds 2021).

Locally there is evidence for potential overharvest of some duck species in Europe (Ellis and Cameron 2022). However, tools to regulate harvest are limited. In Europe, huntable species are mostly managed through the establishment of conservation areas to protect habitats, allowing or prohibiting harvest and, in some cases, adjusting the length of the hunting season. In most European countries, open seasons are fixed and not subject to annual revision and commonly there are no regulatory frameworks to allow such changes (but see Jensen et al. 2023). Unlike in North America, there are furthermore no bag limits and no adjustment of harvest to annual fluctuations in reproductive success or abundance of ducks. The level of protection has historically varied and is still varying among countries (Priklonski 1974; Lampio 1980; Mooi 2005; Cooch et al. 2014; Holopainen et al. 2018a). Accordingly, spatio-temporal harvest regulation is not typical in European waterfowl management, but has recently been applied to management of some species also in Finland. For instance, taiga bean goose (*Anser fabalis fabalis)* and tundra bean goose (*A. f. rossicus*) offer an example of a challenging management situation, since the two subspecies have different conservation statuses and population trends, but are both harvested. However, with spatio-temporal regulation, harvest can be targeted at the abundant tundra bean goose (Piironen et al. 2022). Our results show that stable isotope techniques can be ideally suited to combine with GPS-tracking to reveal spatio-temporal occurrence of sub-populations and their distribution in harvest bags, thus offering effective tools for management actions.

The task of sustainably managing migratory waterfowl is urgent. Currently, we do not know how different populations distribute themselves from their respective breeding areas during winter, and even our current limited knowledge might be rendered obsolete by the impacts of climate change (Guillemain et al. 2013; Lehikoinen et al. 2013). Furthermore, habitat changes and predation at the Fennoscandian breeding sites may lower reproductive success (Piha et al. 2023; Pöysä et al. 2023; Holopainen et al. 2024; see also Pöysä and Väänänen 2018). Under these circumstances wigeon might be exposed to potential overexploitation. Periodically revised spatio-temporal regulation of harvest could guarantee sustainable harvest levels for this Finnish declining species.

Conclusions

Efficient and wise harvest regulation is a challenge for waterfowl managers in Europe. Population units and associated harvest pressures are typically not known in Europe (Holopainen et al. 2018a, b), which would be crucial knowledge to ensure sustainable harvest rates. Integrating modern methods such as stable isotopes and GPS-tracking offers a level of resolution that was not available previously and can be utilised to address the challenge of migratory species and their connectivity (see also Christensen et al. 2017; Guillemain et al. 2023). These methods could substantially improve our knowledge of the structure of populations at the time of the annual harvest (Cooch et al. 2014). While it seems that harvest is not driving duck population trends in Finland (Pöysä et al. 2013), wise use of populations would demand adjusting harvest pressure according to population status and management/conservation objectives. Concerning the wigeon, local breeding adult females in Finland appear to be harvested in the early season. Implementing spatio-temporal harvest management for breeding wigeon females at the breeding areas seems plausible based on our results. Temporal restriction of harvest could potentially decrease harvest pressure of the local female birds and thus support the national breeding population.

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Author contributions SH, AP and TL designed research. AP and SH collected field data. JK and KH executed laboratory analyses and AP made statistical analyses. SH wrote the manuscript and all authors reviewed the manuscript. TL, AP, SH, IHS, MBE and HW contributed to funding acquisition.

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Data availability Data for putative origin (δ 2Hf values of flight feathers) for wigeons harvested is available in the supplementary material.

Declarations

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with legal hunting.

Competing interests The authors declare no competing interests.

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