Author(s): Jong, Adriaan de; Torniainen, Jyrki; Bourski, Oleg V.; Heim, Wieland; Edenius, Lars

Title: Tracing the origin of vagrant Siberian songbirds with stable isotopes : the case of Yellow-browed Warbler (Abrornis inornatus) in Fennoscandia

Year: 2019

Version: Published version

Please cite the original version:

Jong, A. D., Torniainen, J., Bourski, O. V., Heim, W., & Edenius, L. (2019). Tracing the origin of vagrant Siberian songbirds with stable isotopes : the case of Yellow-browed Warbler (Abrornis inornatus) in Fennoscandia. Ornis Fennica, 96(2), 90-99.
https://www.ornisfennica.org/pdf/latest/19Jong.pdf

Ornis Fennica 96: 90–99. 2019

Tracing the origin of vagrant Siberian songbirds with stable isotopes: the case of Yellow-browed Warbler (*Abrornis inornatus*) in Fennoscandia

Adriaan de Jong*, Jyrki Torniainen, Oleg V. Bourski, Wieland Heim & Lars Edenius

*A. de Jong, L. Edenius, Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden. * Corresponding author's e-mail: adriaan.de.jong@slu.se*
J. Torniainen, Open Science Centre and Department of Biological and Environmental Science, P. O. Box 35, FI-40014 University of Jyväskylä, Finland
O. G. Bourski, A.N. Severtsov Institute of Animal Ecology and Evolution RAS, Leninsky prospect 33, 119071 Moscow, Russia
W. Heim, Institute of Landscape Ecology, University of Münster, Heisenbergstraße 2, 48149 Münster, Germany

Received 20 January 2019, accepted 8 April 2019

Vagrant birds are mesmerizing birdwatchers worldwide, but the nature of vagrancy and the true origin of the vagrants are poorly known. To Western Europe, the massive Siberian land mass delivers most of the vagrant songbirds, e.g. Yellow-browed Warbler (YBW) (*Abrornis inornatus,* formerly *Phylloscopus inornatus*). In this study we used stable hydrogen isotope ratios in tail feathers (δ^2H_f) from two ringing stations in northern Fennoscandia in an attempt to link vagrant YBW to potential regions of origin. We could do this thanks to a collection of samples from nestling and breeding adult YBW in Central Siberia. Compared with the nestling samples, the Fennoscandian δ^2H_f data indicated origins in the western and/or southern parts of the breeding range. The assignment map created in IsoMAP showed high probabilities of origins in the Komi Republic, N/NW of the Ural Mountains. Although our study rules out a large proportion of the YBW breeding range, our method could not pin-point a precise region of origin. The main reason for this is the similarity of environmental hydrogen isotope ratios across longitudes in Eurasia. For increased precision, we propose a multi-method approach (e.g. stable isotopes and genetics) based on significantly more data from across the vast and challenging Siberian territory. More international collaboration will be vital for this endeavour.

1. Introduction

Vagrants fascinate birdwatchers and the general public, but their origin and the causes behind their appearance are often poorly known. In Western Europe, vagrant songbird numbers are dominated by boreal species from the massive Siberian land mass, e.g. Pine Bunting (*Emberiza leucocephalos*), Pallas's Leaf-warbler (*Abrornis proregulus*) and Yellow-browed Warbler (*Abrornis* *inornatus*) (hereafter YBW). This paper focuses on Siberian songbirds arriving in NW Europe after the breeding season, the YBW in particular.

Among the theories attempting to explain the tempo-spatial pattern of occurrences of Siberian vagrants, "weather" (Baker 1977, Bozó *et al.* 2016), "reverse migration" (Rabøl 1969, Thorup 2004, Pfeifer *et al.* 2007) and "(post-juvenile) dispersion" (Folvik 1992, Gilroy & Lees 2003) prevail. As an extension of the latter, especially when observations of vagrants are increasing, recently established, yet undiscovered wintering areas in Western Europe or West Africa are recurrently suggested (Gilroy & Lees 2003). If that were the case, these "pseudo-vagrants" would be scarce migrants rather than true vagrants (Gilroy & Lees 2003). Increasing numbers are also sometimes hypothesised to relate to range expansions (Veit 2000, De Juana 2008).

A weak spot in all these theories is that the actual origin of the individuals arriving as vagrants from Siberia is basically unknown. To date, ringing and tracking technologies have provided virtually no clues about the starting point of their journeys. This is because ringing activities in this immense, remote territory are very sparse and current tracking technologies inappropriate for small birds. In this study we used deuterium-to-hydrogen ratios (δ^2H) in an attempt to trace the origins of vagrant Yellow-browed Warbler arriving in Fennoscandia after the breeding season.

