

Article (refereed) - postprint

Stefanescu, Constantí; Páramo, Ferran; Åkesson, Susanne; Alarcón, Marta; Ávila, Anna; Brereton, Tom; Carnicer, Jofre; Cassar, Louis F.; Fox, Richard; Heliölä, Janne; Hill, Jane K.; Hirneisen, Norbert; Kjellén, Nils; Kühn, Elisabeth; Kuussaari, Mikko; Leskinen, Matti; Liechti, Felix; Musche, Martin; Regan, Eugenie C.; Reynolds, Don R.; Roy, David B.; Ryrholm, Nils; Schmaljohann, Heiko; Settele, Josef; Thomas, Chris D.; van Swaay, Chris; Chapman, Jason W. 2013 Multi-generational long-distance migration of insects: studying the painted lady butterfly in the Western Palaearctic. *Ecography*, 36 (4). 474-486. [10.1111/j.1600-0587.2012.07738.x](https://doi.org/10.1111/j.1600-0587.2012.07738.x)

© 2012 The Authors

This version available <http://nora.nerc.ac.uk/21064/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

This document is the author's final manuscript version of the journal article, incorporating any revisions agreed during the peer review process. Some differences between this and the publisher's version remain. You are advised to consult the publisher's version if you wish to cite from this article.

The definitive version is available at <http://onlinelibrary.wiley.com>

Contact CEH NORA team at
noraceh@ceh.ac.uk

1 **Multi-generational long-distance migration of insects: studying**
2 **the painted lady butterfly in the Western Palaearctic**

3
4
5 Constantí Stefanescu,^{1,2} Ferran Páramo,¹ Susanne Åkesson,³ Marta Alarcón,⁴ Anna Ávila,⁵
6 Tom Brereton,⁶ Jofre Carnicer,^{2,7} Louis F. Cassar,⁸ Richard Fox,⁶ Janne Heliölä,⁹ Jane K.
7 Hill,¹⁰ Norbert Hirneisen,¹¹ Nils Kjellén,³ Elisabeth Kühn,¹² Mikko Kuussaari,⁹ Matti
8 Leskinen,¹³ Felix Liechti,¹⁴ Martin Musche,¹² Eugenie C. Regan,^{15,16} Don R. Reynolds,^{17,18}
9 David B. Roy,¹⁹ Nils Ryrholm,²⁰ Heiko Schmaljohann,²¹ Josef Settele,^{12,22} Chris D.
10 Thomas,¹⁰ Chris van Swaay,^{22,23} and Jason W. Chapman^{17,24}

11
12 ¹ *Butterfly Monitoring Scheme, Museu de Granollers de Ciències Naturals, Francesc Macià,*
13 *51, E-08402 Granollers, Spain*

14 ² *Global Ecology Unit, CREAM-CEAB-CSIC, Edifici C, Campus de Bellaterra, E-08193*
15 *Bellaterra, Spain*

16 ³ *Department of Animal Ecology, Lund University, Ecology Building, SE-223 62 Lund,*
17 *Sweden*

18 ⁴ *Departament de Física i Enginyeria Nuclear, Universitat Politècnica de Catalunya,*
19 *c/Urgell 187, E-08036 Barcelona, Spain*

20 ⁵ *Center for Ecological Research and Forestry Applications, Edifici C, Universitat Autònoma*
21 *de Barcelona, Bellaterra 08193, Spain*

22 ⁶ *Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset BH20 5QP, UK*

23 ⁷ *Community and Conservation Ecology Group, Centre for Life Sciences, Nijenborgh 7,*
24 *Groningen 9747, The Netherlands*

25 ⁸ *Institute of Earth Systems (IES), Division of Environmental Management and Planning,*
26 *University of Malta, MSD 2080, Malta*

27 ⁹ *Finnish Environment Institute, Natural Environment Centre, Ecosystem Change Unit, P.O.*
28 *Box 140, FI-00251 Helsinki, Finland*

29 ¹⁰ *Department of Biology, Wentworth Way, University of York, York, YO10 5DD, UK*

30 ¹¹ *science4you, von-Müllenark-Str. 19, 53179 Bonn, Germany*

31 ¹² *Department of Community Ecology, Helmholtz Centre for Environmental Research–UFZ,*
32 *Theodor-Lieser Str. 4, 06120 Halle, Germany*

33 ¹³ *Department of Physics, Division of Atmospheric Sciences, University of Helsinki, P.O. Box*
34 *64, FI-00014 University of Helsinki, Finland*

35 ¹⁴ *Swiss Ornithological Institute, Luzernerstrasse 6, Sempach 6204, Switzerland*

36 ¹⁵ *National Biodiversity Data Centre, WIT West Campus, Carriganore, Waterford, Ireland*

37 ¹⁶ *Department of Zoology, Trinity College Dublin, Dublin 2, Ireland*

38 ¹⁷ *Plant and Invertebrate Ecology Department, Rothamsted Research, Harpenden,*
39 *Hertfordshire AL5 2JQ, UK*

40 ¹⁸ *Natural Resources Institute, University of Greenwich, Chatham, Kent ME4 4TB, UK*

41 ¹⁹ *NERC Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh*
42 *Gifford, Oxfordshire OX19 8BB, UK*

43 ²⁰ *Department of Electronics, Mathematics and Natural Sciences, Faculty of Engineering and*
44 *Sustainable Development, University of Gävle, S-801 76 Gävle, Sweden*

45 ²¹ *Institute of Avian Research “Vogelwarte Helgoland”, An der Vogelwarte 21,*
46 *Wilhelmshaven 26386, Germany*

47 ²² *BCE, Butterfly Conservation Europe, c/o Vlinderstichting, P.O. Box 506, Wageningen*
48 *6700, The Netherlands*

49 ²³ *De Vlinderstichting, Dutch Butterfly Conservation, P.O. Box 506, Wageningen 6700, The*
50 *Netherlands*

51 ²⁴ *Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10*
52 *9EZ, UK*

53

54

55

56

57 Word count (excluding acknowledgements and references): 5959. Abstract 273, Introduction
58 673, Material and methods 1437, Results 2259, Discussion 1316, Acknowledgements 225; 59
59 references, 2 tables and 6 figures (plus Supplementary material, 6 appendixes)

60 *Abstract.* Long-range, seasonal migration is a widespread phenomenon among insects,
61 allowing them to track and exploit abundant but ephemeral resources over vast geographical
62 areas. However, the basic patterns of how species shift across multiple locations and seasons
63 are unknown in most cases, even though migrant species comprise an important component of
64 the temperate-zone biota. The painted lady butterfly, *Vanessa cardui*, is such an example; a
65 cosmopolitan continuously-brooded species which migrates each year between Africa and
66 Europe, sometimes in enormous numbers. The migration of 2009 was one of the most
67 impressive recorded, and thousands of observations were collected through citizen science
68 programmes and systematic entomological surveys, such as high altitude insect-monitoring
69 radar and ground-based butterfly monitoring schemes. Here we use *V. cardui* as a model
70 species to better understand insect migration in the Western Palaearctic, and we capitalise on
71 the complementary data sources available for this iconic butterfly. The migratory cycle in this
72 species involves six generations, encompassing a latitudinal shift of thousands of kilometres
73 (up to 60 degrees of latitude). The cycle comprises an annual poleward advance of the
74 populations in spring followed by an equatorward return movement in autumn, with returning
75 individuals potentially flying thousands of kilometres. We show that many long-distance
76 migrants take advantage of favourable winds, moving downwind at high elevation (from
77 some tens of metres from the ground to altitudes over 1,000 m), pointing at strong similarities
78 in the flight strategies used by *V. cardui* and other migrant Lepidoptera. Our results reveal the
79 highly successful strategy that has evolved in these insects, and provide a useful framework
80 for a better understanding of long-distance seasonal migration in the temperate regions
81 worldwide.

82

83 **Introduction**

84

85 Large parts of the world are characterised by the seasonal abundance of resources,
86 interspersed by periods when resources are unavailable or when the physical environment is
87 inhospitable for survival. Species can exploit such resources *in situ* by means of diapausing
88 stages (Tauber et al. 1986) or, alternatively, by some form of migration, breeding when
89 temporary resources become available and then retreating to locations where survival is
90 possible at other times of the year (Southwood 1977, Dingle 1996, Dingle and Drake 2007).
91 This phenomenon has been best studied in vertebrates and other long-lived animals (e.g.
92 Newton 2008), which have generation times comparable to or longer than the annual seasonal
93 cycle. Individuals of these species either migrate with conspecifics and learn traditional
94 routes, or immatures migrate in genetically-determined seasonal directions, and then retrace
95 their steps back to the breeding grounds in the following season or year.

96 Investigation of migration in species with generation times shorter than the seasonal cycle
97 or year is generally more difficult, and this is the case for the majority of migratory insects
98 (Drake and Gatehouse 1995, Holland et al. 2006). Insects that track suitable environments
99 (arising from responses to spatially and temporally variable conditions) must exhibit patterns
100 of movement that encompass multiple generations. Inhabitants of arid/semi-arid regions, such
101 as desert locusts and African armyworm moths, *Spodoptera exempta*, allow themselves to be
102 carried towards large-scale convergence zones where seasonal rains are likely to occur, and
103 hence survive by exploiting successive areas where the vegetation is temporally lush and
104 suitable for reproduction (Pedgley 1981, Pedgley et al. 1995). However, the precise means by
105 which the very large number of migratory insect individuals and species that occur in the
106 temperate zone survive throughout the course of the year is largely unknown. The only well-
107 documented species is the monarch butterfly, *Danaus plexippus*, which is probably atypical of

108 most other insect migrants because it migrates southwards in North America to enter diapause
109 at specific over-wintering sites, notably in Mexico (Solensky 2004). By contrast, most other
110 insect migrants probably have far more widely-distributed (but currently unknown) over-
111 wintering sites, and breed continuously throughout the year, including during winter.

112 In this study, we analyse data for the highly migratory painted lady butterfly, *Vanessa*
113 *cardui*, in Europe, to better understand insect migration in the Western Palaearctic. We
114 concentrate on the exceptional migration events recorded in 2009. Each year, this butterfly
115 colonizes the European continent from its African overwintering quarters (Pollard et al. 1998,
116 Stefanescu et al. 2011). In 2009, numbers of *V. cardui* migrating across Europe were so high
117 that they raised awareness among the general public, with the result that a large number of
118 people contributed to online surveys and made it possible to investigate with unprecedented
119 detail the migration system in this part of the range. Additional data were also obtained
120 through more systematic surveys based on established protocols, such as the extensive
121 network of butterfly recording schemes operating in many European countries (van Swaay et
122 al. 2008), and the continuous monitoring of high-altitude insect migrations by radars
123 operating in southern England and Finland (Chapman et al. 2011a, Leskinen et al. 2011).

124 Here we bring together a combination of ground and aerial (radar) observations to
125 evaluate the following hypotheses, that may also apply to many other migratory insects in the
126 temperate regions: (a) Does this species exhibit a succession of seasonal population shifts,
127 allowing it to track suitable environments and to breed continuously throughout the year?; (b)
128 Does it show a seasonal reversal of migratory direction in spring and autumn generations?; (c)
129 Is migration wind-assisted and at least partly at high altitude or, in common with other
130 migratory butterflies, largely restricted to within the Flight Boundary Layer (i.e. the layer of
131 the atmosphere close to the ground where the wind speeds are slow enough for the insect to
132 make progress in any direction; Srygley and Oliveira 2001)?

133 Using our results, we quantify the pattern and timing of one of the longest insect
134 migrations on Earth, and discuss the mechanisms by which multi-generational long-distance
135 migration could be achieved.

136

137

138

139 **Material and methods**

140

141

142 **Study species**

143

144 *Vanessa cardui* is widely distributed across the world and migrates over vast distances
145 (Shields 1992). It is extremely polyphagous, using larval hostplants from a number of
146 different plant families (Ackery 1988). In the Western Palaearctic, oviposition occurs mostly
147 on thistles (tribe Cardueae, family Asteraceae) and common mallow, *Malva sylvestris* (family
148 Malvaceae), growing in disturbed habitats (e.g. Stefanescu 1997, Asher et al. 2001,
149 Stefanescu et al. 2011). Eggs are laid singly, each female potentially laying about 500 eggs
150 (Hammad and Raafat 1972). On hatching, larvae make a characteristic silken tent on the
151 foodplant leaf and, when fully developed, they leave the plant in search of suitable pupation
152 sites. Developmental time is highly dependent on temperature, the completion of the lifecycle
153 ranging between 33 and 44 days in subtropical areas (Boorman and Taylor 1977, Hammad
154 and Raafat 1972) and ≥ 60 days under cool conditions in the temperate region (C. Stefanescu
155 pers. obs.). It is continuously-brooded and, under favourable laboratory-conditions, may
156 complete as many as eight generations in a year (Hammad and Raafat 1972).

157

158

159 **Study regions**

160

161 The present analysis covers the Western Palaearctic region (i.e. the biogeographical region
162 that includes the western part of the Eurasian landmass and northernmost Africa) and West
163 Africa (i.e. the region of western Africa between the Sahara Desert and the Gulf of Guinea).
164 In order to understand patterns of movement, we divided this geographical area of the species
165 range into the following five subregions, which coincide with broadly recognized
166 biogeographic regions: (1) Western Africa (5-25°N, 26°W-0°W), (2) Northwestern Africa (26-
167 35°N, 19°W-15°E), (3) Western and Central Mediterranean (36-45°N, 10°W-15°E), (4)
168 Western and Central Europe (46-55°N, 11°W-25°E), and (5) Northern Europe (56-71°N,
169 25°W-31°E) (Fig. 1).

170 For simplicity, subregions (3) and (4) are referred to as Mediterranean and Central
171 Europe, respectively. In order to document the European migration pattern in more detail, the
172 last three subregions have been further divided into a western and an eastern part along the
173 5°E meridian (for the Mediterranean) or the 2°E meridian (for Central and Northern Europe)
174 in some analyses.

175

176

177 **Datasets**

178

179 We used three independent datasets (for further details see Supplementary material Appendix
180 1):

181 (1) *Ad-hoc distribution records*. 30,002 observations of adults or immatures that encompass
182 the latitudinal range 5°-71° N and 67 countries/regions were obtained from a diversity of

183 sources. Data were gathered during 2009, except for a subset of 1,337 records from earlier
184 years. Records prior to 2009 have mainly been used to improve knowledge of the timing and
185 location of the species' breeding quarters in Africa. Each record contained at least information
186 on location and date of the observation. In many cases there was also information on relative
187 abundance, adult behaviour (e.g. reproductive or migratory behaviours) and condition of
188 butterflies (i.e. fresh, worn). We classified butterflies as migrating within the Flight Boundary
189 Layer (FBL) whenever they showed sustained and undistracted low altitude flights (i.e. up to
190 20 m from the ground, generally within 3 m) (Dingle and Drake 2007). The main heading
191 direction was classified into eight compass directions (north, northeast, east, etc.).

192 (2) *Butterfly Monitoring Scheme (BMS) records*. 30,358 weekly estimates of adult densities
193 (butterflies/100 m) were extracted from standardized transect counts carried out between
194 March and September 2009 in eight European countries/regions: Andorra, Balearic Islands,
195 Catalonia (NE Spain), Finland, Germany, Ireland, The Netherlands and the UK. Data were
196 pooled into three different latitudinal bands (Northern Europe, Central Europe and
197 Mediterranean), matching the geographical subregions defined above. For Central Europe we
198 distinguished two subsets of the data: that covering Britain and Ireland and the Dutch-German
199 data, respectively, as we had good evidence that migratory waves arriving into these areas
200 frequently had different origins and timings.

