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

3

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13 Running title: *Autographa gamma* migration

14 ABSTRACT

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

28

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

31 INTRODUCTION

32

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

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

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

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

60

61 MATERIALS AND METHODS

62 *Sampling*

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

70

71 *Isotope analysis*

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

80

81 *Spatial assignment*

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

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

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

99

100 *Statistics*

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

106

107 RESULTS

108 *Wing isotope values*

109 Samples' $\delta^2\text{H}_w$ mean values were significantly dependent of generation/species, i.e., whether
110 they were from spring generation, autumn generation, or *P. napi*. ($F = 45.20$, d.f. = 2, $P <$
111 0.001). Post hoc test revealed that spring generation values were higher than autumn
112 generation ($P < 0.001$). *P. napi* $\delta^2\text{H}_w$ values were lower compared to spring generation $\delta^2\text{H}_w$
113 ($P < 0.001$), but did not differ from *A. gamma* autumn generation $\delta^2\text{H}_w$ ($P > 0.05$) (Figure 1).
114 There was also a significant year effect ($F = 2.53$, d.f. = 8, $P = 0.027$) (Figure 1). Spearman's
115 correlation coefficient showed a negative relationship between spring generation $\delta^2\text{H}_w$ values
116 and year ($r_s = -0.545$, $N = 24$, $P = 0.002$), but not for autumn generation $\delta^2\text{H}_w$ values and year
117 ($P > 0.05$). Autumn generation $\delta^2\text{H}_w$ values were similar between sampling locations ($F =$
118 2.23, d.f. = 8, $P > 0.05$) (Table S1).

119

120 *Evaluated provenance of the migrants*

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

125

126 DISCUSSION

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

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

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

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

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

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

157

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165

166 SUPPORTING INFORMATION

167 Figure S1. Weekly *Autographa gamma* adult observations in years 1990–2014 in Finland (N
168 = 5904 inds.).

169

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

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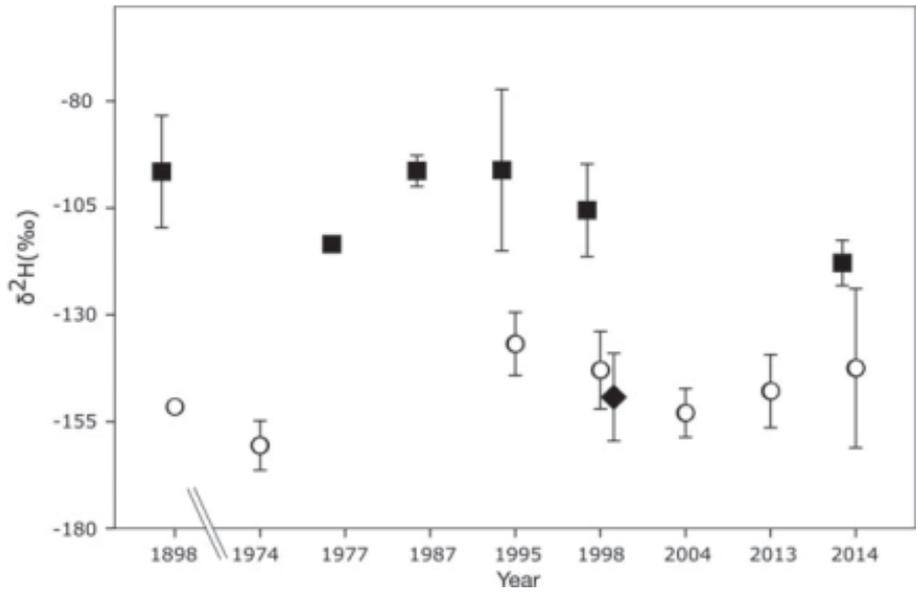
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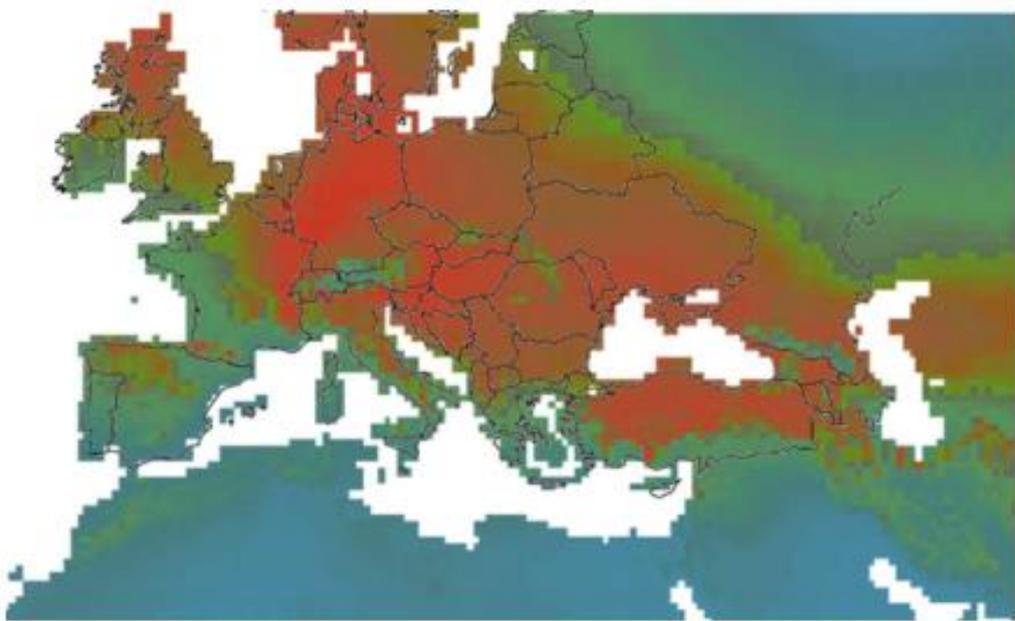
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222 Stefanescu, C., Soto, D. X., Talavera, G., Vila, R., & Hobson, K. A. (2016) Long-distance
223 autumn migration across the Sahara by painted lady butterflies: exploiting resource pulses
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225 Figure 1. *A. gamma* $\delta^2\text{H}_w$ values for spring (squares) and autumn (circles) generation
226 between years 1898–2014. Resident *Pieris napi* values are denoted with a diamond. Whiskers
227 represent standard deviations.



228
229 Figure 2. Estimated origin of spring generation *A. gamma* caught in Finland. The assignment
230 is based on comparison of hydrogen stable isotopes of annual precipitation ($\delta^2\text{H}_p$) and adult
231 wing material ($\delta^2\text{H}_w$). Red colour represent high probability and blue low probability of
232 origin.



233
12