The YBW is a foliage-gleaning insectivore inhabiting boreal forest and forest-tundra, from the western foothills of the Ural Mountains (c. 56° E) to easternmost Siberia (c. 175° E) (Dementiev & Gladkov 1954, IUCN 2017). Hagemeijer and Blair (1997) describe the Western Palearctic breeding population estimated at 45,000–46,000 pairs to be confined to the Komi Republic W of the Ural Mountains. YBW is locally common along the eastern slopes of the Ural Mountains (Jones *et al.* 2015, Meshcheryagina *et al.* 2015), but occurs at lower densities in the western parts of the Siberian lowlands. It becomes increasingly abundant again first from the Taz River (81° E) and further eastward into Central Siberia (Rogacheva *et al.* 1991, Vartapetov 1998, Sokolov *et al.* 2012). In the Yenisei Mid Taiga, Central Siberia, Rogacheva (1992) classified YBW as a semi-colonial breeder with breeding groups of 10–50 pairs. Other autecological traits in YBW are low site tenacity and large inter-annual variation in local breeding densities (Bourski 1994, Bourski & Forstmeier 2000). The known wintering range of YBW is confined to South-East Asia (Clement 2018), and YBW populations are proposed to migrate along the East Asian flyway (Irwin & Irwin 2005, Yong *et al.* 2015).

Adult YBW undergo a complete post-nuptial moult once per year at the breeding grounds whereas juveniles have a partial post-juvenile, pre-migration moult, including only body and wing covert feathers (Svensson 1992, Demongin 2016, O. Bourski pers. obs.). Consequently, both adult and juvenile YBW encountered in Europe during autumn and early winter carry tail feathers with isotope signatures reflecting the same year's breeding sites. The general perception is that first-year YBW dominate strongly in Western Europe during autumn (Gilroy & Lees 2003, M. Hellström pers. com.). These juveniles have tail feathers that were grown in the nest and thus, tail feathers sampled from nestlings within the breeding range are the best hallmark for assessment of origin.

Stable isotopes are widely used as a tool to unravel geographic origin of migratory birds; the method is particularly useful in small birds, for which logger/transmitter technology is of limited use or missing (Hobson & Wassenaar 1997, Hobson 2005a, Hobson & Wassenaar 2008, Hobson 2011). Like for example human hair and fish scales (Torniainen *et al.* 2014), keratinous bird feathers are inert tissues that retain their isotope ratios built in during formation (West *et al.* 2006). Consequently, bird feathers reflect isotopic ratios of the moulting area (place of feather growth) and can be analyzed retrospectively until the next moult.

For migration studies, deuterium-to-hydrogen ratios (δ^2H) are most commonly used (Hobson 2005b). The main source of deuterium is oceanic water delivered across the continents by precipitation. The geographically variable concentrations of deuterium in precipitation create a pattern of environmental hydrogen isotope ratios: an isoscape (West *et al.* 2010, Hobson *et al.* 2010).

The gradient in environmental precipitation-based δ^2H (hereafter δ^2H_p) values across temperate-arctic Eurasia goes from higher values in the western and southern parts to gradually lower val-

Table 1. Yellow-browed Warbler feather collection details.

Site	Country	Location	Sampling Date(s)	Location relative to known breeding range
Stora Fjäderägg ringing station	Sweden	63°49’ N, 21°00’ E	14–23 Sept 2016	c. 1,700 km W of western border
Tauvo ringing station	Finland	64°49’ N, 24°33’ E	16 Sept 2016	c. 1,600 km W of western border
Mirnoye Ecological Research Station	Russia	62°20’ N, 89°00 ’E	19 June–7 July 2017 (breeders) 2–8 July 2017 (nestlings)	Central

ues in the eastern and northeastern parts (Bowen *et al.* 2005). Perpendicular to this gradient (i.e., NW–SE), the variation in predicted δ^2H_p values is significantly smaller and thus, the precision of geographical assignments lower. We used hydrogen stable isotope ratios in tail feathers (hereafter δ^2H_f) to evaluate geographical origins of vagrant YBW ringed in Sweden and Finland during autumn migration. For comparisons, we used δ^2H_f ratios in a unique collection of tail feathers from nestlings and breeding YBW in Central Siberia.

2. Material and methods

2.1. Sampling

Twenty YBW tail feathers from the autumn 2016 catching season were provided by the Stora Fjäderägg ($N = 16$) and Tauvo ($N = 4$) bird ringing stations, located at opposite sides of the Gulf of Bothnia in Sweden and Finland, respectively (Table 1 for details). These ringing stations catch the highest numbers of YBW of the ringing stations in their country. The Central Siberian samples were collected in early July 2017 from one nestling each in 22 nests in Birch (*Betula spp.*) dominated habitats near Mirnoye village located on the eastern bank of the Yenisei River (62.3° N, 89.0° E). In this same area, nine individuals supposed to be local breeders were also sampled. Due to documented low site tenacity (Bourski 1994, Bourski and Forstmeier 2000), the sites where these individuals had grown their tail feathers during the previous postbreeding season was unknown. Feathers were stored dry in paper envelopes at room temperature. Altogether feathers from 51 birds were analysed for this study.