201 (3) *Radar observations of insect migrations*. Data were obtained from radars located in
202 England and Finland (for 2009) and in Mauritania (for 2003 and 2004). English data were
203 obtained from a vertical-looking entomological radar (VLR) situated in Chilbolton,
204 Hampshire (51°8'40'' N, 1°26'13'' W), which provided information on the intensity of high-
205 altitude flights (i.e. the number of butterflies actively migrating through a 1 km² 'window' of
206 the atmosphere), the altitude of flights, ground speed and direction of movements. Finnish
207 data were obtained from three weather radars situated in southern Finland: Helsinki-Kumpula

208 (60°12'16" N, 24°57'47" E), Järvenpää (60°29'4" N, 25°4'55" E), and Kerava (60°23'17" N,
209 25°6'50" E). Mauritanian data were collected by two ornithological radars, running in either a
210 fixed-beam mode or tracking mode, operated by the Swiss Ornithological Institute in 24
211 August-25 October 2003 and 15 March-10 May 2004 in central Mauritania, near the oasis of
212 Ouadâne (20° 56' N, 11°35' W), and on the Mauritanian coast, near Nouakchott (18°6'
213 N, 15°57' W).

214

215

216 **Data analysis**

217

218 *Phenology and frequency of migrations*

219 To study the seasonal shift of *V. cardui*, distribution records were divided into the five
220 geographical subregions, and then plotted as abundance through the season. To allow for a
221 direct comparison with BMS data, observation dates were transformed into BMS weeks,
222 according to the calendar of the Catalan BMS: week 1 corresponds to 1-7 March, week 2 to 8-
223 14 March, and so on.

224 Phenological curves showing different generations and waves of migration were fitted
225 using the cubic spline method, using the JMP package (SAS Institute 1989-2002). This
226 method uses a set of third-degree polynomials spliced together such that the resulting curve is
227 continuous and smooth at the splices (knot points). The estimation is done by minimizing an
228 objective function composed by a combination of the sum of squares error and a penalty for
229 curvature integrated over the curve extent. We used direct observations of migration within
230 the FBL to calculate the frequency of migratory waves in different regions and to identify
231 those days when peaks of ground-level migration occurred across Europe.

232

233 ***Migration directions***

234 Standard circular statistical methods (Fisher 1993) were used to calculate and compare the
235 mean migration directions during different periods and in different subregions. To estimate
236 the relative number of butterflies migrating within the FBL on a given date in each of the
237 geographical subregions, each observation reporting more than 100 individuals was assumed
238 to be the same as 10 observations reporting 11-100 individuals and 100 observations reporting
239 1-10 individuals.

240 For ground-based *ad-hoc* distribution records, we aggregated data by date: all migrations
241 recorded on the same day in a given subregion were used to calculate the mean track direction
242 on that date (alleviating potential pseudoreplication issues caused by individuals being
243 recorded when they were experiencing the same local conditions; Alerstam et al. 2011), and
244 the Rayleigh test of uniformity for circular data was applied. We excluded data from days
245 with <20 individuals to reduce the likelihood of individual recorder measurement error. The
246 same procedure was used for the many thousands of migrant butterflies detected by the
247 ornithological tracking radars deployed in Mauritania in 2003.

248 In the case of VLR radar data at Chilbolton, we analysed individual high-flying targets
249 attributable to *V. cardui*, rather than daily means, because they are not subject to human
250 measurement error. The number of individuals detected on most days was small (<20 per
251 day), and butterflies were flying over a long period (8 hours) and wide altitude range (150-
252 1,200 m above ground level (a.g.l.)), such that very few individuals will have been flying
253 under the same wind conditions; thus the potential for pseudoreplication to skew the results is
254 also very low in these data. We therefore carried out circular statistics on all individual radar-
255 detected butterflies to find the mean seasonal migration directions, and in addition we
256 calculated the mean daily direction for the two principal spring migration dates in the UK (25

257 and 29 May 2009), which together accounted for 43% of all spring radar-detected butterflies
258 at Chilbolton during 2009.

259

260 *Comparison of high-altitude and ground-level migrations*

261 Radar observations from the UK, Finland and Mauritania were used to seek evidence of high-
262 altitude migration and, in combination with ground-level observations, the progression of
263 migratory waves and the existence of return migrations. Migration intensities detected by the
264 UK entomological radar were used to estimate the total number of *V. cardui* that migrated in
265 seasonally-appropriate directions (i.e. towards the north in spring and towards the south in
266 summer/autumn) at high altitudes over a 300-km long stretch of the southern British mainland
267 (Chapman et al. 2010).

268 Estimates of migratory intensity from the VLR at Chilbolton were correlated with daily
269 frequency of ground-level flights in different regions using ordinary least squares regression
270 models (OLS). However, because the variance greatly exceeded the mean in all datasets, we
271 also applied generalized linear regression models (GLM), in particular quasi-Poisson and
272 negative binomial regression models (Ver Hoef and Boveng 2007). Analyses were conducted
273 with the R statistics package (R Development Core Team 2009).

274

275

276

277 **Results**

278

279

280 **Seasonal distribution of populations**

281

282 During 2009, *V. cardui* occupied an area of the Western Palaearctic-West African regions
283 ranging from latitude 10°N (Ghana) to 71°N (northern Norway), and covering a distance of
284 over 6,500 km south to north (Fig. 1). The extent of the butterfly's occurrence shifted through
285 the seasons as populations migrated northwards and then southwards.

286 From December 2008 to February 2009, moderate numbers of adults and larvae were
287 recorded in Morocco, the Canary Islands and, more rarely, in several Mediterranean Islands
288 and coastal areas in southern Spain (Fig. 2). Populations built up in Northwestern Africa in
289 March and early April, with large numbers of fresh adults migrating northward being
290 recorded in central-western Morocco (Figs 2, 3). Butterflies also started to appear all over the
291 western Mediterranean and on transects in north Spain and the Balearic Islands in a
292 succession of distinct migratory waves (Fig. 3, Supplementary material Appendix 2).
293 Although sightings also occurred further north in Central Europe at this time (Supplementary
294 material Appendix 3), they mostly consisted of single butterflies and contributed very little to
295 the general pattern of abundance in the region (Fig. 2).

296 Mating behaviour and egg-laying were observed as soon as migrants arrived in the
297 Mediterranean, while larvae were recorded in large numbers soon after, giving rise to the
298 emergence of a local adult generation from mid May to the beginning of June. The
299 appearance of this new generation coincided with the second critical period of the expansion
300 in Europe (Fig. 2, Supplementary material Appendix 3). The eastern part of Central Europe
301 was colonized in a continuous succession of migratory waves between 10-25 May, while the
302 western part had two distinct peaks of immigration, the first on 24-25 May and the second
303 between 28 May and 1 June (Fig. 3). Butterflies from the first peak probably belonged to the
304 same migrants colonising eastern Central Europe from the southern Mediterranean coast, part
305 of which eventually progressed in a north-westward direction. Migrants from the second peak
306 originated in the Iberian Peninsula and further south (e.g. northern Morocco and north-

307 western Algeria), as deduced from a mixture of worn and fresh butterflies in northward flights
308 in coastal areas of Portugal, southern Spain and the Balearic Islands. In Northern Europe,
309 migrants were not recorded in abundance until the third week of May, and secondary peaks of
310 migration occurred during the second half of June (Fig. 3).

311 Massive breeding in Central and Northern Europe started immediately after the arrival of
312 migrants (Fig. 2). In Central Europe, the local generation emerged from mid July to mid
313 August. In accordance with the timing of earlier migrations, local emergence occurred
314 somewhat earlier in the eastern part than in the western part. A further delay was noted in
315 Northern Europe, where the local generation peaked by mid August (Fig. 2, Supplementary
316 material Appendix 2). Coupled with radar observations of southward flights (see below), the
317 rapid disappearance of European summer-emerging generations indicates the start of a return
318 migration to lower latitudes. Part of the migrant population stopped to breed in Central
319 Europe and, to a lesser extent, the Mediterranean in the second half of the summer, eventually
320 producing new generations in late September and October (Fig. 2). Moreover, coinciding with
321 the disappearance of this second local Central European generation by the end of October, a
322 small additional generation started to develop in the Mediterranean (e.g. in southern Spain).
323 Although breeding was recorded there in November, fresh adults in winter were exceedingly
324 rare, suggesting very low reproductive success (Fig. 2).

325 Data from 2009 and previous years show an increase in the number of records in the
326 African continent in August and subsequent months, coincident with the disappearance of
327 European populations (Fig. 2). The few systematic counts that have been carried out in the
328 Sahel and further south in Western Africa confirm the sudden arrival of *V. cardui* from the
329 end of August to early October (e.g. data from Mauritania, The Gambia and Sierra Leone).
330 However, this population is apparently soon gone again, given its complete absence from
331 extensive areas in the Sahel from December to March (e.g. comprehensive surveys in Senegal

332 and Mali in 2009 and 2010). Immigrations into Northwestern Africa occurs mainly in October
333 and early November (more rarely in late September), with the species being recorded at
334 relatively low densities all through the winter months (Fig. 2).

335

336

337 **Frequency and direction of migratory flights near the ground**

338

339 We compiled a total of 3,174 observations of ground-level migratory flights, of which 2,894
340 were from Europe in 2009 (Supplementary material Appendix 1). Notably, ground-level
341 spring migration was observed much more commonly than summer/autumn migration in
342 Europe (Fig. 4). Migrations showed a very clear seasonal pattern for direction, with spring
343 flights being essentially northward and summer/autumn flights being southward (Table 1,
344 Supplementary material Appendix 4). The change in the direction of migrations occurred by
345 mid July: the few flights recorded in the Mediterranean in the first fortnight of July still
346 showed northward direction, while those recorded in Central and Northern Europe during the
347 second fortnight of July were predominantly southward. Overall mean directions in spring
348 were very similar across subregions, although in the western part of Central Europe there was
349 a distinct westward tendency which contrasted with a slight eastward tendency in the eastern
350 part (Table 1). The two distributions were found to be significantly different (mean directions
351 of 329° and 18° respectively; test for a common mean direction: $Y_r = 24.5$, $p < 0.0001$).

352 Data from ground-level migratory flights in Africa were too scarce to draw any firm
353 conclusion. In Northwestern Africa, northward flights precipitating the colonization of the
354 Mediterranean region clearly predominate in the spring but the situation becomes more
355 complex in the autumn, when southward and northward flights were equally recorded, which
356 may genuinely represent immigration from both the south (Sahel) and north (Central Europe

357 and Mediterranean). In Western Africa there were a few reports of southward and westward
358 flights from August to November, while a single massive northward flight of several
359 thousands of butterflies was observed in Mali in early November 2009.

360

361

362 **Frequency and direction of high-altitude migratory flights**

363

364 High-altitude migration was recorded by European radars in 2009. At Chilbolton, the VLR
365 detected large numbers of *V. cardui*-like targets moving mostly in a northward direction
366 between ~150-1,200 m a.g.l. from April to June, with two major influxes occurring on 25 and
367 29 May (Fig. 5). Extrapolating from the radar sensed volume, it was estimated that ~2.3
368 million and ~1.7 million high-flying butterflies would have crossed a 300-km stretch of the
369 English coast on those two days respectively (mean migration direction on 25 May: 76°, n =
370 64 individuals, $r = 0.70$, $p < 0.001$; mean migration direction on 29 May: 0°, n = 37
371 individuals, $r = 0.77$, $p < 0.001$, Supplementary material Appendix 4). During the whole of
372 May and June, we estimate that ~11.1 million high-flying *V. cardui* passed through southern
373 UK; of these, 65% (~7.2 million) moved generally towards the north, i.e. between 270° and
374 90°, and the overall mean direction of all individuals was towards the north-east (mean
375 migration direction: 52°, n = 202 individuals, $r = 0.33$, $p < 0.001$). The mean ground speed of
376 the windborne high-flying *V. cardui* in the spring migrations was 13.3 m/s (~50 km/h).

377 Migratory activity remained rather low through June and July, but increased again from
378 the beginning of August to mid October, when it peaked on certain days, e.g. 7 August with
379 ~1.2 million, 5 September with ~1.0 million, and 19 September with ~1.6 million high-flying
380 butterflies passing southward (Fig. 5). Over the whole late-summer/autumn period (August–
381 October), we estimate that ~25.9 million *V. cardui* engaged in high-altitude flights, but of

382 these only 55% (~14.1 million) were transported in a generally southwards direction, i.e.
383 between 90° and 270°. However, the overall mean direction of all butterflies was in a south-
384 westward direction (mean migration direction: 236°, n = 446 individuals, r = 0.16, p < 0.001)
385 and there was a distinct absence of flights close ($\pm 20^\circ$) to north (Supplementary material
386 Appendix 4). The mean migration direction was thus almost 180° opposite to the mean spring
387 direction, albeit with a greater dispersion of individual tracks. The mean migration direction
388 (towards the south-west) contrasts with the patterns of high-altitude winds (measured at 300
389 m) during the autumn migration period, which had a significant mean direction blowing from
390 the WSW towards the ENE (wind from: 251°, n = 63 days, r = 0.22, p = 0.048), and a
391 comparative shortage of northerly winds favourable for autumn return migration. Thus there
392 is some evidence that butterflies preferentially migrated on winds with a northerly component
393 (resulting in a significant tendency for southward displacement), even though many of the
394 individuals were displaced in unfavourable directions (towards the north-west or north-east)
395 due to the shortage of suitable tailwinds. The mean displacement speed during
396 summer/autumn migrations was 12.7 m/s (~45 km/h).

397 *V. cardui*-like targets migrated at hundreds of metres above the ground in both spring and
398 summer/autumn, but declined towards the greatest heights (at ~1,200 m, where very few
399 butterfly-type targets were recorded) (Supplementary material Appendix 5). In spring, the
400 highest densities were recorded in the lowest elevation band, implying that many additional
401 migrants are likely to be closer to the ground (when many were observed by ground-based
402 recorders). In autumn, the peak density was above 300 m, when fewer individuals were
403 observed by ground-based observers.

404 Southward migration across the Gulf of Finland was also recorded by radars at Kerava
405 and Kumpula between 3-6 August 2009 (Fig. 6a-b). On 5 August, the Kumpula radar vertical
406 sections over the land and over the sea showed that these insects were flying mostly in the

407 layer 500-700 m a.g.l. During the morning hours of 6 August, however, the wind direction
408 changed from northerly to south-easterly and the insects drifted towards west and north-west
409 to end up back on the Finnish coast and several nearby southern islands (Fig. 6c-d).
410 Thousands of *V. cardui* were then recorded in this area, pointing towards a massive southward
411 windborne flight that was interrupted by a sudden change in the formerly favourable weather
412 conditions for migration. High-altitude southward migrations of large-sized insects across the
413 Gulf of Finland were recorded again by Finnish radars throughout August (see details in
414 www.helsinki.fi/~mleskine/vaellus/Vcar2009.html), suggesting the existence of regular return
415 flights of *V. cardui* out of sight from ground-level observers.

416 High-altitude migration of *V. cardui* was also recorded by the Swiss Ornithological
417 Institute's radar group in Mauritania between 25 August and 25 October 2003: large numbers
418 of high-flying, radar-detected insects were present at the radar site on the coast moving
419 generally towards the south on northerly winds, as would be expected at that time of year
420 (mean migration direction: 188°, n = 20 days, r = 0.33, p = 0.107; wind from: 35°, n = 1,250, r
421 = 0.48, p < 0.001). Although other insects were also present, *V. cardui* was the most abundant
422 insect at ground-level, as indicated by periodic transect counts (Swiss Ornithological Institute
423 unpubl. data). A similar abundance of ground-level *V. cardui* was recorded 500 km inland, at
424 Ouadâne, although there the high-flying insects were displaced westward (mean migration
425 direction: 283°, n = 49 days, r = 0.61, p < 0.001), on easterly winds (wind from: 85°, n =
426 2,680, r = 0.43, p < 0.001). On 18 October it was possible to demonstrate unequivocally that
427 most insects detected by the radar from ground level up to 2,000 m were *V. cardui*: its
428 presence at high altitude was confirmed by using telescopes trained on the radar 'sensed-
429 volume'. A ground speed of 25.1 ± 3.8 km/h (mean \pm sd) was estimated for a subset of 7
430 individuals flying at 241 ± 62 m, but speeds at higher altitude were not recorded.

