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The origins of northern European *Autographa gamma* individuals evaluated using hydrogen stable isotopes

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ABSTRACT

1. Many insect species are migratory. As the spring progresses, adults gradually depart from their over-wintering habitats and arrive in northern zones where they reproduce during the summer. Understanding this transgenerational and highly adaptive migratory behaviour is crucial when interpreting lifecycle dynamics of many insect pests.
2. Origins of migratory Silver Y moths, *Autographa gamma* (Linnaeus, 1758), captured from Finland were studied with stable hydrogen analysis of their wings ($\delta^2\text{H}_w$).
3. The difference between spring and autumn generation $\delta^2\text{H}_w$ values indicate different geographical natal origins. Probability surface map shows that the spring generation likely emerged in central Europe (Benelux countries, Germany and parts of France).
4. A negative correlation between the $\delta^2\text{H}_w$ values and the migrants' capture year suggests that warming climate may have driven the transgenerational migratory stages northwards during the last century.

Keywords: *Autographa gamma*, climate change, insects, stable isotopes, transgenerational migration

INTRODUCTION

Many insect species are migratory (Chapman *et al.*, 2004; Holland *et al.*, 2006). Adult life stages arrive each spring from lower-latitude winter habitats to temperate zones in order to use the temporary resources and to reproduce (Cardé, 2008; Chapman *et al.*, 2012). Completion of the full migratory route often consists of several generations and thus determining the emerging areas of the migratory individuals is not straightforward (Stefanescu *et al.*, 2013).

The agricultural pest silver Y moth (*Autographa gamma*) is a migratory species in Europe (Ellis, 2016). Its occurrence in northernmost Europe, where it's unable to overwinter (Chapman *et al.*, 2012), is bimodal during the summer suggesting two primary generations of adults (Figure S1). In the spring adults arrive from their winter localities, supposedly via intermediate generations along the way (Stefanescu *et al.*, 2016). From the late summer to autumn, a second, domestic generation emerges. These offspring then engage in migration back towards the overwintering grounds (Chapman *et al.*, 2010). The high-latitude-emerging individuals that exploit abundant resources in the north form the primary breeding population of the species, whereas unfavourable conditions during the low-latitude winter decrease reproduction and thus limit the overall population size (Chapman *et al.*, 2012). *Autographa gamma* larvae feed on various crops e.g, potato and tomato (Carter, 1984). They are capable of causing serious outbreaks in agricultural settings throughout Africa, Asia, and Europe (Carter, 1984). Thus, it is important to localize the origin of migrants and to increase the overall understanding of insect pest migratory ecology.

Similarly to feathers, hair, and fish scales (all keratin), insect wings (chitin) are inert after moulting (e.g. Hobson *et al.*, 1999; Brättström *et al.*, 2010). Therefore, *A. gamma* wing isotope composition reflects the values in the resident larvae and consequently emerging

areas of the adults. We evaluated the geographical origins of *A. gamma* spring generation in Finland using hydrogen stable isotope analysis (SIA) from adult wings. The relationship between capture year and SIA values was explored to see if temporal changes in the emergence area of migrants have occurred, for example due to ongoing climate change.

MATERIALS AND METHODS

Sampling

Hind wings from 54 *A. gamma* individuals (capturing years 1898–2014) were analysed for hydrogen isotopes ($\delta^2\text{H}_w$). Wings were obtained from University of Jyväskylä Open Science Centre collections and from the field. Five resident (but see: Dal & Irhammar 1980) butterflies (*Pieris napi*) were also analysed. The preliminary segregation of individuals to spring and autumn generations was based on distribution of the adult observations in Finland (Figure S1). The latest individual assigned to spring was caught on June 27th and the earliest autumn moth on July 30th (Table S1).

Isotope analysis

Wings were cleaned in 2:1 chloroform/methanol, dried overnight, and cut to 0.35 ± 0.05 mg pieces into silver capsules. $\delta^2\text{H}_w$ were measured using Isoprime 100 CF-SIRMS (Isoprime UK), coupled with an Elementar Pyrocube elemental analyser (Elementar, Germany). Two keratin laboratory reference materials from Environment Canada were used to normalize the results (KHS: $\delta^2\text{H} = -54.1\text{‰}$ and CBS: $\delta^2\text{H} = -197\text{‰}$). Results are expressed using the standard δ -notation ($\delta^2\text{H}$) as parts per thousand (‰) differences from the international standard. The reference material used was IAEA standard of VSMOW – SLAP scale for hydrogen. Standard deviation of reference replicates was lower than 2.2‰.

Spatial assignment

Cyber-GIS online tool IsoMAP (<http://isomap.org>) by Bowen et al. (2014) was used for evaluating the individuals' natal origins. IsoMAP creates a probability surface map of the match between precipitation hydrogen values ($\delta^2\text{H}_p$) and study material, $\delta^2\text{H}_w$.

A rectangle-shaped $\delta^2\text{H}_p$ model fitting was created with latitude range of -37.9 to 71.5 degrees and longitude range of -19.3 to 87.2 degrees using $\delta^2\text{H}_p$ data from Anon. (2011). The following variables were applied to the regression model: elevation (Anon. 1998), latitude squared, longitude squared and precipitation ($R^2 = 0.77$). Annual interval from 1960 to 2000 precipitation $\delta^2\text{H}_p$ survey was used to ensure inclusion of sufficient $\delta^2\text{H}_p$ survey data points (altogether 311 stations) for the required geographic area (model key: 43462 in IsoMAP).