2.2. Isotope analysis

As a pre-treatment, tail feathers were rinsed in 2:1 chloroform/methanol. Feather vane material was cut into 0.35 ± 0.10 mg pieces and placed into silver capsules. Following Wassenaar & Hobson (2003), samples were left for at least four days in laboratory atmosphere prior to analysis. δ^2H_f was measured using an Isoprime 100 CF-SIRMS (Isoprime UK) coupled with an Elementar Pyrocube analyser (Elementar, Germany) at the University of Jyväskylä isotope laboratory, Finland. Two keratin laboratory reference materials obtained from Environment Canada were used to standardize the results (KHS: $\delta^2H = -54.1‰$ and CBS: $\delta^2H = -197‰$) (Wassenaar & Hobson 2010). Results are expressed in standard δ^2H-notation as parts per thousand (‰) differences from the international VSMOW-SLAP standard (International Atomic Energy Agency). Based on the standard deviation of repeated measurements of the reference materials, instrumental error was estimated at $SD = 2.4‰$. All sample measurements were numerically corrected according to the protocol of Soto *et al.* (2017).

2.3. Geographical assignment of feathers

We used the web-based GIS and software tool IsoMAP (http://isomap.org) to geographically relate YBW δ^2H_f sample values to predicted δ^2H_p

Table 2. Yellow-browed Warbler δ^2H_f statistics for the sampling sites.

Sampling sites	*N*	Mean ‰	*SD* ‰	Value range ‰	Margin of error[1],%
Fennoscandian vagrants	20	–96.8	11.0	–119.2 to –73.4	5.1
Mirnoye-breeders	9	–101.1	7.4	–109.6 to –89.9	5.6
Mirnoye-nestlings	22	–107.9	8.9	–127.2 to –97.0	3.9

1) Estimated by power analysis (95% *CL*, 2-sided *CI*)

values across Eurasia (Bowen *et al.* 2014a,b). The underlying δ^2H_p model was based on data for precipitation, elevation, average temperature, longitude and latitude from 1960–2010 (public IsoMAP key 64735). For the parameterization of the prediction map we used the same variables across the same geographic range, but for the 1981–2000 period (public IsoMAP key 64737). This way we avoided detrimental data deficiency from the sparse network of climate stations in northern Eurasia. Based on AIC values, we chose geostatistical (kriging) models instead of regression models throughout our analyses.

From the kriging-based δ^2H_p map (IsoMAP key 64737), we extracted the predicted δ^2H_p values and their *SD*s for the grid cells ($N = 6$) in a 75 × 110 km square surrounding the Mirnoye sampling site. These δ^2H_p values were used to establish the feather-to-precipitation conversion coefficient (Hobson & Wassenaar 1997) based on δ^2H_f values of tail feathers from 22 nestlings collected in separate nests in Mirnoye 2–8 July 2017 (Table 2). We used a Monte Carlo process with 10,000 iterations to calculate this coefficient. This process combined (a) the individual grid cell estimate error, (b) between grid cells variation and (c) instrumental error. Coefficients were averaged across sampled individuals and the *SD* for this averaged value calculated. The resulting value for the coefficient was 1.116 and for its SD 0.087. δ^2H_f values for all sampled YBW were then precipitation-adjusted by multiplying the δ^2H_f value with the conversion coefficient. In order to account for instrumental error and conversion coefficient variance, this was done in another Monte Carlo loop with 10,000 iterations. The resulting estimates and their *SD* were used to geographically assign all sampled YBW individually in IsoMAP against the same kriging-based δ^2H_p map used to calculate the conversion coefficient (IsoMAP key 64737).

2.4. Post-processing

We imported assignment maps for the individual Fennoscandian samples into ArcGIS 10.6 in TIFF format against the National Geographic World base map. Maps for these individual samples were

Table 3. ANOVA (A) and 95% Tukey test statistics (B) for the δ^2H_f values of Fennoscandian vagrants, Mirnoye breeders and Mirnoye nestlings (the three levels in the analyses). Means that do not share a letter are significantly different.

A

Source	*DF*	*Adj SS*	*Adj MS*	*F*-value	*P*-value
Level	2	1,305	652.5	7.16	0.002
Error	48	4,375	91.1		
Total	50	5,680			

B

Level	*N*	Mean	Grouping	
Fennoscandian vagrants	20	–96.8	A	
Mirnoye breeders	9	–101.1	A	B
Mirnoye nestlings	22	–107.9		B