431

432

433 **Relationship between ground-level migrations and vertical looking radar data**

434

435 A comparison between the temporal distribution of daily high-altitude and ground-level
436 migratory flights in 2009 is provided in Table 2. In the spring, high-altitude flights in south
437 England were positively correlated with ground-level flights across all western Europe ($p <$
438 0.001 , 1,398 flights). The correlation was significant for the Central Europe subregion ($p <$
439 0.001 , 1,213 flights), but not for the Mediterranean (148 flights) and Northern Europe (37
440 flights) subregions. High-altitude flights were also correlated with ground-level flights across
441 all of eastern Europe ($p < 0.001$, 1,020 flights), as well as with particular subregions
442 (Mediterranean: 46 flights; Central Europe: 910 flights; Northern Europe: 64 flights). The
443 correlations were stronger if it was assumed that the peak of windborne flight would occur
444 one day earlier in the Mediterranean than in southern England, which in turn would be one
445 day behind the flight peak in Northern Europe (Table 2). In the summer/autumn, high altitude
446 flights were only correlated with ground-level flights across all eastern Europe ($p < 0.01$, 557
447 flights) and the eastern Central Europe subregion ($p < 0.01$, 534 flights), probably because of
448 the very low number of records of ground-level migrations in this part of the season (Fig. 4).

449 These results strongly suggest a high synchrony in the spring migrations across Europe
450 (Fig. 3), mediated by windborne migration occurring well above the species' FBL. The lack
451 of correlation between high-altitude flights in south England and western Mediterranean
452 ground-level flights is explained by the high number of migrations that were recorded in the
453 latter subregion in April, which did not progress further north (Supplementary material
454 Appendix 3). On the other hand, the lack of a significant correlation with western Northern
455 Europe is probably the consequence of the very low number of records.

456

457

458

459 **Discussion**

460

461 The results of this study show a succession of generations of *V. cardui* populations, exhibiting
462 a northwards spread out of Africa into a warming European continent, as spring develops,
463 followed by a southwards reversal in late summer and autumn. As with some migrant moths
464 (Chapman et al. 2008a,b, 2010, Alerstam et al. 2011), the reversal of direction appears to
465 involve complex behaviour, including both the adoption of seasonally-favourable headings
466 (see also Nesbit et al. 2009) and the selection of favourable tailwinds when available. Exodus
467 from each region takes place before the environment becomes directly inhospitable, in
468 anticipation of the arrival of conditions unsuitable for continued breeding in the location of
469 adult emergence. Adverse seasonal conditions not only include extreme temperatures and the
470 decreasing availability of ephemeral resources for larvae and adults, but also increasing levels
471 of natural enemies such as specialist parasitoids (Stefanescu et al. 2012).

472 Although further details of the African legs of the migration are still needed, the basic
473 pattern appears to be that of the successive displacement and reproduction of a population that
474 in years of high abundance may attain a size of thousands of millions of individuals, through
475 ca. six generations (see Supplementary material Appendix 6 for a full description of the
476 migratory model). The extremities of the migration go from the Sahel region of Western
477 Africa (at least for a large portion of the population) through North Africa, the Mediterranean,
478 Central and Northern Europe, before retreating back to Africa in one or two steps. In addition,
479 the predominant population movement described here meets additional populations in Eastern
480 Europe and into Asia, and other populations apparently circulate within central and southern
481 Africa (e.g. Williams 1930, Larsen 1976, John 2001). The extent to which there is gene flow

482 between these different populations is unknown, although the low levels of genetic
483 substructuring across continents (Wahlberg and Rubinoff 2011) suggests that it might be high.
484 A strong gene flow leading to genetic homogeneity of populations has also been found in
485 other migratory insects, and seems to be a common pattern in highly mobile species (Peterson
486 and Denno 1998).

487 Although the precise mechanisms are not known, it is likely that a combination of
488 temperature and photoperiod and, perhaps, hostplant cues (e.g. related to senescence)
489 experienced by developing larvae trigger directional movement in northern or southern
490 directions in emerged butterflies. All these factors induce diapause in *D. plexippus*
491 undergoing long-distance migration in autumn (Goehring and Oberhauser 2002) and have
492 been shown to have similar effects in *V. cardui* (Herman and Dallmann 1981). Current
493 research aimed at identifying which genes are involved in migration and which ones are
494 involved in diapause of *D. plexippus* (Zhu et al. 2008, 2009) will greatly contribute to the
495 understanding of the environmental stimuli triggering migration not only in this species but
496 probably also in *V. cardui*.

497 We believe that a key aspect for the whole migratory system to be maintained is the
498 ability of *V. cardui* to use favourable high altitude winds to move rapidly in appropriate
499 seasonal directions (see also Stefanescu et al. 2007). This would seem to be necessary
500 particularly in the autumn given the distances that must be covered during this part of the
501 annual cycle. Indeed, our results strongly suggest that butterflies leaving the European
502 continent on their return flight travel far above the ground and mostly remain unnoticed by
503 observers (Fig. 4). The radar data from southern England in autumn 2009 indicate that
504 migrating *V. cardui* were not very successful at selecting suitable winds, given that only 55%
505 of the radar-detected high-flying butterflies were displaced in a southwards direction.
506 However, analysis of wind directions during this period indicated that there was a

507 preponderance of winds blowing from the south-west and WSW, and relatively few days
508 when winds blew from the north, and so presumably the shortage of suitable transport
509 opportunities resulted in butterflies being forced to move on less than ideal winds. Radar
510 observations from previous *V. cardui* invasions of the UK have shown much clearer
511 southward return migrations (Chapman et al. 2010), and the Finnish radar data in the present
512 study also demonstrate the ability of high-flying *V. cardui* to preferentially select suitable
513 winds. We thus conclude that transport on fast-moving high-altitude winds is an essential part
514 of the annual cycle, particularly during the autumn. Although windborne migration above the
515 FBL has been widely described in insects showing long-range seasonal movements,
516 particularly pest species (Chapman et al. 2011a,b), its presence had been questioned in some
517 large day-flying insects such as butterflies and dragonflies (e.g. Baker 1978, Walker 1980,
518 Walker and Riordan 1981). However, strong similarities in the strategies used by *V. cardui*
519 and other migrant Lepidoptera, such as noctuids and hawk-moths (Chapman et al. 2010),
520 raises the possibility that high-altitude windborne flights may be, in fact, much more
521 widespread among migrant butterflies than has been assumed. The scarcity of records could
522 be simply due to the difficulty of collecting data from the ground (see also Gibo 1981,
523 Mikkola 2003). In this respect, radar technology is a useful complementary tool, as has been
524 shown in our study.

525 However important high-altitude migration is, ground-level observations of movements
526 along fixed compass bearings are very commonly reported in the spring, indicating that
527 migration at ground level is still a major feature of *V. cardui*. The high synchrony that we
528 found between high-altitude and ground-level migration shows that the two are linked.
529 Whether higher and lower altitude flights represent distinct behaviours or phases of migration,
530 as first suggested by Mikkola (1986), requires further work. This might be affected by both

531 the prevailing weather conditions and individual physiological and reproductive
532 characteristics (cf. Johnson 1969, McNeil et al. 1995).

533 The predominant pattern of movement and responses is somewhat "noisy" in that there
534 may be stragglers left behind when the majority of the population emigrates, and some
535 portions of the population are not found in the locations where the majority of the population
536 is present, at a given time (Supplementary material Appendix 6). Further work is needed to
537 assess whether the noise and stragglers represent individuals obeying different genetically-
538 based behavioural rules (e.g. Hill and Gatehouse 1993), or whether they are simply
539 individuals that, after experiencing particular conditions (e.g. late emerging individuals that
540 experienced unfavourable winds), failed to migrate with the majority. It is also interesting to
541 speculate whether this noise is in fact important to the persistence of the migratory system, in
542 the event that unusual winds in some years deposit a high proportion of the population in
543 unfavourable locations (e.g. in the middle of the Atlantic ocean: Williams 1958, Bowden and
544 Johnson 1976). Indeed, migrant insects (apart from *D. plexippus*) do not head for very
545 specific destination areas, so the risks associated with windborne displacement in terms of
546 direction of travel will be offset by the benefits of very rapid transport (Alerstam et al. 2011)
547 and by r-type reproduction rates (Loxdale and Lushai 1999).

548 In summary, we have documented a continuously-breeding migration path, in which a
549 species undertakes a round-trip migration of up to 15,000 km (up to 60 degrees of latitude and
550 back) from tropical Africa to northern Europe. This is close to double the latitudinal migration
551 distance of the famed monarch butterfly (Solensky 2004), and potentially exceeds the distance
552 achieved by the globe-skimmer dragonfly *Pantala flavescens* (Anderson 2009). The capacity
553 of *V. cardui* to exploit winds and maintain migratory direction enables it to maintain this
554 exceptionally long inter-generation migration route. We believe that our findings provide a
555 useful framework for the study of insect migration in the temperate regions worldwide,

556 especially for those species sharing common life-history traits with *V. cardui* (e.g. continuous
557 breeding, strong polyphagy and habitat generalism) and predictable patterns of seasonal
558 movements. Because these species include some of the most serious agricultural pests and
559 may act as vectors of infections and diseases (Cannon 1998, Reynolds et al. 2006),
560 understanding their migratory strategies is undoubtedly an essential issue.

561

562

563

564 *Acknowledgements* – We thank the many thousands of butterfly recorders and members of the
565 public who contributed the sightings of *V. cardui* that we have analysed in this study. A
566 special mention is due to Mauri Leivo and Jaakko Kullberg for their painted lady observations
567 and a valuable newspaper article on the southward migration of the painted lady along the
568 south coast of Finland, and to Gerard Troost and Trektellen for allowing us to use their
569 counting records. Wilfred Alblas, Jon Baker, Torben Larsen, Theunis Piersma, and Martin
570 Wiemers kindly provided useful information of the painted lady in Western Africa and the
571 Canary Islands. Jason Lim provided technical support for the Rothamsted radars. CS, DBR,
572 EK, MM, and JS were partly supported by the project CLIMIT (Climate Change Impacts on
573 Insects and their Mitigation; Settele and Kühn 2009) funded by DLR-BMBF (Germany),
574 NERC and DEFRA (UK), ANR (France), Formas and Swedish EPA (Sweden), through the
575 FP6 BiodivERsA Eranet. CS was also supported by grant CSD2008-00040 (Consolider
576 Ingenio MONTES). The UKBMS is operated by the Centre for Ecology & Hydrology and
577 Butterfly Conservation and funded by a consortium of government agencies. The CBMS is
578 funded by the Department de Territori i Sostenibilitat de la Generalitat de Catalunya.
579 Rothamsted Research is a national institute of bioscience strategically funded by the UK
580 Biotechnology and Biological Sciences Research Council (BBSRC).

581
582
583
584
585
586
587
588
589
590
591
592
593
594
595
596
597
598
599
600
601
602
603
604
605

References

- Ackery, P. R. 1988. Hostplants and classification: a review of nymphalid butterflies. – Biol. J. Linn. Soc. 33: 95-203.
- Alerstam, T., J. et al. 2011. Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. – Proc. R. Soc. B 278: 3074-3080.
- Anderson, R.C. 2009. Do dragonflies migrate across the western Indian Ocean? – J. Trop. Ecol. 25: 347-358.
- Asher, J. et al. 2001. The millennium atlas of butterflies in Britain and Ireland. – Oxford Univ. Press.
- Baker, R. R. 1978. The evolutionary ecology of animal migration. – Holmes and Meier.
- Boorman, J. and Taylor, W. P. 1977. The breeding of the Painted Lady butterfly, *Vanessa cardui*, in Nigeria. – The Nigerian Field 42: 84-87.
- Bowden, J. and Johnson, C. G. 1976. Migrating and other terrestrial insects at sea. – In: Cheng, L. (ed.), Marine insects. North Holland, pp. 97-117.

- 606 Cannon, R. J. C. 1998. The implications of predicted climate change for insect pests in the
607 UK, with emphasis of non indigenous species. – *Global Change Biol.* 4: 785–796.
608
- 609 Chapman, J. W. et al. 2011a. Recent insights from radar studies of insect flight. – *Ann. Rev.*
610 *Entomol.* 56: 337-356.
611
- 612 Chapman, J. W. et al. 2011b. Animal orientation strategies for movement in flows. – *Curr.*
613 *Biol.* 21: R861-R870.
614
- 615 Chapman, J. W. et al. 2010. Flight orientation behaviors promote optimal migration
616 trajectories in high-flying insects. – *Science* 327: 682-685.
617
- 618 Chapman, J. W. et al. 2008a. Wind selection and drift compensation optimize migratory
619 pathways in a high-flying moth. – *Curr. Biol.* 18: 514-518.
620
- 621 Chapman, J. W. et al. 2008b. A seasonal switch in compass orientation in a high-flying
622 migrant moth. – *Curr. Biol.* 18: R908-R909.
623
- 624 Dingle, H. 1996. *Migration: the biology of life on the move.* – Oxford Univ. Press.
625
- 626 Dingle, H. and Drake, V. A. 2007. What is migration? – *BioScience* 57: 113-121.
627
- 628 Drake, V. A. and Gatehouse, A.G. 1995. *Insect migration: tracking resources through space*
629 *and time.* – Cambridge Univ. Press.
630

- 631 Fisher, N. I. 1993. Statistical analysis of circular data. – Cambridge Univ. Press.
632
- 633 Gibo, D.L. 1981. Altitudes attained by migrating monarch butterflies, *Danaus plexippus*
634 (Lepidoptera: Danaidae), as reported by glider pilots. – Can. J. Zool. 59: 571-572.
635
- 636 Goehring, L. and Oberhauser, K. S. 2002. Effects of photoperiod, temperature, and host plant
637 age on induction of reproductive diapause and development time in *Danaus plexippus*. – Ecol.
638 Entomol. 27: 674-685.
639
- 640 Hammad, S. M. and Raafat, A. M. 1972. The biology of the painted lady butterfly, *Vanessa*
641 (*Pyrameis*) *cardui* L. (Lepidoptera: Nymphalidae). – Bull. Soc. Entomol. Égypte 56: 15-20.
642
- 643 Herman, W. S. and Dallmann, S. H. 1981. Endocrine biology of the Painted Lady butterfly
644 *Vanessa cardui*. – J. Insect Physiol. 27: 163-168.
645
- 646 Hill, J. K. and Gatehouse, A.G. 1993. Phenotypic plasticity and geographic variation in the
647 pre-reproductive period of *Autographa gamma* (Lepidoptera: Noctuidae) and its implications
648 for migration in this species. – Ecol. Entomol. 18: 39-46.
649
- 650 Holland, R. A. et al. 2006. How and why do insects migrate? – Science 313: 794-796.
651
- 652 John, E. 2001. Migration of *Vanessa cardui* (L.) (Lep.: Nymphalidae) through Cyprus, March
653 2001. – Entomol. Rec. J. Var. 113: 269-281.
654
- 655 Johnson, C. G. 1969. Migration and dispersal of insects by flight. – Methuen.