A prediction model for $\delta^2\text{H}_p$ "isoscape" was created from the abovementioned $\delta^2\text{H}_p$ model rectangle to include latitudinal and longitudinal range of -35 to 59.1 degrees and -15.1 to 60.5 degrees, respectively (key: 43473). For the final assignment (i.e. probability surface), *Vanessa atalanta* and *Inachis io* transfer function ($\delta^2\text{H}_w = 1.096 \times \delta^2\text{H}_p - 40.56$), according to Brättström et al. (2010), was used to directly compare $\delta^2\text{H}_w$ with $\delta^2\text{H}_p$. IsoMAP requires mean (-58.3‰) and standard deviation (14.1) from the calibration curve $\delta^2\text{H}_w$ values for creating a probability surface map. Interpolations were made using the kriging method (probability surface map key: 49258).

Statistics

Nested ANOVA-GLM (year nested within generation/species) and Spearman's correlation coefficient (r_s) were used to test whether the capture year and generation/species had effects on $\delta^2\text{H}_w$ values. One-way ANOVA was used to compare $\delta^2\text{H}_w$ values from different sampling locations (i.e. municipalities). Post hoc tests (LSD) were Bonferroni-corrected. Statistics were performed using SPSS 21.0 (SPSS Inc., Chicago, IL, USA).

RESULTS

Wing isotope values

Samples' $\delta^2\text{H}_w$ mean values were significantly dependent of generation/species, i.e., whether they were from spring generation, autumn generation, or *P. napi*. ($F = 45.20$, d.f. = 2, $P < 0.001$). Post hoc test revealed that spring generation values were higher than autumn generation ($P < 0.001$). *P. napi* $\delta^2\text{H}_w$ values were lower compared to spring generation $\delta^2\text{H}_w$ ($P < 0.001$), but did not differ from *A. gamma* autumn generation $\delta^2\text{H}_w$ ($P > 0.05$) (Figure 1). There was also a significant year effect ($F = 2.53$, d.f. = 8, $P = 0.027$) (Figure 1). Spearman's correlation coefficient showed a negative relationship between spring generation $\delta^2\text{H}_w$ values and year ($r_s = -0.545$, $N = 24$, $P = 0.002$), but not for autumn generation $\delta^2\text{H}_w$ values and year ($P > 0.05$). Autumn generation $\delta^2\text{H}_w$ values were similar between sampling locations ($F = 2.23$, d.f. = 8, $P > 0.05$) (Table S1).

Evaluated provenance of the migrants

IsoMAP output for *A. gamma* provenance shows high probability in Central Europe, especially in Germany, the Benelux countries, northern France and in the east side of the Alps. In contrast, Mediterranean region, North Africa and areas northeast from southwest Russia show the lowest probabilities (Figure 2).

DISCUSSION

The difference between Finnish *A. gamma* spring and autumn generation $\delta^2\text{H}_w$ values indicates clearly separate emergence areas. Autumn generation values were on average ~30% lower than spring generation values, and similar to resident *P. napi* from the same areas. This strongly suggests that autumn generation *A. gamma* individuals have emerged in the same

region as *P. napi*, whereas spring generation values indicate more southern origin. Results are not surprising due to the species' inability to overwinter in the very northernmost areas of its occurrence range (Hill & Gatehouse, 1992), although overwintering larvae have been observed in central Europe (Honěk *et al.*, 2002).

Map localizes the highest likely provenance of spring generation to central Europe. The known distribution of the species also covers northern parts of Africa (Carter, 1984). Based on our results it is not likely that individuals observed in northern Europe arrive from that far regularly, although exceptional wind conditions might occasionally make it possible (Chapman *et al.*, 2010). On the contrary, based on the negative correlation of $\delta^2\text{H}_w$ and year, the spring generation might be arriving from more northern latitudes than it used to in the past. Confirmation for this trend would benefit from further research.

Similarly to butterflies like *Vanessa cardui*, *A. gamma* likely exhibits transgenerational migration between the primary overwintering grounds and the northern temperate zones (Chapman *et al.*, 2014; Stefanescu *et al.*, 2016), especially because it can produce up to five generations a year (Carter, 1984; Chapman *et al.*, 2012). This is very well in concordance with our data, because the high-likelihood areas for migrants' emergence include relatively cold regions that cannot support the mid-winter population. These areas are more likely to form an intermediate but crucial step in the transgenerational migratory route.

The unfavourable conditions in the overwintering areas have been shown to cause annual bottlenecks and to form the main limiting factor to *A. gamma* population size (Chapman *et al.*, 2012). Consequently, it is essential to recognize changes in the migratory patterns of this insect pest. Human-driven climate change has vast potential to affect the yearly dynamics of not only migratory pests, but also beneficial species, by making resources spatially and temporally more available during the more unfavourable months (Bale, 2010).

This could mean higher initial population sizes and/or earlier arrival for the primary breeding population in the temperate zone.

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SUPPORTING INFORMATION

Figure S1. Weekly *Autographa gamma* adult observations in years 1990–2014 in Finland (N = 5904 inds.).

Table S1. *Autographa gamma* $\delta^2\text{H}_w$ ($\pm\text{SD}$) spring and autumn generation values, sampling dates, capture locations in Finland and numbers (N).

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Figure 1. A. *gamma* $\delta^2\text{H}_w$ values for spring (squares) and autumn (circles) generation between years 1898–2014. Resident *Pieris napi* values are denoted with a diamond. Whiskers represent standard deviations.

Figure 2. Estimated origin of spring generation *A. gamma* caught in Finland. The assignment is based on comparison of hydrogen stable isotopes of annual precipitation ($\delta^2\text{H}_p$) and adult wing material ($\delta^2\text{H}_w$). Red colour represent high probability and blue low probability of origin.