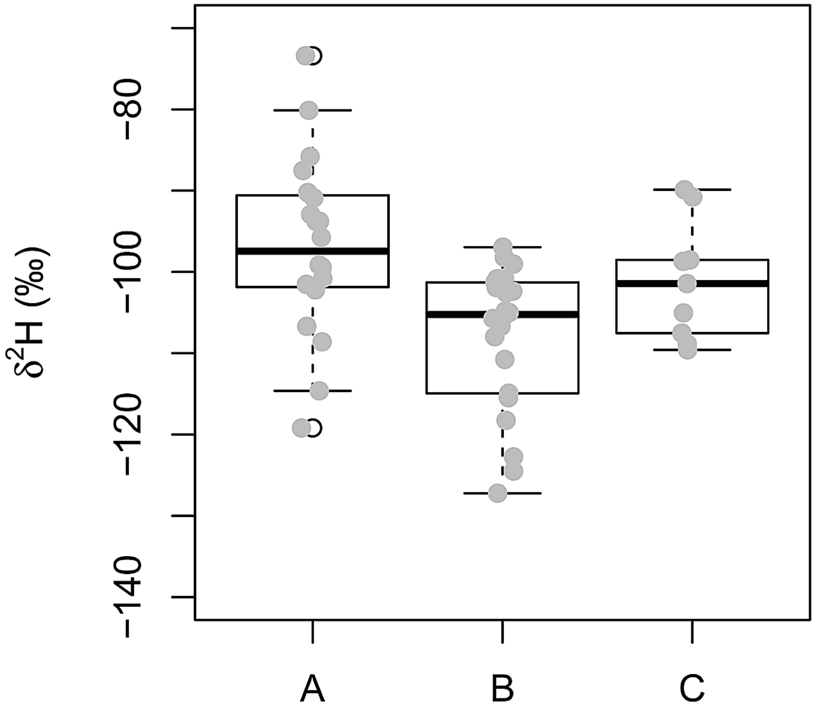

Fig. 1. Boxplot of δ^2H_f values in Yellow-browed Warbler samples from A = Fennoscandian vagrants (N = 20), B = Mirnoye nestlings (N = 22) and C = Mirnoye breeders (N = 9). Thick horizontal lines mark the median values, the boxes represent the 50% interquartile range, and the whiskers extend to 1.5 times the interquartile range from the top and bottom of the box; outliers are marked individually (open circles). Overlain in grey are the original data points, horizontally jittered for separation.

then summed to a combined probability map (ArcGIS tool Raster Calculator). This probability maps was clipped with the YBW breeding range polygon (IUCN 2017) and sampling locations added.

2.5. Statistical analysis

Differences in δ^2H_f means of the Fennoscandian vagrants, the Mirnoye breeders and the Mirnoye nestlings were tested by ANOVA with *post hoc* Tukey test. Boxplots of sample δ^2H_f values for the three groups were produced to visualize the within group variation and the overlap between groups. These analyses and plots were carried out in Minitab, version 18.

3. Results

The results of the ANOVA showed that the δ^2H_f values of Fennoscandian vagrants, the Mirnoye nestlings and the Mirnoye breeders were unlikely to belong to the same pool $F_2 = 7.16$, $P = 0.002$ (Table 3A). The Tukey *post hoc* test placed the Fennoscandian vagrants and the Mirnoye nestling values in separate groups, the latter with significantly lower (more depleted) δ^2H_f values than the former (Table 3B, Fig. 1). The Mirnoye breeders had intermediate δ^2H_f values and could not be (collectively) associated to either one of the groups.

The combined probability map for the Fennoscandian samples (Fig. 2) shows that the highest probabilities within the known breeding range were found just W–NW of the Northern Ural Mountains (Komi Republic) and in some minor regions in the southern parts of the northern boreal zone (e.g. N of Krasnoyarsk and around Irkutsk, *ca*. 2,000 and 3,000 km farther away respectively). The probability map also shows that high probabilities occur across large parts of western and southern Siberia, while origins from NE Siberia are unlikely.

4. Discussion

Averaged across sampling sites, the Fennoscandian YBW had higher δ^2H_f values than the Central Siberian nestlings. If the assumption about a high proportion of juveniles among vagrant YBW was valid, this difference suggests that YBW arriving

Fig. 2. Combined probability map of origin for 20 Fennoscandian Yellow-browed Warblers against a prediction map based on δ^2H value in tail feathers from 22 nestlings in Central Siberia. Grid cell probabilities (originally with very low probability each) are linearly scaled for convenient comparisons. Delineation of the known breeding range (black borders) according to IUCN (2017). Stars represent the three sampling locations in Sweden, Finland and Mirnoye, Russia (west to east). Base map: National Geographic World Map by permission to the Swedish University of Agricultural Sciences.

in Fennoscandia in autumn were born in a region with higher δ^2H_p values than, i.e., W and/or S of Mirnoye in Central Siberia. The observation that Mirnoye breeders had intermediate δ^2H_f values could be an effect of immigration due to low breeding site tenacity (Bourski 1994, Bourski & Forstmeier 2000), but also of deuterium-depletion processes resulting in lower δ^2H_f values in nestlings relative to their parents (Meehan *et al.* 2003, Smith & Dufty Jr. 2005, Betini *et al.* 2009, Marquiss *et al.* 2012). Both factors make δ^2H_f values from breeding adults inadequate for comparisons with autumn vagrant YBW. We suggest feathers from nestlings to be the hallmark of choice for other species with a similar moulting strategy as well.

Although all Mirnoye nestlings were sampled within *ca* 3 km radius, during a limited time period and in similar habitat, their δ^2H_f values showed considerable variation (range –127‰ to –97‰, Table 2). This inherent uncertainty about the relationship between site of origin and δ^2H_f values is important for the interpretation of between-sites comparisons and of geographical assignments. As a consequence, it is unclear whether individual Fennoscandian samples originated from a wide range of different locations (as suggested by the disparate δ^2H_f values in relation to the δ^2H_p prediction map) or from a small area (cf. Oppel *et al.* 2011).