- 656
- 657 Larsen, T. 1976. The importance of migration to the butterfly faunas of Lebanon, East Jordan,
658 and Egypt (Lepidoptera, Rhopalocera). – Notul. Entomol. 56: 73-83.
- 659
- 660 Leskinen, M. et al. 2011. Pest insect immigration warning by an atmospheric dispersion
661 model, weather radars and traps. J. Appl. Entomol. 135: 55-67.
- 662
- 663 Loxdale, H. D. and Lushai, G. 1999. Slaves of the environment: the movement of herbivorous
664 insects in relation to their ecology and genotype. – Phil. Trans. R. Soc. Lond. B 354: 1479-
665 1495.
- 666
- 667 McNeil, J. N. et al. 1995. Physiological integration of migration in Lepidoptera. – In: Drake,
668 V. A. and Gatehouse, A.G. (eds), Insect migration: tracking resources through space and time.
669 Cambridge Univ. Press, pp. 279-302.
- 670
- 671 Mikkola, K. 1986. Direction of insect migrations in relation to the wind. – In:
672 Danthanarayana, W. (ed.), Insect flight: dispersal and migration. Springer-Verlag, pp. 152-
673 171.
- 674
- 675 Mikkola, K. 2003. Red Admirals *Vanessa atalanta* (Lepidoptera: Nymphalidae) select
676 northern winds on southward migration. – Entomol. Fenn. 14: 15-24.
- 677
- 678 Nesbit, R. L. et al. 2009. Seasonally-adaptive migratory headings mediated by a sun compass
679 in the painted lady butterfly (*Vanessa cardui*). – Anim. Behav. 78: 1119-1125.
- 680

- 681 Newton, I. 2008. The migration ecology of birds. – Elsevier Ltd.
682
- 683 Pedgley, D. E. 1981 (ed.). Desert Locust forecasting manual. Volumes 1 and 2. – Centre for
684 Overseas Pest Research.
685
- 686 Pedgley, D. E. et al. 1995. Long-range insect migration in relation to climate and weather:
687 Africa and Europe. – In: Drake, V. A. and Gatehouse, A.G. (eds), Insect migration: tracking
688 resources through space and time. Cambridge Univ. Press, pp. 3-29.
689
- 690 Peterson, M. A. and Denno, R. F. 1998. The influence of dispersal and diet breadth on
691 patterns of genetic isolation by distance in phytophagous insects. – Am. Nat. 152: 428-446.
692
- 693 Pollard, E. et al. 1998. Migration of the painted lady butterfly *Cynthia cardui* in Europe:
694 evidence from monitoring. – Div. Distrib. 4: 243-253.
695
- 696 R Development Core Team. 2009. R: A language and environment for statistical computing
697 (ed. Computing RFFS). Vienna, Austria. ISBN 3-900051-07-0. Available at: [www.R-](http://www.R-project.org)
698 [project.org](http://www.R-project.org).
699
- 700 Reynolds, D. R. et al. 2006. The migration of insect vectors of plant and animal viruses. –
701 Adv. Virus Res. 67: 453-517.
702
- 703 SAS Institute. 1989-2002. JMP. Version 70. – SAS Institute.
704
- 705 Settele, J. and Kühn, E. 2009. Insect conservation. – Science 325: 41–42.

- 706
- 707 Shields, O. 1992. World distribution of the *Vanessa cardui* group (Nymphalidae). – J. Lepid.
708 Soc. 46: 235-238.
- 709
- 710 Solensky, M. J. 2004. Overview of Monarch migration. – In: Oberhauser, K. S. and Solensky,
711 M. J. (eds), The Monarch butterfly. Biology and conservation. Cornell Univ. Press, pp. 79-83.
- 712
- 713 Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? – J. Anim. Ecol. 46:
714 337-365.
- 715
- 716 Srygley, R. B. and Oliveira, E. G. 2001. Orientation mechanisms and migration strategies
717 within the flight boundary layer. – In: Woiwod, I. P. et al. (eds), Insect movement:
718 Mechanisms and consequences. CABI, pp. 183-206.
- 719
- 720 Stefanescu, C. 1997. Migration patterns and feeding resources of the Painted Lady butterfly,
721 *Cynthia cardui* (L.) (Lepidoptera, Nymphalidae) in the northeast of the Iberian peninsula. –
722 Misc. Zool. 20: 31-48.
- 723
- 724 Stefanescu, C. et al. 2007. Migration of the painted lady butterfly, *Vanessa cardui*, to north-
725 eastern Spain is aided by African wind currents. – J. Anim. Ecol. 76: 888-898.
- 726
- 727 Stefanescu, C. et al. 2011. Moroccan source areas of the painted lady butterfly *Vanessa cardui*
728 (Nymphalidae: Nymphalinae) migrating into Europe in spring. – J. Lepid. Soc. 65: 15-26.
- 729

- 730 Stefanescu, C. et al. 2012. Parasitism and migration in southern Palaearctic populations of the
731 painted lady butterfly, *Vanessa cardui* (Lepidoptera: Nymphalidae). – Eur. J. Entomol. 109:
732 85-94.
- 733
- 734 Tauber, M. J. et al. 1986. Seasonal adaptations of insects. – Oxford Univ. Press.
- 735
- 736 Van Swaay, C. A. M. et al. 2008. Butterfly monitoring in Europe: methods, applications and
737 perspectives. – Biodiv. Conserv. 17: 3455-3469.
- 738
- 739 Ver Hoef, J. M. and Boveng, P. L. 2007. Quasi-Poisson vs. negative binomial regression: how
740 should we model overdispersed count data? – Ecology 88: 2766-2772.
- 741
- 742 Wahlberg, N. and Rubinoff, D. 2011. Vagility across *Vanessa* (Lepidoptera: Nymphalidae):
743 mobility in butterfly species does not inhibit the formation and persistence of isolated taxa. –
744 Syst. Entomol. 36:362-370.
- 745
- 746 Walker, T. J. 1980. Migrating Lepidoptera: are butterflies better than moths? – Fla. Entomol.
747 63: 79-98.
- 748
- 749 Walker, T. J. and Riordan, A. J. 1981. Butterfly migration: are synoptic-scale winds systems
750 important? – Ecol. Entomol. 6: 433-440.
- 751
- 752 Williams, C. B. 1930. The migration of butterflies. – Oliver & Boyd.
- 753
- 754 Williams, C. B. 1958. Insect migration. – Collins.

755

756 Zhu, H. et al. 2008. Chasing migration genes: a brain expressed sequence tag resource for
757 summer and migratory monarch butterflies (*Danaus plexippus*). – PLoS ONE, 3(1): e1345.

758

759 Zhu, H. et al. 2009. Defining behavioral and molecular differences between summer and
760 migratory monarch butterflies. – BMC Biology 7: 14.

761

762

763 Table 1. Directional data for spring (March-June) and summer/autumn (July-November)
 764 ground-level migrations in different subregions of Europe and Africa in 2009 (see Material
 765 and methods and Fig. 1, for definition of subregions). Overall mean directions have been
 766 calculated from daily means (N) using a second-order Rayleigh test for non-uniformity in a
 767 circular distribution. ‘p’ values indicate the probability of a uniform distribution. The mean
 768 vector length ‘r’ is a measure of the clustering of the angular distribution, ranging from 0 to 1.
 769 The mean displacement direction is not available for all combinations of subregions × season
 770 because of insufficient number of daily observations of migrations (especially in the
 771 summer/autumn period and in both of the African subregions, which have been pooled into a
 772 single region to increase sample size).

773

774

775

Subregion	Direction (°)	r	N	Rayleigh P-value
Spring				
Africa	10.8	0.797	37	<0.001
western Mediterranean	0.2	0.922	26	<0.001
eastern Mediterranean	2.3	0.986	20	<0.001
Mediterranean	1.2	0.95	46	<0.001
western Central Europe	328.7	0.874	15	<0.001
eastern Central Europe	18.2	0.811	31	<0.001
Central Europe	1.7	0.764	46	<0.001
Northern Europe	13.6	0.918	8	<0.001
Summer/Fall				
Africa	---	0.364	14	0.157
Mediterranean	---	0.223	8	0.686
eastern Central Europe	181.1	0.855	43	<0.001
Central Europe	180.4	0.805	47	<0.001

776

777

778

779 Table 2. Correlations between daily migration flux at high-altitude (150-1,188 m a.g.l.) in Chilbolton, southern England (as revealed by the
 780 vertical looking radar), and the daily frequency of ground-level migratory flights in different subregions of Europe in spring (April-June) and
 781 summer/fall (July-November). OLS: ordinary least squares regression models; GLM: quasi-Poisson regression models. Med: Mediterranean,
 782 CEur: Central Europe, NEur: Northern Europe, All: all subregions pooled. Correlations were calculated with lags of one day for LagMed and
 783 LagNEur, under the hypothesis that windborne migrants passing over the Mediterranean would arrive one day later in southern England, and
 784 migrants passing over southern England would arrive one day later in Northern Europe. Significance levels: ** $p < 0.01$, *** $p < 0.001$.

785

786

787

			Western Europe						Eastern Europe					
			Med	LagMed	CEur	NEur	LagNEur	All	Med	LagMed	CEur	NEur	LagNEur	All
Spring	OLS	R ²	0	0	34.45***	0	0	33.64***	0	15.41***	8.7**	11.57***	25.81***	11.63***
	GLM	% Deviance	0	0	33.59***	0	0	32.55***	0	20.59***	13.51**	15.10***	29.12***	17.98***
Fall	OLS	R ²	0	0	0	0	0	0	0	0	5.68**	0	0	6.03**
	GLM	% Deviance	0	0	0	0	0	0	0	0	6.91**	0	0	7.45**

788

789

790

791 Fig. 1. Geographical extent of the *ad-hoc* distribution records used for the analysis of
792 migrations of *Vanessa cardui* in the western Palaearctic-West African regions (see
793 Supplementary material Appendix 1 for details on country records). For analytical
794 purposes, the area has been divided into five different subregions: Western Africa,
795 Northwestern Africa, Mediterranean, Central Europe, and Northern Europe. Another
796 30,000 records (not shown) from BMS networks in European countries were also used
797 to better define phenological patterns between March-September 2009. Additional
798 information was provided by radar sites in Mauritania, southern England and southern
799 Finland.

800

801

802 Fig. 2. Phenology of the *ad-hoc* distribution records in the five geographical subregions
803 considered in the analysis. Red line shows adult records; blue line shows records of
804 adults showing reproductive behaviour (courtship by males and egg-laying females);
805 green line shows records of immatures (i.e. larvae and pupae).

806

807

808 Fig. 3. Phenology of records of ground-level migrations in Northern Europe (a-b),
809 Central Europe (c-d), Mediterranean (e-f) and Northwestern Africa (g-h) in 2009. Each
810 subregion has been further divided into a western and an eastern subregion (see text for
811 definitions) to reveal differences in the timing of migratory events.

812

813

814 Fig. 4. Temporal distribution of 2,894 records of ground-level migrations in Europe in
815 2009, classified according to three categories of relative abundance: low abundance (1-
816 10 individuals recorded), medium abundance (11-100 individuals recorded), high
817 abundance (more than 100 individuals recorded).

818

819

820 Fig. 5. Migration intensity for *Vanessa cardui*-like targets detected by the Chilbolton
821 (England) vertical looking radar in 2009 between 150-1,188 m a.g.l. Intensity is
822 expressed as the number of butterflies estimated daily across a 300 km line running
823 west-east (i.e. perpendicular to the migration direction). Spring data (1 April - 30 June)
824 is only for those radar-detected butterflies that were moving in a northward direction
825 (i.e. seasonal migrants that were moving between 270 degrees through to 90 degrees).
826 Summer data (July) is for all butterflies (irrespective of movement direction). Autumn
827 data (1 Aug - 30 Nov) is only for southward moving butterflies (from 90 degrees
828 through to 270 degrees).

829

830

831 Fig. 6. Southern migration of *Vanessa cardui* recorded in the Gulf of Finland on 5 and 6
832 August 2009. a-d, Kerava radar images. Kerava is about 25 km north of the coastline
833 (NNE from the Helsinki city centre), and the map overlay shows the coastline of the
834 Gulf of Finland that lies between Finland (north) and Estonia (south). (a) 5 August,
835 05:00 UTC. Insects get airborne at the Finnish coastline, but not farther inland. The
836 strongest reflectivity corresponds to a few rain showers over the Estonian coast and to
837 birds near the radar in Finland. (b) 09:03 UTC. Insects flying over the land area cause
838 most of the widespread echoes. Long-range migration continues over the sea, especially

839 in the SW and SE, where many insects are seen flying over the Gulf of Finland. Rain
840 showers have developed over Estonia, south of the coastline, and over Finland (125 km
841 to the WNW, and 110-120 km to the NNE). Southward migration of *V. cardui* up in the
842 air was recorded by this time on the outer islands 70-80 km ESE of the radar (M. Leivo
843 pers. obs.). (c) 6 August, 09:45 UTC. Strong and wide spread echoes are caused by
844 insects, especially over the land areas both in Finland and in Estonia. Many insects are
845 flying over the sea towards SW, especially in the SW sector. (d) 12:46 UTC. Only a few
846 insects are now flying over the sea, after a sea-breeze has started to blow from SE in the
847 coastal region. Insects flying below about 500 m are carried back to the Finnish
848 coastline by the sea-breeze. Thousands of *V. cardui* were observed coming from the
849 south while flying north-westward on tailwinds, and landing on the island of Öro, about
850 150 km WSW from the radar (J. Kullberg pers. obs.).
851

Fig. 1.

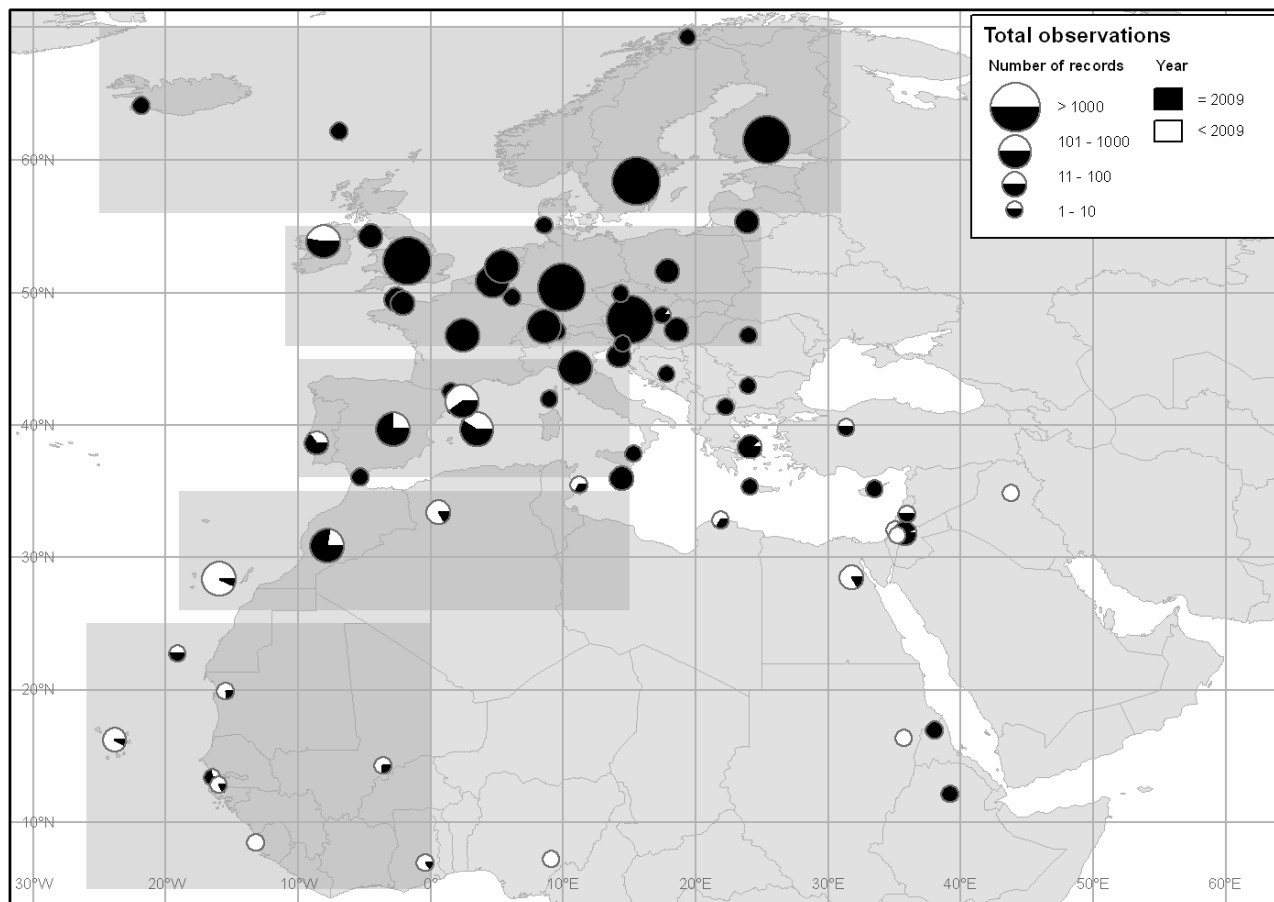


Fig. 2.