Inter-annual variation in δ^2H_f values is a potentially confounding factor, because the Fennoscandian vagrants were sampled in 2016 (assumed to have grown their feathers the same year) and the Mirnoye nestlings in 2017. To the best of our knowledge, no multi-year data set of δ^2H_f values for Siberian songbirds exists that could have enabled us to estimate the importance of this variance component. Until the full role of inter-annual variation has been clarified, this factor calls for extra caution in the interpretation of the geographical assignment results.

The averaged assignment map (Fig. 2) shows a wide belt of relatively high probabilities of origin, from W of the Ural Mountains to Sakhalin in the Sea of Okhotsk. A number of regions stand out with even higher probabilities, e.g. the Komi Republic W of the Northern Ural Mountains and a region between Mirnoye and Krasnoyarsk in central Siberia. The latter is *ca* 1800 km further away from NW Europe than the Komi Republic, and one could argue that this region is a less likely source due to distance related losses and dilution during dispersion (Thorup 2004, Pfeifer *et al.* 2007).

Virtually no δ^2H_f data of known origin are available from Siberia, neither from YBW nor other breeding songbirds (but see Pekarsky *et al.* 2015). The Common Crossbill samples reported in Marquiss *et al.* (2012) were from Archangelsk Oblast, > 500 km W of the Ural Mountains. Instead of picking a published feather-to-precipitation conversion coefficient for another species in another environment, we chose a novel method for relating observed δ^2H_f values to predicted δ^2H_p values. We used data from nestlings (with juvenile feathers corresponding with the juvenile feathers of the vagrants) sampled under a very limited time period within a small area in the core of the YBW breeding range.

The robustness of the coefficient was ensured by including (a) the variation in observed δ^2H_f values, (b) the variation in δ^2H_p values in the local isoscape and (c) the use of a Monte Carlo process. Under these circumstances, a regression model for precipitation-to-feather conversion (e.g. Marquiss *et al.* 2012) was not feasible. The intercepts in regression models are generally small in relation to the dynamic part, e.g. 9.81 vs –173‰ (1.42 × –121.6‰) at the Mirnoye sampling site when applying a regression model for European songbirds (Marquiss *et al.* 2012). With these values, the regression model virtually converges to a single factor model, equivalent to the use of a linear conversion coefficient. The potential bias of the single point connection between the prediction map and the modelled δ^2H_f isoscape is also limited by the lack of variation in δ^2H_p values across large parts of the prediction map. Until more feather samples from Siberia are collected and analysed, we conclude that this way to geographically assign δ^2H_f data is a feasible method.

A recent westward range expansion in YBW has been proposed by De Juana (2008) as an explanation of the increasing numbers of YBW vagrants in Europe. The shape of the δ^2H_p isoscape across Eurasia (Bowen *et al.* 2005, IsoMAP key 64737) does not contradict that the δ^2H_f values found in the Fennoscandian vagrants originated from European Russia. Until new evidence for the distribution and densities of YBW in European Russia is presented, claims of origins outside the known breeding range remain speculative.

Although our results rule out a large proportion of YBW breeding range, our insight into the true origin of YBW arriving in Europe in autumn remains vague. We agree with Gilroy & Lees (2003) that increased observer coverage and awareness are important for a deeper understanding of vagrancy, but better observations alone cannot take us to the Holy Grail of vagrancy; information about origins is vital. Massive ringing in regions where vagrants stage or winter will not provide the necessary migratory connectivity data, because very few of the marked birds are likely to return to their site of origin, let alone be recaptured there.

Massive ringing in the breeding areas could potentially help, but the logistical challenges would be enormous and the rarity of the vagrancy events would require prohibitively large numbers of marked potential vagrants. The same is true for loggers that require recaptures, e.g. geolocators and passive GPS-loggers, particularly in species with low site tenancy. Waiting for active tags small enough to be safely carried by small songbirds will probably leave us with none or sparse data for a very long time, too.

Intrinsic markers appear to be our best bet for short-term success, but as shown by this study, δ^2H ratios alone can only describe origins with very limited levels of precision (cf. Farmer *et al.* 2008, Marquiss *et al.* 2012). To really pin-point the key sites of migratory connectivity for an observed (caught) vagrant, combinations of different methods should be considered. These could encompass (a) multiple element stable isotopes (e.g. Fox *et al.* 2016), (b) genetic markers (Chamberlain *et al.* 2000, Veen 2013), (c) fine scale weather and deuterium deposition data (Tonra *et al.* 2015), (d) trace elements (Norris *et al.* 2007, Kaimal *et al. 2009*, Szép *et al.* 2009), and probably even (e) anthropogenic pollutants and (f) internal and external organisms of various sorts (antibodies against them included).

Each of these methods will come with costs and complications, and stitching the resulting data together to form solid conclusions will be highly demanding. The key issue, though, is the need for reliable range-wide ground-truth data on each of these characteristics to create value maps equivalent to the isoscapes developed for stable isotopes. Most of these data would need to be collected “on the ground”, which obviously is an immense task.

Overall, we suggest that vagrancy is acknowledged as a genuine research topic rather than just a twitcher's delight. Birdwatchers and ringers can contribute significantly to the development of this field, especially if they are willing to work in new places. Once a dataset of migratory connection points is established, the various theories of vagrancy can be evaluated. We predict that the emerging insight will unveil a complex phenomenon with multiple internal and external drivers, e.g. anthropogenic environmental changes. During the process, we hope that international collaboration will strengthen and necessary conservation actions be founded.

Acknowledgements. Isak Vahlström and Aron Dynesius collected the Mirnoye feather samples during their work at the Mirnoye Ecological Research Station (headed by Oleg Bourski). The ringing teams at the Stora Fjäderägg and Tauvo stations kindly provided us feathers from the birds they handled. Nomenclature of scientific names according to Howard and Moore Complete Checklist of the Birds of the World (https://www.howardandmoore.org/, downloaded 9th of January 2019). This research was financially supported by the Gustafsson and C F Lundström Foundations (grants to LE), Bröderna Edlund's Foundation (grants to AdJ), the University of Jyväskylä Open Science Centre (grant to JT) and Russian Foundation for Basic Research (grant 18-04-00269 to OB).

Siperialaisten vaelluslintujen alkuperä: esimerkkitapauksena taigauunilintu Fennoskandiassa

Vaelluslinnut tai harhailijat ovat kiehtova osa lintuharrastusta ja -tutkimusta. Kuitenkin syyt lintujen vaelluksille, harhailuille ja erityisesti sille, mistä ne saapuvat on varsin heikosti tunnettua. Läntisessä Euroopassa alkuperäpohdiskelujen kohteena ovat pääasiassa idästä, Siperian valtavalta maa-alueelta saapuvat monilajiset harhailijat, kuten esimerkiksi nykyään syksyisin yleisehkönä tavattava taigauunilintu (*Abrornis inornatus*, aikaisemmin *Phylloscopus inornatus*).

Tämän tutkimuksen tarkoituksena on antaa ensi kertaa viitettä syksyllä tavattavien taigauunilintujen lähtöalueista vedyn isotooppianalyysillä kahdella lintuasemalla (Stora Fjäderägg ja Tauvo) tavattujen taigauunilintujen pyrstösulista. Vertailuaineistona käytettiin Keski-Siperiasta saatuja taigauunilinnun pesäpoikasia sekä niiden emoja. Vertailtaessa syksyllä lintuasemilta saatujen taigauunilintujen vedyn isotooppiarvoja pesiviin lintuihin, näyttää siltä, että syksyiset linnut ovat saapuneet lajin pesimisalueen länsi- tai/ja eteläosista. Suurimmat lähtöaluetodennäköisyydet osuvat Komin tasavallan ja Uralvuoriston pohjois-/luoteisosiin.

Vaikka menetelmällä onnistutaan rajaamaan valtaosa taigauunilinnun mahdollisista lähtöalueista ulos, isotooppianalyysin tarkkuus ei riitä osoittamaan yhtä tiettyä hyvin tarkkaa aluetta. Suurimpana syynä tähän on taigauunilinnun pesimisympäristön samankaltaisuus Euraasiassa ja siten myös vedyn isotoopin vaihtelu on rajallista. Lähtöalueen osoitustarkkuus voisi parantua, jos isotooppimenetelmän rinnalle saataisi myös muita mittareita (esim. mahdolliset geneettiset erot) ja enemmän mittausaineistoa valtavalta Siperian maa-alueelta. Keskeisessä osassa on kansainvälinen yhteistyö.

References

Baker, K. 1977: Westward vagrancy of Siberian passerines in autumn 1975. — Bird Study 24: 233–242.

Betini, G.S., Hobson, K.A., Wassenaar, L.I. & Norris, D.R. 2009: Stable hydrogen isotope (δD) values in songbird nestlings: effects of diet, temperature, and body size. — Canadian Journal of Zoology 87: 767–772.

Bourski, O.V. & Forstmeier, W. 2000: Does interspecific competition affect territorial distribution of birds? A long-term study on Siberian *Phylloscopus* warblers. — Oikos 88: 341–350.

Bourski, O.V. 1994: Breeding bird dynamics in the Yenisei middle taiga: a 13-year study. — In: Hagemeijer, E. J. M. & Vestrael, T. J. (eds.). Bird Numbers 1992. Distribution, monitoring and ecological aspects. Proceedings of the 12th International Conference of IBCC and EOAC, Noordwijkerhout, The Netherlands. Statistics Netherlands, Voorburg/Heerlen and SOVON, Beek-Ubbergen, pp. 143–149.

Bowen, G.J., West J.B., Miller C.C., Zhao L. & Zhang T. 2014a: IsoMAP: Isoscapes Modeling, Analysis and Prediction (version 1.0). — The IsoMAP Project. http://isomap.org.

Bowen, G.J., Liu, Z., Van der Zanden, H.B., Zhao, L. & Takahashi, G. 2014b: Geographic assignment with stable isotopes in IsoMAP. — Methods in Ecology and Evolution 5: 201–206.

Bowen, G.J., Wassenaar. L.I. & Hobson, K.A. 2005: Global application of stable hydrogen and oxygen isotopes to wildlife forensics. — Oecologia 143: 337–348.