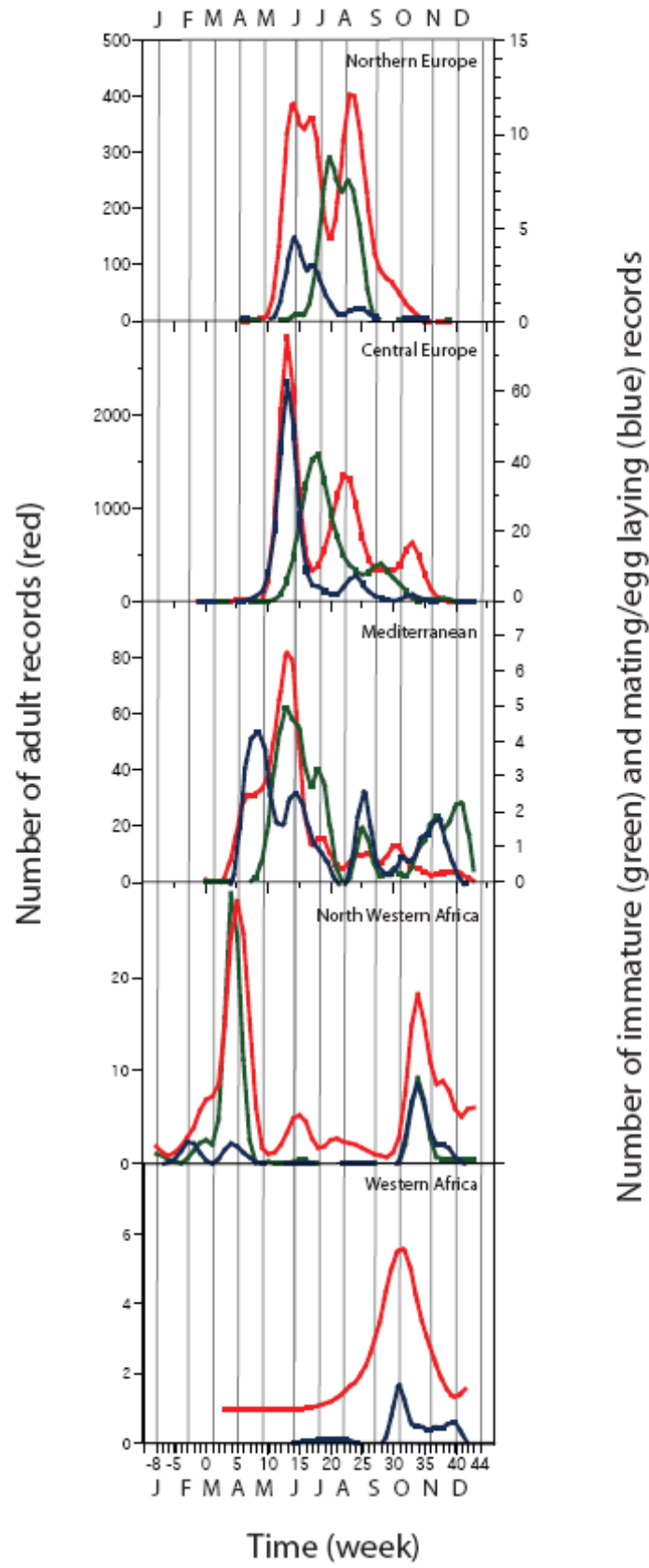


Fig. 3.

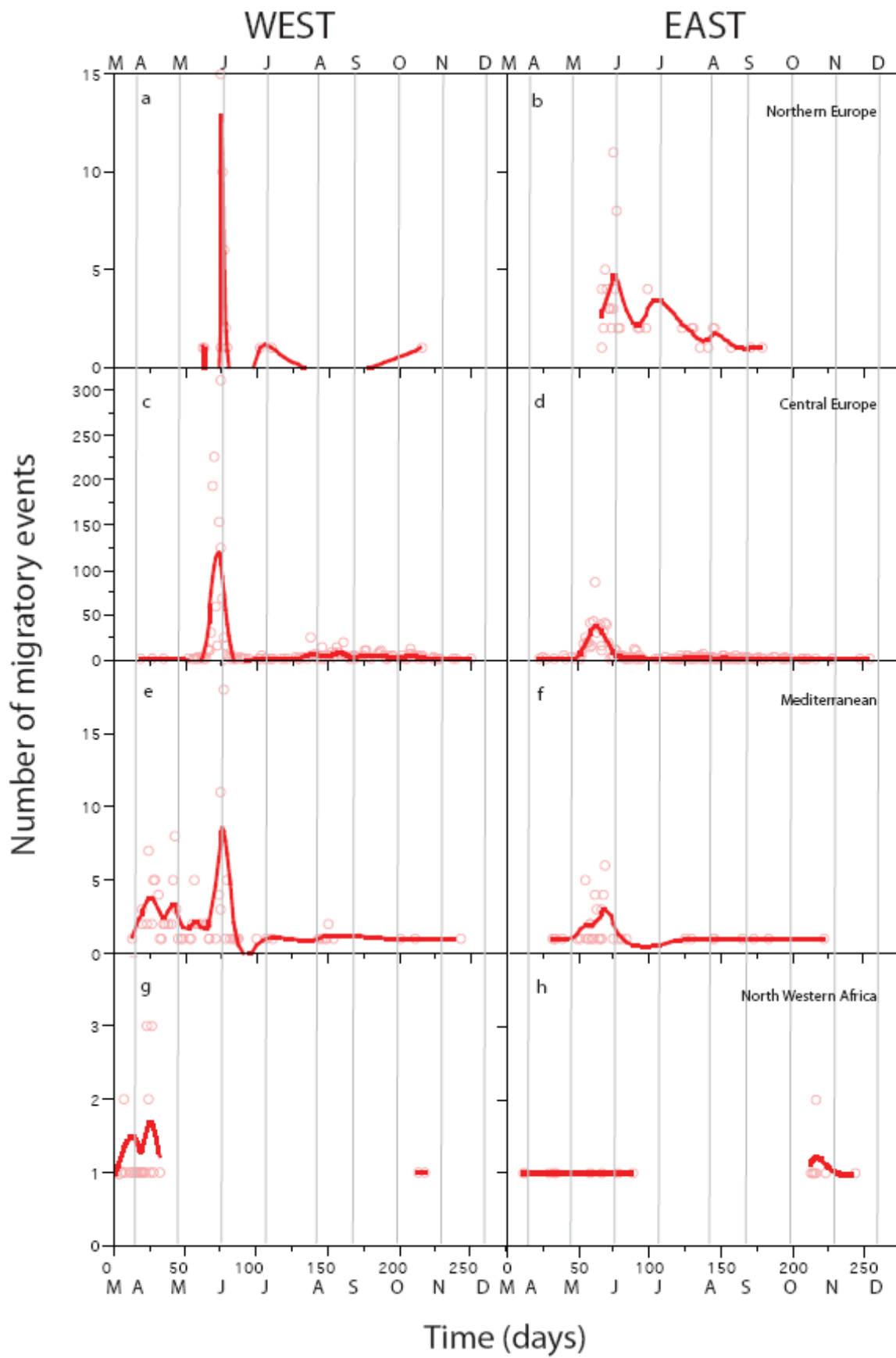


Fig. 4.

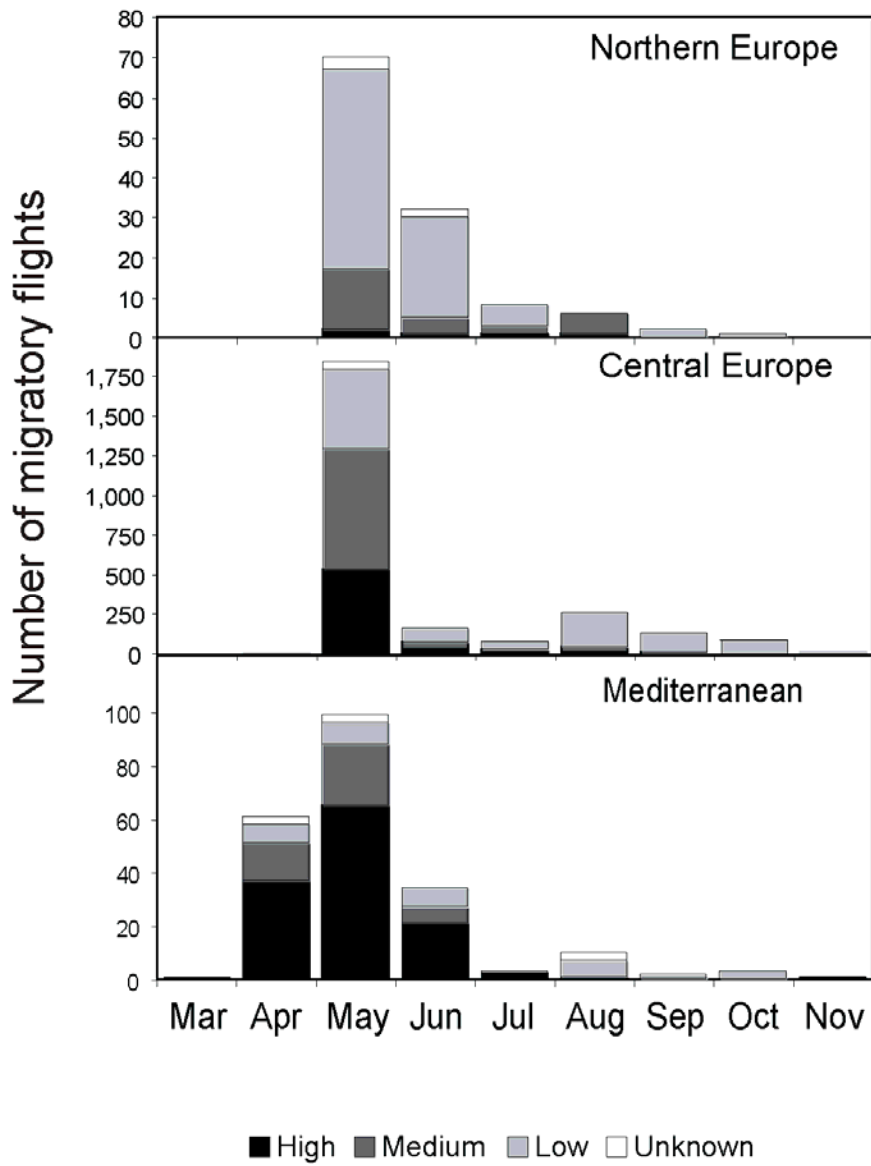


Fig. 5.

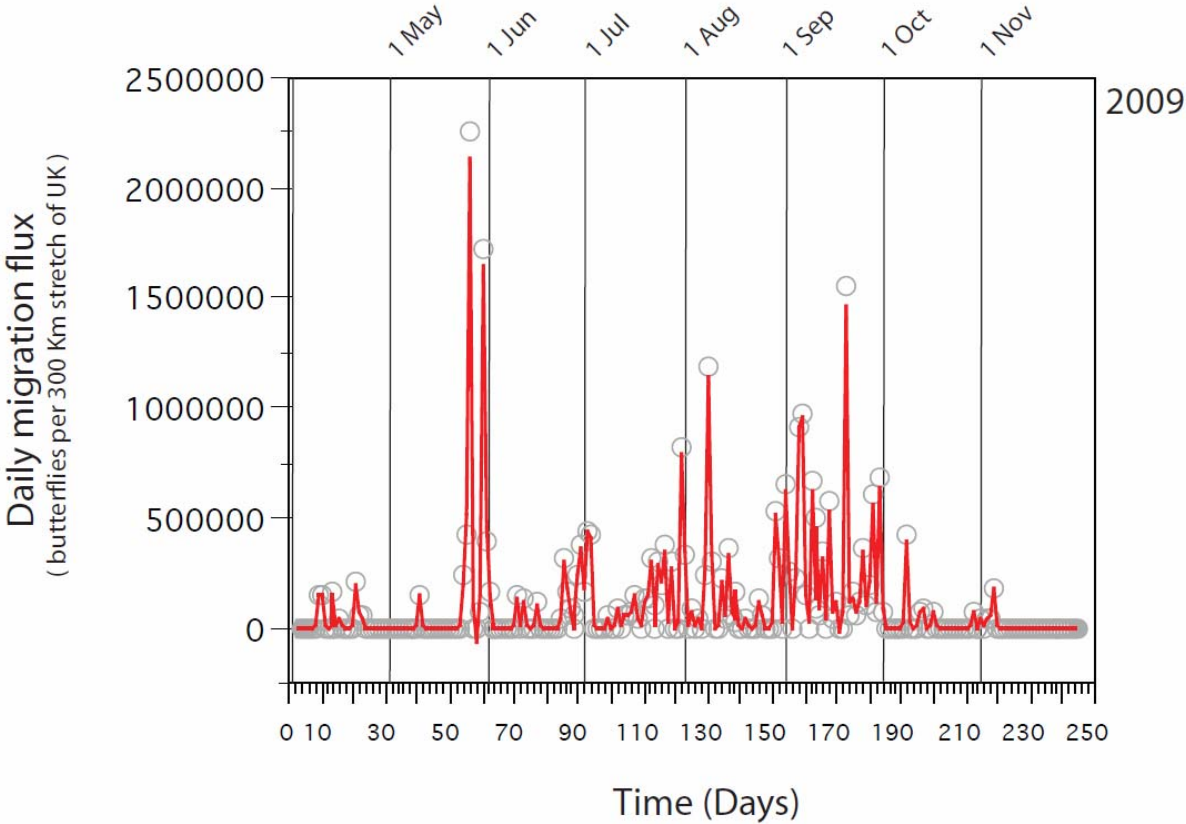
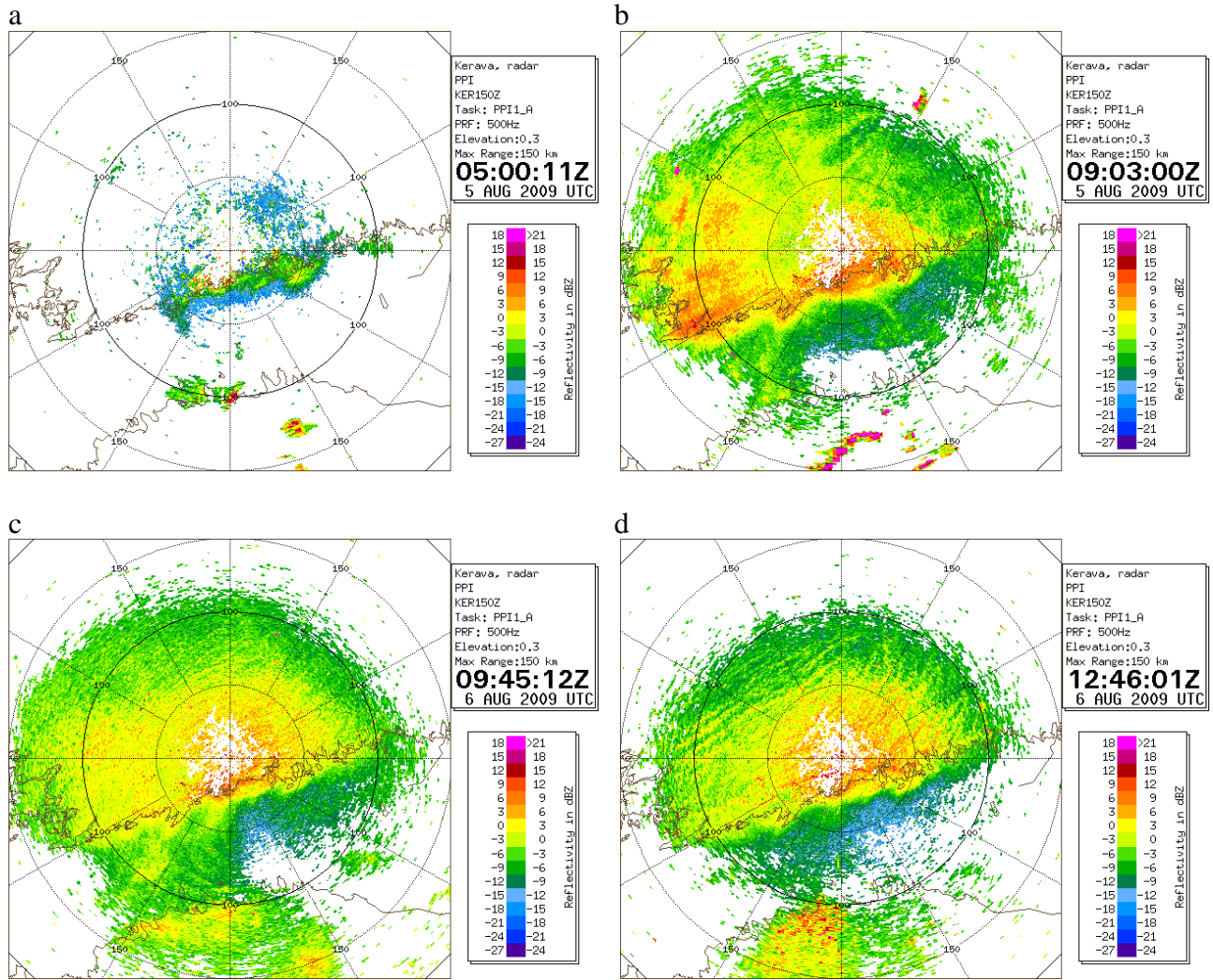