Bozó, L., Heim, W., Harnos, A. & Csörgő, T. 2016: Can we explain vagrancy in Europe with the autumn migration phenology of Siberian warbler species in East Russia? — Ornis Hungarica 24: 150–171.

Chamberlain, C.P., Bensch, S., Feng, X., Åkesson, S. & Andersson, T. 2000: Stable isotopes examined across a migratory divide in Scandinavian Willow Warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. — Proceedings of the Royal Society of London. Series B 267: 43–48.

Clement, P. 2018: Yellow-browed Warbler (*Phylloscopus inornatus*). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). Handbook of the Birds of the World Alive. — Lynx Edicions, Barcelona. https://www.hbw.com/node/58883. Downloaded on 6 April 2018.

De Juana, E. 2008: Where do Pallas's and Yellow-browed Warblers (*Phylloscopus proregulus*, *Ph. inornatus*) go after visiting Northwest Europe in autumn? An Iberian perspective. — Ardeola 55: 13–25.

Dementiev, G.P. & Gladkov, N.A. 1954: Birds of the Soviet Union, Volume VI. — Sovetskaya Nauka, Moscow.

Demongin, L. 2016: Identification guide to birds in the hand. — Bauregaard-Vendon, France.

Farmer, A., Cade, B.S. & Torres-Dowdall, J. 2008: Fundamental limits to the accuracy of deuterium isotopes for identifying the spatial origin of migratory animals. — Oecologia 158: 183–192.

Folvik, A. 1992: Norwegian records of Yellow-browed Warblers *Phylloscopus inornatus*. — Fauna Norvegica Series C. Cinclus 15: 31–36.

Fox, A.D., Hobson, K.A., de Jong, A., Kardynal, K.J., Koehler, G. & Heinicke, T. 2016: Flyway population delineation in Taiga Bean Geese *Anser fabalis fabalis* revealed by multi-element feather stable isotope analysis. — Ibis 159: 66–75.

Gilroy, J.J. & Lees, A. C. 2003: Vagrancy theories: are autumn vagrants really reverse migrants? — British Birds 96: 427–438.

Hagemeijer, E.J.M. & Blair, M.J. (eds.) 1997: The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. — T & A D Poyser, London.

Hobson, K.A. 2005a: Using stable isotopes to trace long-distance dispersal in birds and other taxa. — Diversity and Distributions 11: 157–164.

Hobson, K.A. 2005b: Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. — Auk 122: 1037–1048.

Hobson, K.A. 2011: Isotopic ornithology: a perspective. — Journal of Ornithology 152 (Suppl 1): 49–66.

Hobson, K.A. & Wassenaar, L.I. 1997: Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. — Oecologia 109: 142–148.

Hobson, K.A. & Wassenaar, L.I. 2008: Tracking animal migration with stable isotopes. — Terrestrial Ecology Series Vol. 2. — Academic Press, Elsevier, Amsterdam.

Hobson, K.A., Barnett-Johnson, R. & Cerling, T. 2010: Using isoscapes to track animal migration. In: West, J. B. *et al.* (eds.), Isoscapes: understanding movement, pattern, and processes in Earth through isotope mapping. — Springer Science. Doi: 10.1007/978-90-481-3354-3_13.

Irwin, D.E. & Irwin, J.H. 200:. Siberian migratory divides. — In: Greenberg, S. & Marra, P. P. (eds.), Birds of two worlds: the ecology and evolution of migration. John Hopkins University Press. pp. 27–40.

IUCN 2017: The IUCN Red List of Threatened Species. — http://maps.iucnredlist.org/map.html?id=22715310. Downloaded on 15 Dec 2017.

Jones, J., Monticelli, D. & Crochet, P.A. 2015: Birding in European Russia: Ural Mountains, Yekaterinburg and Orenburg region. — Dutch Birding 37: 302–320.

Kaimal, B., Johnson, R. & Hannigen, R. 2009: Distinguishing breeding populations of mallards (*Anas platyrhynchos*) using trace elements. — Journal of Geochemical Exploration 102: 176–180.

Marquiss, M., Newton, I., Hobson, K.A. & Kolbeinsson, Y. 2012: Origins of irruptive migrations by Common Crossbills *Loxia curvirostra* into northwestern Europe revealed by stable isotope analysis. — Ibis 154: 400–409.

Meehan, T.D., Rosenfield, R.N., Atudore, V.N., Bielefeldt, J., Rosenfield, L.J., Stewart, A. C., Stout, W. E. & Bozek, M. A. 2003: Variation in hydrogen stable-isotope ratios between adult and nestling Cooper's Hawks. — Condor 105: 567–572.

Meshcheryagina, S.G., Vurdova, I.F., Polyakov, V.E. & Golovatin, M.G. 2015: On Yellow-browed Warbler breeding in the northern parts of the Sverdlovsk and Perm regions. Fauna of the Urals and Siberia, Regional Faunistic Journal No. 2 2015. — Russian Academy of Sciences, Ural branch, Institute of Plant and Animal Ecology, pp. 125–135. (In Russian with English summary).

Norris, D.R., Lank, D.B., Pither, J., Chipley, D., Ydenberg, R.C. & Kyser, T.K. 2007: Trace element profiles as unique identifiers of western sandpiper (*Calidris mauri*) populations. — Canadian Journal of Zoology 85: 579–583.