Fig. 6.



1 **Supplementary material**

2

3

4

5 **Appendix 1**

6

7 Datasets.

8

9 (1) *Ad-hoc* distribution records

10 Description of sources used for building the '*ad-hoc* distribution records' dataset:

11

12 - BCE (Butterfly Conservation Europe): In spring 2009, coordinators of BCE partners
13 were asked to collate observations of migrations of *V. cardui* in their countries. A
14 recording spreadsheet was distributed among partners to collect standardized data on the
15 number of migratory butterflies per unit time and area, and heading direction.

16

17 - BIBLIOGRAPHY: Published records on the abundance, breeding and migratory
18 behaviour of *V. cardui* in North and West Africa, and the Mediterranean region. Data
19 were extracted from original articles and books, including the most comprehensive
20 monographs on the subject (e.g. Williams 1930, Olivier 1993, Owen 1971, Wiemers
21 1995, Larsen 2005).

22

23 - CITES: Records gathered by C. Stefanescu and colleagues, mainly from field work in
24 the Iberian Peninsula and North and West Africa. Apart from observations on migratory

25 behaviour, a special effort was made in obtaining direct and indirect evidence of
26 breeding in these regions (i.e. data from immature stages and mating behaviour).
27
28 - CITIZEN: Records on the abundance and migrations of *V. cardui* were gathered from
29 the general public via an online ‘citizen science’ recording scheme, set up by Butterfly
30 Conservation in 2009 (Fox 2010). The scheme was promoted widely in the media,
31 including on BBC television’s *Springwatch* and *Autumnwatch* and in national
32 newspapers and magazines. Although the scheme was focused on Britain and Ireland, a
33 small fraction (1%) of observations were from other countries.

34
35 - FINLAND: The Finnish data were extracted from an open online database (Insect
36 Database: <http://hyonteiset.luomus.fi/insects/main/EntDatabase.html>), which is
37 maintained by the Finnish Museum of Natural History (University of Helsinki). The
38 database is open for all registered volunteers, and anyone can download data from it
39 even without registration. Observations were not specifically requested for *V. cardui* in
40 2009. The database is widely used among active lepidopterologists but virtually
41 unknown to the general public, meaning that the data quality is very good.

42
43 - IRELAND: Records of migrations of *V. cardui* in Ireland in 2009 were collated by
44 The National Biodiversity Data Centre in Ireland (www.biodiversityireland.ie).

45
46 - MILLENNIUM: Records for immature stages of *V. cardui* in the UK and Ireland,
47 gathered within the project ‘Butterflies for the New Millennium’ (Asher et al. 2001, Fox
48 et al. 2006) from 1995 to 2009.

49

50 - S4Y (science4you): Butterfly records were submitted to DFZS (www.falterfunde.de),
51 BUND and ÖNB (www.naturbeobachtung.at), and subsequently information on *V.*
52 *cardui* was collated and extracted by science4you (www.science4you.org). Most data
53 were from central Europe (Germany, Austria, Switzerland), but records were also
54 submitted from other European and African countries.

55

56 - SWEDEN: Observations made by lepidopterologists and other people with interest in
57 butterflies, among these a considerable number of ornithologists. Most records were
58 gathered in the Swedish report log (www.ArtDatabanken.se), but other data were
59 retrieved directly from the observers. A subset of records correspond to observations of
60 migrations carried out by ornithologists from Lund University working at the Falsterbo
61 Peninsula (55°23'N, 12°49'E), in SW Sweden, between 1 August and 25 October 2009
62 (see Brattström et al. 2008 for further details).

63

64 - TREKTELLEN: www.Trektellen.org is a private initiative aimed at monitoring bird
65 migration in The Netherlands and Belgium. In 2009, standardised counts between May
66 and October were carried out by ornithologists at 64 sites, mainly along the coast.
67 Numbers and direction of *V. cardui* migrants were also recorded during the whole
68 period.

69

70 Records were first compiled into a single database and individually checked, and
71 only those containing unequivocal information on location and date of the observation
72 were retained. Most of the records (97%) also included qualitative or quantitative
73 estimates of abundance, which were reclassified and standardized into three categories:
74 low abundance (1-10 individuals), medium abundance (11-100 individuals), high

75 abundance (more than 100 individuals). Complementary information on the timing of
76 the observation, adult behaviour (e.g. feeding, searching and egg-laying, territorial and
77 courtship, roosting, active migratory flight), condition of butterflies (i.e. fresh, worn)
78 was heterogeneously distributed among records and extracted whenever available.

79 An important fraction of the observations (ca. 10% of the records in both the whole
80 dataset and the subset for year 2009) referred to butterflies that were classified as
81 migrating within the Flight Boundary Layer. Additional information on the direction of
82 travel and an estimation of the numbers of butterflies flying per unit area and time was
83 given in many cases. For analytical purposes, abundance of migrants was standardized
84 into the three categories defined above (i.e. low, medium and high). The main heading
85 direction – and a secondary direction, whenever part of the population was moving in a
86 different direction – was classified into eight classes (north, northeast, east, etc.).
87 Finally, a subset of 949 records referred to immature stages (eggs, larvae and pupae),
88 allowing breeding to be attributed to a given region and date.

89

90 (2) Butterfly Monitoring Scheme (BMS) records

91 Density estimates were obtained at each monitored site on a weekly basis, between
92 March and September (Andorra: 6 sites; Balearic Islands: 18 sites; Catalonia: 53 sites),
93 April and September (Germany: 284 sites; Ireland: 69 sites; The Netherlands: 531 sites;
94 UK: 849 sites), or May and September (Finland: 63 sites).

95 Distribution of data into latitudinal bands was as follows: (a) Northern Europe - all
96 the Finnish data and 984 records from Scotland (i.e. northern UK); (b) Central Europe -
97 data from England and Wales, Germany, Ireland, and The Netherlands; and (c)
98 Mediterranean - data from Andorra, Balearic Islands and Catalonia.

99

100 (3) Radar observations of insect migrations

101 UK radar: Individual high-flying insects passing through the vertical beam of the radar

102 were continuously monitored throughout 2009, within 15 different height-bands from

103 150 m to 1,188 m above ground level (a.g.l.). Migrating insects most likely to

104 correspond to *Vanessa cardui* were identified based on measures of body size (mass)

105 and shape, and also on timing of activity (i.e. day-flying insects). To set the criteria for

106 selecting *V. cardui*-like radar targets, we first weighed a sample of wild-caught *V.*

107 *cardui* and determined the mean body mass and standard deviation of the sample (n =

108 21, mean mass = 175 mg, s.d. = ± 62 mg). A sub-sample of these butterflies (n = 5) were

109 then used to determine the principal radar back-scattering terms (the maximum

110 reflectivity (σ_{xx} term) divided by the minimum reflectivity (σ_{yy} term); see Chapman et

111 al. 2002a), using an established laboratory technique for measuring radar back-

112 scattering values (Chapman et al. 2002b, 2005, 2006). The ratio of these two terms ($\sigma_{xx} /$

113 σ_{yy}) gives an indication of the insect's body shape, with ratios close to 1 indicating an

114 insect with a circular underside aspect (e.g. a ladybird), and larger values indicating

115 longer and thinner-bodied insects. The mean ratio (9.2, range = 7.2 – 13.0) was typical

116 for a relatively long-bodied species such as a vanessid butterfly, and smaller than would

117 be expected for very long-bodied insects like dragonflies or green lacewings (Chapman

118 et al. 2005, 2006). Based on these laboratory measurements, a size range of 100-250 mg

119 was used to select day-flying insects detected by the radar during the spring, summer

120 and autumn of 2009 that might correspond to *V. cardui*. The radar back-scattering terms

121 of these targets were then examined, and it was found that the great majority of the

122 targets had $\sigma_{xx} / \sigma_{yy}$ values that would be expected for a butterfly like *V. cardui* (i.e.

123 ratios falling between 5 and 15). A few targets with ratios that fell well outside the

124 expected values were excluded from further analysis, and so we are confident that the

125 majority of the selected radar signals were produced by insects that closely resembled *V.*
126 *cardui* in both size and shape. Given the huge invasion of *V. cardui* that occurred in
127 2009, the very close association of radar peaks of abundance with visual observations of
128 ground-level migrations (see results section of main paper), and the shortage of other
129 likely candidate species of similar size and shape, we conclude that the majority of this
130 data did indeed relate to high-flying *V. cardui*. For technical details of the vertical-
131 looking entomological radar (VLR) operating procedures, see Chapman et al. (2002a,
132 2003, 2011). High-altitude wind directions were obtained from the UK Met Office's
133 numerical weather prediction model, the 'Unified Model' (Wood et al. 2006).

134

135 Finnish radars: Kumpula and Kerava are dual-polarimetric scanning radars with similar
136 fundamental parameters (Leskinen et al. 2011), allowing large moths and butterflies to
137 be observed at ranges of a few tens of kilometres. The Järvenpää system is a vertical-
138 looking Doppler weather radar (one fixed linear polarization), sensitive enough to
139 observe single large insects from 500 m upwards. For the present study we selected one
140 example from Finland, corresponding to a southward migration in August 2009 (for full
141 details see: <http://www.helsinki.fi/~mleskine/vaellus/Vcar2009.html>).

142

143 Mauritanian radar: See more details in Schmaljohann et al. (2007).

144

145

146 **References**

147

148 Asher, J. et al. 2001. The Millennium Atlas of Butterflies in Britain and Ireland. –
149 Oxford Univ. Press.

150

151 Brattström, O. et al. 2008. Effects of wind and weather on red admiral, *Vanessa*
152 *atalanta*, migration at a coastal site in southern Sweden. – Anim. Behav. 76:335-344.

153

154 Chapman, J. W. et al. 2002a. Development of vertical-looking radar technology for
155 monitoring insect migration. – Computers and electronics in agriculture 35: 95-110.

156

157 Chapman J.W. et al. 2002b. High-altitude migration of the diamondback moth, *Plutella*
158 *xylostella*, to the UK: a study using radar, aerial netting and ground trapping. – Ecol.
159 Entomol. 27: 641-650.

160

161 Chapman, J. W. et al. 2003. Vertical-looking radar: a new tool for monitoring high-
162 altitude insect migration. – BioScience 53: 503-511.

163

164 Chapman, J. W. et al. 2005. Mass aerial migration in the carabid beetle *Notiophilus*
165 *biguttatus*. – Ecol. Entomol. 30: 264-272.

166

167 Chapman J. W. et al. 2006. Seasonal variation in the migration strategies of the green
168 lacewing *Chrysoperla carnea* species complex. – Ecol. Entomol. 31: 378-388.

169

170 Chapman, J. W. et al. 2011. Recent insights from radar studies of insect flight. – Annu.
171 Rev. Entomol. 56: 337-356.

172

173 Fox, R. 2010. 2009: The year of the Painted Lady *Vanessa cardui* (L.). – Atropos 40: 3-
174 14.

175

176 Fox, R. et al. 2006. The state of butterflies in Britain and Ireland. – Information Press.

177

178 Larsen, T.B. 2005. Butterflies of West Africa. – Apollo Books.

179

180 Leskinen, M. et al. 2011. Pest insect immigration warning by an atmospheric dispersion

181 model, weather radars and traps. – J. Appl. Entomol. 135: 55-67.

182

183 Olivier, A. 1993. The butterflies of the Greek Island of Ródos: taxonomy, faunistics,

184 ecology and phenology. – Vlaamse Vereniging Entomologie.

185

186 Owen, D.F. 1971. Tropical butterflies. – Clarendon Press.

187

188 Schmaljohann, H. et al. 2007. Songbird migration across the Sahara: the non-stop

189 hypothesis rejected! – Proc. R. Soc. B 274: 735-739.

190

191 Wiemers, M. 1995. The butterflies of the Canary Islands. A survey on their distribution,

192 biology and ecology (Lepidoptera: Papilionoidea and Hesperioidea) (second part). –

193 Linn. Belgica 15: 87-118.

194

195 Williams, C. B. 1930. The migration of butterflies. – Oliver & Boyd.

196

197 Wood C.R. et al. 2006. The influence of the atmospheric boundary layer on nocturnal

198 layers of moths migrating over southern Britain. – Int. J. Biometeor. 50: 193-204.

199

200 Table S1a. Number of 'ad-hoc' distribution records and the subset of observations of
 201 migratory flights (all years and 2009) obtained from different data sources.
 202

Source	nr records		nr records migrations	
	total	2009	total	2009
BCE	214	214	161	161
BIBLIOGRAPHY	200	0	42	0
CITES	1588	784	346	162
CITIZEN	12595	12594	1294	1293
FINLAND	1192	1192	7	7
IRELAND	24	24	24	24
MILLENNIUM	491	159	0	0
S4Y	9854	9854	751	751
SWEDEN	3358	3358	81	81
TREKTELLEN	486	486	468	468
Total	30002	28665	3174	2947

203 Table S1b. Number of ‘ad-hoc’ distribution records obtained for 67 countries/regions in
 204 the study of the western Palaearctic-west African migratory system of *Vanessa cardui*.
 205 Most records were for year 2009 and gave only general information on adult abundance,
 206 but 10.5% records corresponded to observations of migrations and 3.2% to observations
 207 of immature stages. Also indicated are the countries/regions for which BMS and radar
 208 data were available.
 209

country / region	latitude (°N)	longitude (°E)	BMS	Radar	nr records		nr records migrations		nr records immatures	
					total	2009	total	2009	total	2009
Iceland	64.13	-21.87			8	8	2	2	0	0
Norway	62.70	14.00			10	10	0	0	1	1
Faroe Islands	62.18	-6.94			5	5	0	0	0	0
Finland	61.51	25.36	Yes	Yes	1208	1208	20	20	0	0
Sweden	58.39	15.51			3365	3365	81	81	5	5
Denmark	55.09	8.56			5	5	0	0	2	2
Lithuania	55.35	23.90			16	16	16	16	0	0
Isle of Man	54.27	-4.53			17	17	0	0	0	0
Ireland	53.86	-8.11	Yes		190	100	36	36	104	14
United Kingdom	52.41	-1.79	Yes	Yes	12697	12458	1236	1236	371	151
The Netherlands	51.99	5.36	Yes		397	397	367	367	1	1
Poland	51.63	17.86			18	18	8	8	0	0
Belgium	50.88	4.66			158	158	118	118	0	0
Germany	50.39	9.87	Yes		7028	7028	607	607	157	157
Czech Republic	49.96	14.32			5	5	2	2	0	0
Guernsey	49.47	-2.61			24	21	0	0	4	3
Jersey	49.20	-2.12			33	33	2	2	10	10
Luxembourg	49.66	6.14			3	3	0	0	0	0
Slovakia	48.32	17.48			7	6	3	3	1	1
Austria	47.95	15.05			1527	1527	90	90	15	15
Liechtenstein	47.12	9.54			1	1	0	0	0	0
Switzerland	47.48	8.55			932	930	36	36	22	22
Hungary	47.21	18.53			23	23	10	10	0	0
France	46.81	2.39			188	187	87	86	1	1
Romania	46.78	23.96			1	1	0	0	0	0
Slovenia	46.19	14.45			3	3	1	1	0	0
Croatia	45.24	14.19			30	30	0	0	0	0
Italy	44.34	10.90			144	141	24	22	8	8
Bosnia and Herzegovina	43.90	17.81			6	6	6	6	0	0
Bulgaria	42.98	23.93			3	3	3	3	0	0
Andorra	42.56	1.49	Yes		3	3	2		1	0
Corsica	42.00	8.94			2	2	2	2	0	0
Catalonia	41.81	2.38	Yes		652	252	247	88	71	18
Macedonia	41.41	22.24			1	1	0	0	0	0
Turkey	39.86	31.32			8	4	3	1	0	0

country / region	latitude (°N)	longitude (°E)	BMS	Radar	nr records		nr records migrations		nr records immatures	
					total	2009	total	2009	total	2009
Spain	39.72	-2.86			324	225	41	33	34	26
Balearic Islands	39.71	3.47	Yes		245	144	11	5	6	6
Portugal	38.68	-8.61			32	21	4	4	0	0
Greece	38.38	24.07			37	33	9	5	1	1
Gibraltar	36.14	-5.35			1	1	0	0	0	0
Sicily	37.84	15.28			2	2	0	0	0	0
Tunisia	35.48	11.17			3	1	1	0	0	0
Malta	35.93	14.41			17	13	9	9	0	0
Crete	35.31	24.08			6	6	4	4	0	0
Cyprus	35.14	33.47			10	10	2	2	0	0
Iraq	34.83	43.76			4	0	1	0	1	0
Algeria	33.36	0.58			20	3	5	2	4	1
Syria	33.26	35.94			2	1	2	1	0	0
Libya	32.80	21.86			3	1	2	0	0	0
Israel	32.08	35.03			5	1	4	1	1	0
Jordan	31.81	35.79			26	24	4	2	1	1
West Bank	31.68	35.19			2	0	1	0	0	0
Morocco	30.85	-7.85			292	175	39	32	107	59
Egypt	28.50	31.74			19	3	7	0	0	0
Canary Islands	28.36	-15.98			166	12	9	1	19	0
Western Sahara	22.72	-19.11			2	1	2	1	0	0
Mauritania	19.92	-15.49		Yes	9	2	5	1	0	0
Sudan	16.39	35.70			7	0	1	0	1	0
Eritrea	16.97	38.01			1	1	0	0	0	0
Cape Verde	16.23	-23.87			13	1	1	0	0	0
Mali	14.29	-3.62			4	1	1	1	0	0
The Gambia	13.40	-16.53			7	5	0	0	0	0
Senegal	12.85	-16.02			6	1	0	0	0	0
Ethiopia	12.16	39.19			1	1	0	0	0	0
Sierra Leone	8.48	-13.23			9	0	0	0	0	0
Nigeria	7.26	9.06			2	0	0	0	0	0
Ghana	7.00	-0.42			7	1	0	0	0	0
Total					30002	28665	3174	2947	949	503

210 Table S1c. Number of records across the five latitudinal regions considered in our
 211 analysis, and at different longitudes within each region (all years and 2009).
 212

Latitude	nr records	BMS records	
	total	2009	
>55° N	5035	5013	1600
46-55° N	22808	22495	26805
36-45°N	1513	888	1953
26-35°N	573	255	0
≤ 25°N	73	14	0
	30002	28665	30358

213

Longitude	nr records - total				nr records - 2009			
	<15°W - 0°E	1°- 15°E	16-30°E	31-45°E	<15°W - 0°E	0°- 15°E	15-30°E	30-45°E
>55° N	909	1324	2799	3	887	1324	2799	3
46-55° N	11484	10430	894	0	11188	10414	893	0
36-45°N	371	1091	47	4	247	598	41	2
26-35°N	472	23	21	57	193	11	12	39
≤ 25°N	57	3	0	13	12	0	0	2

214 **Appendix 2**

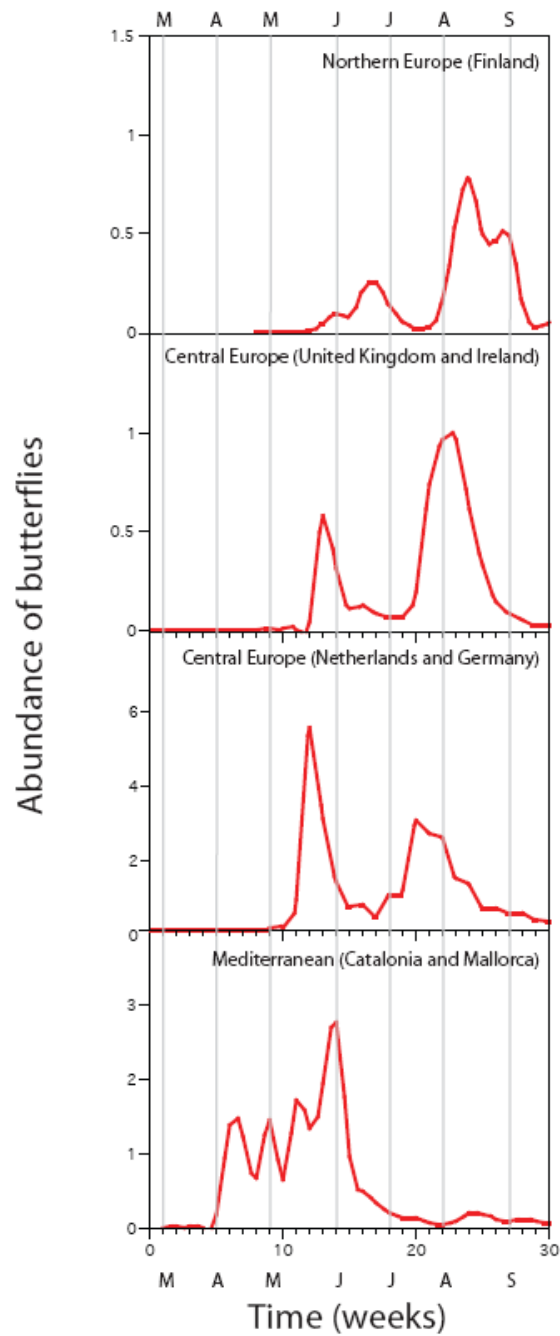
215

216 Population abundance in various European regions as deduced from standardized BMS

217 transect counts between March and September 2009. Abundance data are given as the

218 weekly average of butterflies per 100 m in each region.

219



220

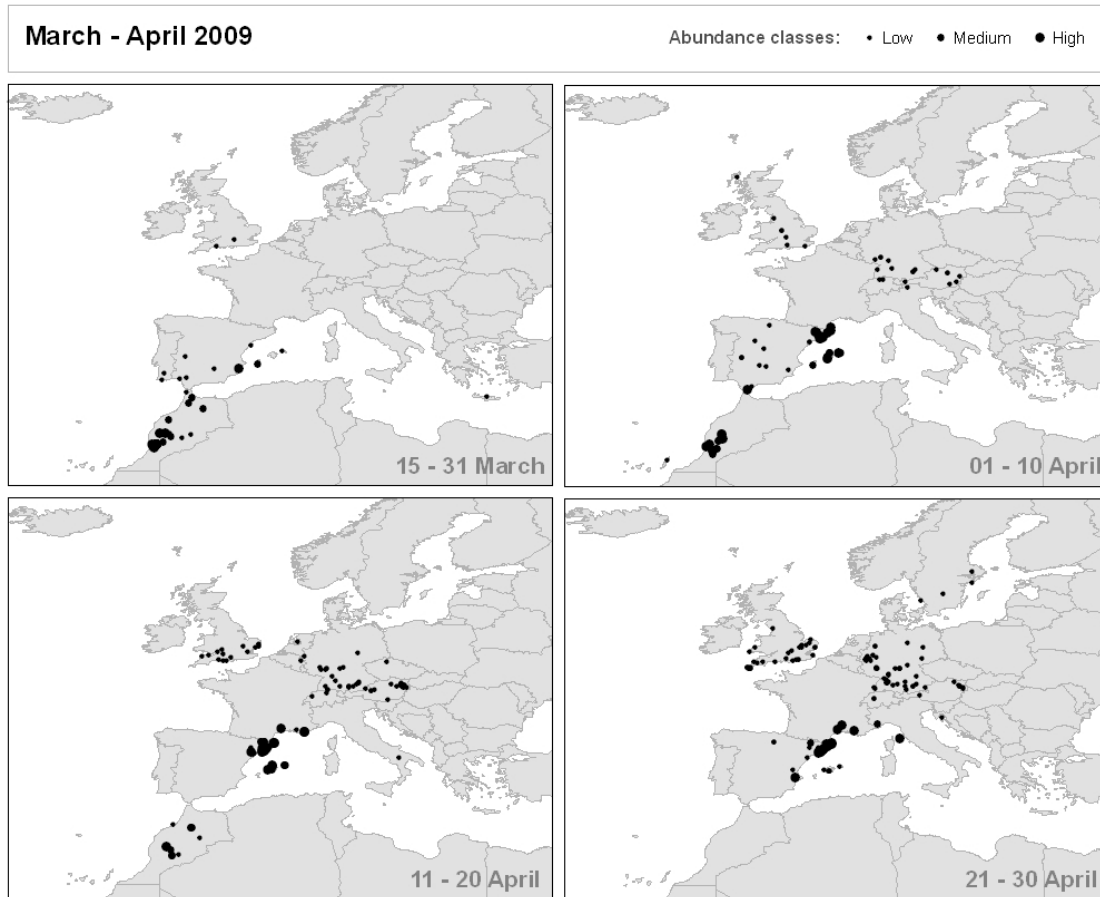
221

Appendix 3

222

223 Maps showing the expansion of *Vanessa cardui* across Europe during the two major

224 periods of northward migration in 2009.



225

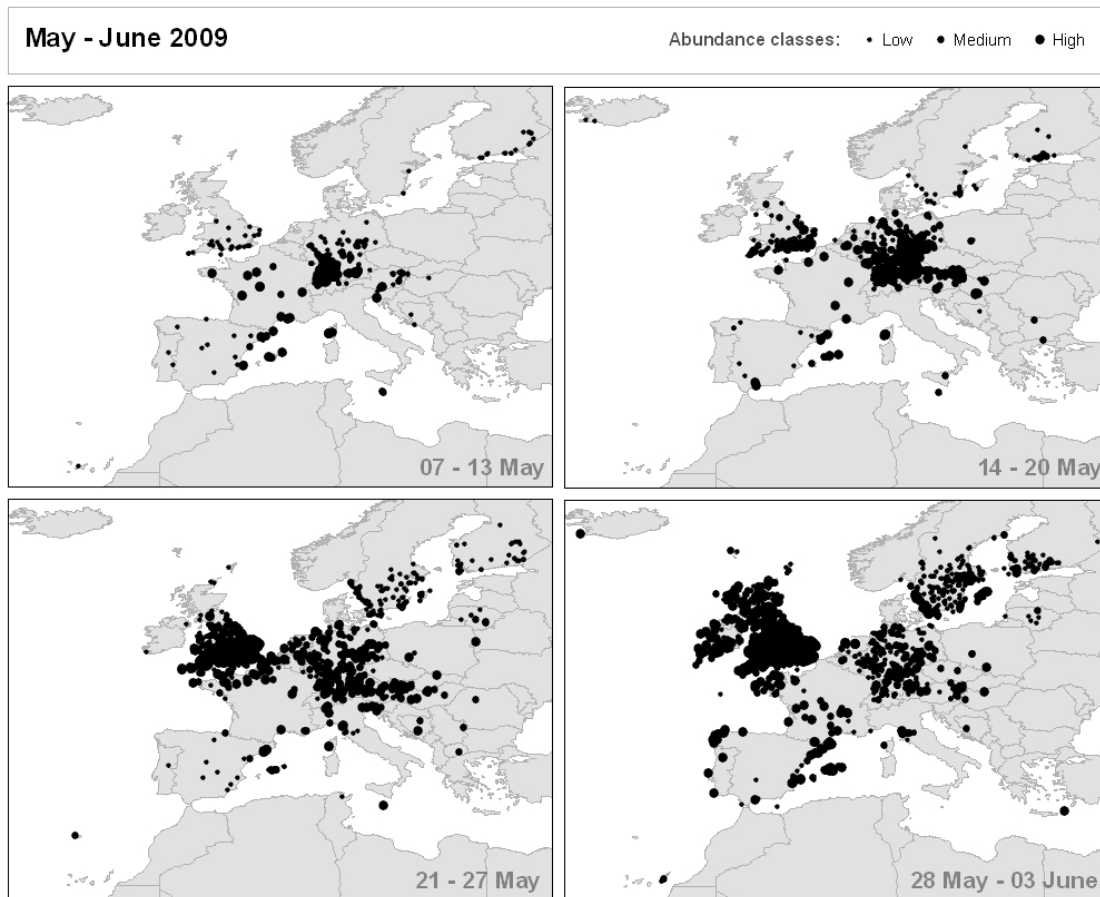
226 Fig. S3a. Colonization of Europe by *Vanessa cardui* in March-April 2009. All European

227 records during this period likely corresponded to migrants originating in western-central

228 Morocco. Note that distributional data are biased due to higher sampling efforts in the

229 UK, Central Europe (Austria, Germany and Switzerland), Sweden and Finland

230 compared to the rest of Europe and North Africa.



231

232 Fig. S3b. Colonization of Europe by *Vanessa cardui* in May-early June 2009. Eastern-
 233 central Europe was colonized by mid May by migrants likely originating in the southern
 234 Mediterranean shore (e.g. eastern Algeria, Tunisia and Libya). By 24-25 May part of
 235 these migrants had moved in a north-westward direction and reached the UK in great
 236 numbers. From 28 May to 2 June a new wave of massive migrations was recorded in
 237 western Europe, with migrants most likely originating in the Iberian Peninsula, northern
 238 Morocco and northwestern Algeria. As in Fig. S3a, note that distributional data are
 239 biased due to higher sampling efforts in the UK, Central Europe (Austria, Germany and
 240 Switzerland), Sweden and Finland compared to the rest of Europe and North Africa.