Oppel, S., Pain, D.J., Lindsell, J.A., Lachmann, L., Diop, I., Tegetmeyer, C., Donald, P.F. Anderson, G., Bowden, C.G.R., Tanneberger, F. & Flade, M. 2011: High variation reduces the value of feather stable isotope ratios in identifying new wintering areas for aquatic warblers *Acrocephahus paludicola* in West Africa. — Journal of Avian Biology 42: 342–354.

Pekarsky, S., Angert, A., Haese, B., Werner, M., Hobson, K.A. & Nathan, R. 2015: Enriching the isotopic toolbox for migratory connectivity analysis: a new approach for migratory species breeding in remote or unexplored areas. — Diversity and Distributions 21: 416–427.

Pfeifer, R., Stadler, J. & Brandl, R. 2007: Birds from the Far East in Central Europe: a test of the reverse migration hypothesis. — Journal of Ornithology 148: 379–385.

Rabøl, J. 1969: Reversed migration as the cause of westward vagrancy by four *Phylloscopus* warblers. — British Birds 62: 89–92.

Rogacheva, E.V., Syroechkovski, E.E., Bourski, O.V., Moros, A.A. & Sheftel, B.I. 1991: Birds of the Central Siberian Biosphere Reserve. 2. Passerine birds. — In: Syroechkovski, E.E. & Rogacheva, E.V. (eds.) Biological resources and ecosystems of the Yenisei taiga. IPEE RAN. Moscow, pp. 32–166. (In Russian)

Rogacheva, H. 1992: The birds of Central Siberia. — Husum Druck und Verlagsgesellschaft, Husum, Germany.

Smith, A.D. & Dufty Jr., A.M. 2005: Variation in the stable-hydrogen isotope composition of Northern Goshawk feathers: relevance to the study of migratory origins. — Condor 107: 547–558.

Sokolov, V., Ehrich, D., Yoccoz, N.G., Sokolov, A. & Lecomte, N. 2012: Bird communities of the arctic shrub tundra of Yamal: habitat specialists and generalists. — PLOS ONE 7: e5035. http://doi.org/10.1371/journal.pone.0050335.

Soto, D.X., Koehler, G., Wassenaar, L.I. & Hobson, K.A. 2017: Re-evaluation of the hydrogen stable isotopic composition of keratin calibration standards for wildlife and forensic applications. — Rapid Communications in Mass Spectrometry 31: 1193–1203.

Svensson, L. 1992: Identification Guide to European Passerines. — Stockholm.

Szép, T., Hobson, K.A., Vallner, J., Piper, S.E., Kovács, B., Szabó, D.Z. & Møller, A.P. 2009: Comparison of trace element and stable isotope approaches to the study of migratory connectivity: an example using two hirundine species breeding in Europe and wintering in Africa. — Journal of Ornithology 150: 621–636.

Thorup, K. 2004: Reverse migration as a cause of vagrancy. — Bird Study 51: 228–238.

Tonra, C.M., Both, C. & Marra, P.P. 2015: Incorporating site and year-specific deuterium ratios (δ^2H) from precipitation into geographic assMay 6, 2019ignments of migratory bird. — Journal of Avian Biology 46: 266–274.

Torniainen, J., Vuorinen, P.J., Jones, R.I., Keinänen, M., Palm, S., Vuori, K.A.M., & Kiljunen, M. 2014: Migratory connectivity of two Baltic Sea salmon populations: retrospective analysis using stable isotopes of scales. ICES J. — Marine Science 71: 336–344.

Vartapetov, L.G. 1998: Birds of the northern taiga of the West Siberian Plain. — Novosibirsk, Nauka. (In Russian)

Veen, T. 2013: Unravelling migratory connections: the next level. — Molecular Ecology 22: 4144–4146.

Veit, R. 2000: Vagrants as the Expanding Fringe of a Growing Population. — Auk 117: 242–246

Wassenaar, L.I. & Hobson, K.A. 2003: Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. — Isotopes in Environmental Health Studies 39: 211–217.

Wassenaar, L.I. & Hobson, K.A. 2010: Two new keratin standards (δ^2H, δ^{18}O) for daily laboratory use in wildlife and forensic isotopic studies. — In: 7th International Conference on Applications of Stable Isotope Techniques to Ecological Studies. University of Alaska, Fairbanks, Alaska, USA.

West, J.B., Bowen, G.J., Cerling, T.E. & Ehleringer, J.R. 2006: Stable isotopes as one of nature's ecological recorders. — Trends in Ecology and Evolution 21: 408–414.

West, J.B., Bowen, G.J., Dawson, T.E. & Tu, K.P. (eds.) 2010: Isoscapes. Understanding movement, pattern, and processes on Earth through isotope mapping. — Springer Nature.

Yong, D.L., Liu, Y., Low, B.W., Española, C.P., Choi, C.-Y. & Kawakami, K. 2015: Migratory songbirds in the East Asian-Australasian Flyway: a review from a conservation perspective. — Bird Conservation International 25: 1–37.