241 **Appendix 4**

242

243 Circular histograms of migratory directions for ground-level flights in different
244 subregions during spring (March-June) and summer/fall (July-November). The area of
245 the black segments is proportional to the number of individual dates within each 22.5°
246 bin (see text for details, and Table 1 for results of Rayleigh tests). The mean
247 displacement direction of the daily migrations, and the degree of clustering of the data
248 set about the mean are given in Table 1. Circular histograms of high-altitude migration
249 (for individual butterflies) recorded by the Chilbolton vertical looking radar in 2009 are
250 also shown for the two principal spring dates for migration into England (a) 25 May,
251 and (b) 29 May, and all summer/fall days.

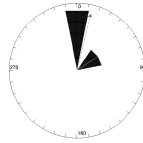
252

253

Spring

Summer/Fall

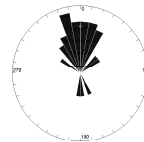
Northern Europe



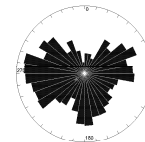
Chilbolton



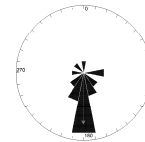
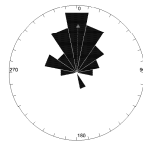
a



b



Central Europe



Mediterranean



Africa



254

255

256

257

258

259 **Appendix 5**

260

261 The density-height profile of *Vanessa cardui*-like targets detected by the Chilbolton

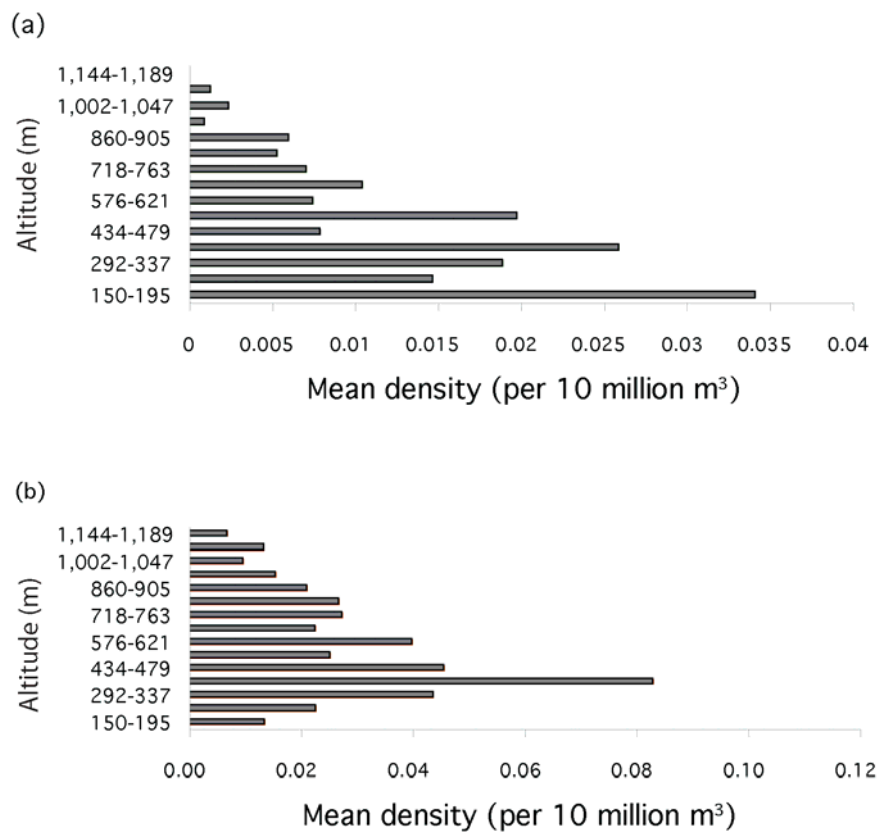
262 vertical looking radar in (a) spring (May-June), and (b) summer/fall (August-

263 September) 2009. Data expressed as mean density of butterflies per 10 million m³.

264 Flying insects were sampled in each of 15 altitude range gates between 150-195 m a.g.l.

265 (gate 1) and 1,144-1,189 m a.g.l. (gate 15).

266



267

268 **Appendix 6**

269

270 A conceptual model of migration of *Vanessa cardui* in the western Palaearctic-Western
271 African regions. In the figure S6, the first four of what is believed to be a total of six
272 annual generations have been identified with sequential numbers. Northward
273 progression in the spring by populations that have developed during the winter in
274 Northern Africa leads to the colonization of the European continent in what basically
275 consists of a two-step process: generation 1 first colonizing the Mediterranean in early
276 spring; then its offspring, generation 2, colonizing Central and Northern Europe in late
277 spring. Butterflies that emerge in these areas by mid summer (generation 3) reverse their
278 migratory direction and engage in a return flight to southern latitudes. Although some
279 migrants will stop in Central Europe and the Mediterranean and produce a fourth
280 generation in early fall (generation 4), a substantial part of the population seems to
281 travel all the way to the Sahel, in Western Africa, partly by movements off the Atlantic
282 coast (see below). The Sahelian region offers optimal conditions for breeding by the end
283 of the rainy season in August-September (Zwarts et al. 2009), and due to the high
284 temperatures a local generation can be produced in little more than one month (again,
285 generation 4). The recolonization of Northwestern Africa, which typically occurs in
286 October and early November, is therefore the result of southward migration by
287 European butterflies (as deduced by vertical looking radar data at Chilbolton and direct
288 observations in e.g. Malta), but probably is also the consequence of northward
289 movements by the Sahelian population. The locations of the remaining two generations
290 requires further documentation, but there is growing evidence indicating that both may
291 develop, without migration, in Northwestern Africa throughout the winter (unpubl. data
292 from winters 2010/2011 and 2011/2012). The actual extent of this region may vary

293 between years according to particular weather conditions, although some areas with a
294 typical mild climate (e.g. the Souss valley in western-central Morocco and the Canary
295 Islands) may prove ideal for winter breeding in a regular basis. In any case, the final
296 generation is expected to emerge by late winter. Offspring of this generation form adult
297 generation 1 in figure S6.

298

299 **Sources of variation and uncertainties of the model**

300 Although our conceptual model satisfactorily explains a large amount of the
301 observations in the western Palaearctic and Western Africa, variation in weather and the
302 physical condition of individual butterflies can affect the directions and distances of
303 migratory flights and result into a more complex pattern of migration. For instance, part
304 of the *V. cardui* population emigrating from central-western Morocco in spring 2009 did
305 not travel further north than northern Morocco, while others progressed well into
306 Central Europe. Because of differences in temperatures experienced by developing
307 larvae, the subsequent generation emerged at different times across a wide geographical
308 range and moved northward in what seemed, in certain European areas, a continuous
309 process of colonization instead of a two-step process. In particular, there is now good
310 evidence to suggest that part of the so-called generation 1 regularly stops and settles in
311 Northwestern Africa (Fig. S6), a wide region which generally offers excellent
312 conditions for breeding in April-May (data from 2010 and 2011; see also Williams
313 1930). Subsequent colonization of Central and Northern Europe is thus accomplished
314 by butterflies emerging on both shores of the Mediterranean.

315 The most serious uncertainties of our model refer to the part of the cycle occurring
316 in the African continent. Firstly, there is a lack of detail about the extremely long-
317 distance migration between the European continent and West Africa for generation 3 in

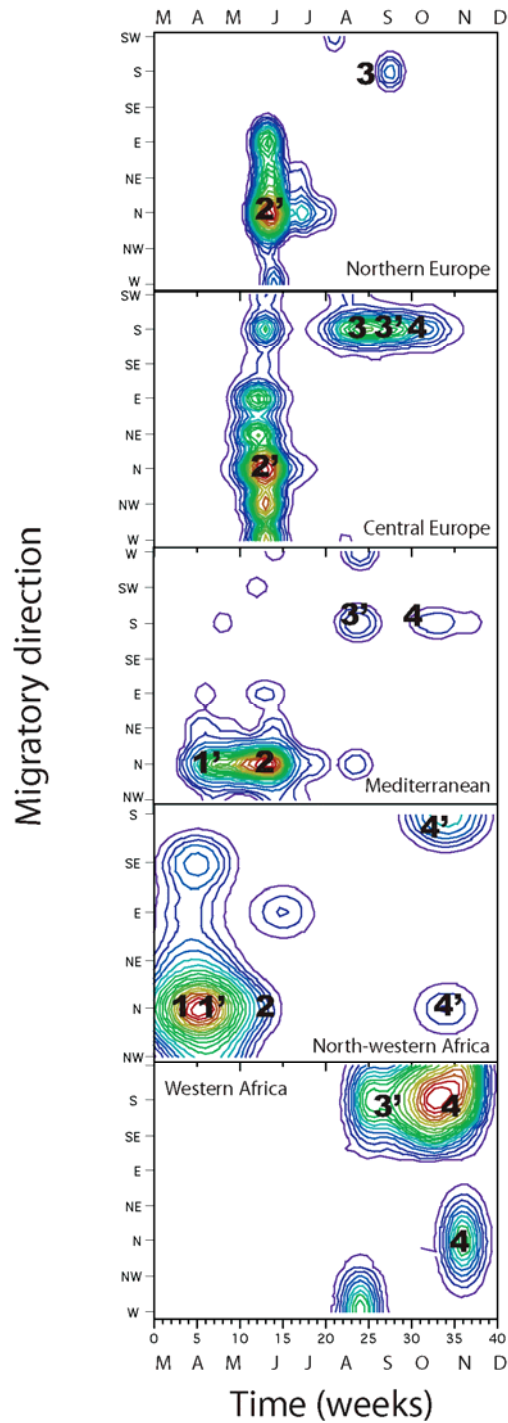
318 our scheme (Fig. S6). Several lines of evidence point at a main migratory route
319 occurring over the Atlantic ocean, favoured by the prevailing northerly winds (Dubief
320 1979, Newell and Kidson 1979). Vertical looking radar data at Chilbolton in August-
321 October were correlated with ground-level flights in eastern Central Europe (Table 2),
322 and showed a predominant south-westward direction of butterflies flying over south
323 England. Both observations seem to indicate a general westward movement of local
324 European populations by the end of summer and fall, which would seemingly result in
325 arrival on the Atlantic shores and the start of an ‘oceanic’ southward movement to West
326 Africa. This would also explain the low number of butterflies appearing in the
327 Mediterranean once the local generations disappear from Central and Northern Europe
328 (Figs 2, 4 and Appendix 2). Moreover, this possibility is in agreement with reports of
329 massive invasions of the Canary and Cape Verde islands in late summer and early fall
330 (compiled in the present study), and the frequent sightings of butterflies in southward
331 flights over the sea and along the African coast during this same period (e.g.
332 observations in Cape Blanc, in Mauritania, in different years, and radar data at
333 Nouakchott in 2003; see also Schouten 1988). In fact, this same idea was previously
334 suggested by Williams (1958), after his observation, in September 1943, of a steady
335 southward movement of *V. cardui* fifty miles at sea off the west coast of Africa, from
336 “the mouth of the Mediterranean to as far as Sierra Leone”. As with other large
337 Lepidoptera, migrant *V. cardui* finding themselves over large expanses of water will
338 continue in flight for very long distances and well outside their normal diel flight
339 period. Nonetheless, alternative routes cannot be discarded, given the great dispersion of
340 individual tracks in the migratory flights in summer and fall (Appendix D).

341 A second aspect that remains speculative at present is the fate of the generation
342 locally produced in the Sahel in the fall (generation 4; Fig. S6). Based on theoretical

343 considerations but also on empirical evidence, it is clear that this generation must
344 immediately leave the region, as it dries up very quickly after the rainy season (Zwarts
345 et al. 2009). However, whether these butterflies engage in regular ‘directed’ migrations
346 or just adopt a nomadic strategy and move according to the prevailing winds is not
347 known. Limited evidence (e.g. radar observations of northeast/eastward movements
348 from Ouadâne in October 2003, and ground-level observations of northward migration
349 in central Morocco in October 2003 and 2009) suggests that at least some of these
350 butterflies will move approximately northward by flying at high altitude under
351 favourable conditions – thus avoiding the prevailing northeasterly Harmattan winds – to
352 end up eventually in Northwestern Africa. Similar seasonal windborne migration
353 between the Sahel and Northwestern Africa has been described in other insects, and is
354 part of a typical seasonal circuit in the desert locust, *Schistocerca gregaria* (Pedgley
355 1981). We do not know, however, how regular this phenomenon might be in *V. cardui*,
356 nor if a variable fraction of the Sahelian population is carried downwind to the south-
357 west, ending up in the savanna zone of West Africa and thus potentially moving out of
358 the North Africa-European migration circuit as defined in this study.

359 Still another gap relates to the dearth of data for the winter period (December-
360 February). Growing evidence suggests that the so-called generations 5 and 6 occur at
361 low densities and widely scattered in Northwestern Africa. This population bottle-neck
362 could result from the scarcity and/or low quality of larval resources during this period
363 (C. Stefanescu unpubl.data), in those parts of the range which are not climatically
364 constrained for larval development (i.e. not too cold). However, in some years,
365 significant winter rainfall events penetrate southward far into the Sahara, and these
366 might provide opportunities for large *V. cardui* populations to develop.

367 According to this model there is an apparent lack of predictable directional
 368 migrations in generations 5, 6, and, perhaps, 4, contrasting with highly predictable
 369 northward or southward migration in generations 1-3. This contrasting behaviour may
 370 arise from the presence or absence of environmental cues that trigger directional
 371 movement in northern or southern directions in emerging butterflies.



373 Fig. S6. A conceptual model for migration of *Vanessa cardui* in the western Palaearctic
374 and West African regions. Smooth surfaces show density of records of migration in five
375 latitudinal bands, together with observed heading directions. Red contour lines indicate
376 maximum point density. Numbers indicate sequential generations (i.e. 1: source area of
377 migrants; 1': area of destination of migrants; 2: offspring of generation 1, and so on).
378 Two more generations (generations 5 and 6) occur in Northwestern Africa from
379 November-December to February-March, but there is a dearth of information about the
380 exact extent of their location. See text for details.

381

382

383

384 **References**

385

386 Dubief, J. 1979. Review of the North African climate with particular emphasis on the
387 production of eolian dust in the Sahel zone and in the Sahara. – In: Morales, C. (ed.),
388 Saharan dust mobilization, transport and deposition. John Wiley and Sons, pp. 27-48.

389

390 Newell, R. E. and Kidson, J. W. 1979. The tropospheric circulation over Africa and its
391 relation to the global tropospheric circulation. – In: Morales, C. (ed.), Saharan dust
392 mobilization, transport and deposition. John Wiley and Sons, pp. 133-169.

393

394 Pedgley, D. E. 1981 (ed.). Desert Locust forecasting manual. Volumes 1 and 2. – Centre
395 for Overseas Pest Research.

396

397 Schouten, J. R. 1988. Notes on terrestrial Gastropoda, Arachnida and insecta of the
398 Knifiss-Tarfaya region. – In: Dakki, M. and De Ligny, W. (eds), The Knifiss lagoon and
399 its surrounding environment (province of La'youne, Morocco). Travaux de l'Institute
400 Scientifique, Rabat, pp. 95-100.
401
402 Stefanescu, C. et al. 2011. Moroccan source areas of the painted lady butterfly *Vanessa*
403 *cardui* (Nymphalidae: Nymphalinae) migrating into Europe in spring. – J. Lepid. Soc.
404 65: 15-26.
405
406 Williams, C. B. 1930. The migration of butterflies. – Oliver & Boyd.
407
408 Williams, C. B. 1958. Insect migration. – Collins.
409
410 Zwarts, L. et al. 2009. Living on the edge: wetlands and birds in a changing Sahel. –
411 KNNV Publishing.