Ecography

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Supplementary material

Supplementary material

Appendix 1

Datasets.

(1) *Ad-hoc* distribution records

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

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

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

- CITES: Records gathered by C. Stefanescu and colleagues, mainly from field work in the Iberian Peninsula and North and West Africa. Apart from observations on migratory behaviour, a special effort was made in obtaining direct and indirect evidence of breeding in these regions (i.e. data from immature stages and mating behaviour).

- CITIZEN: Records on the abundance and migrations of *V. cardui* were gathered from the general public via an online 'citizen science' recording scheme, set up by Butterfly Conservation in 2009 (Fox 2010). The scheme was promoted widely in the media, including on BBC television's *Springwatch* and *Autumnwatch* and in national newspapers and magazines. Although the scheme was focused on Britain and Ireland, a small fraction (1%) of observations were from other countries.

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

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

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

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

- SWEDEN: Observations made by lepidopterologists and other people with interest in butterflies, among these a considerable number of ornithologists. Most records were gathered in the Swedish report log (www.ArtDatabanken.se), but other data were retrieved directly from the observers. A subset of records correspond to observations of migrations carried out by ornithologists from Lund University working at the Falsterbo Peninsula (55º23'N, 12º49'E), in SW Sweden, between 1 August and 25 October 2009 (see Brattström et al. 2008 for further details).

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

Records were first compiled into a single database and individually checked, and only those containing unequivocal information on location and date of the observation were retained. Most of the records (97%) also included qualitative or quantitative estimates of abundance, which were reclassified and standardized into three categories: low abundance (1-10 individuals), medium abundance (11-100 individuals), high abundance (more than 100 individuals). Complementary information on the timing of the observation, adult behaviour (e.g. feeding, searching and egg-laying, territorial and courtship, roosting, active migratory flight), condition of butterflies (i.e. fresh, worn) was heterogeneously distributed among records and extracted whenever available.

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

(2) Butterfly Monitoring Scheme (BMS) records

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

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

(3) Radar observations of insect migrations

UK radar: Individual high-flying insects passing through the vertical beam of the radar were continuously monitored throughout 2009, within 15 different height-bands from 150 m to 1,188 m above ground level (a.g.l.). Migrating insects most likely to correspond to *Vanessa cardui* were identified based on measures of body size (mass) and shape, and also on timing of activity (i.e. day-flying insects). To set the criteria for selecting *V. cardui*-like radar targets, we first weighed a sample of wild-caught *V. cardui* and determined the mean body mass and standard deviation of the sample (n = 21, mean mass = 175 mg, s.d. = ±62 mg). A sub-sample of these butterflies (n = 5) were then used to determine the principal radar back-scattering terms (the maximum reflectivity (σ_{xx} term) divided by the minimum reflectivity (σ_{yy} term); see Chapman et al. 2002a), using an established laboratory technique for measuring radar back-scattering values (Chapman et al. 2002b, 2005, 2006). The ratio of these two terms (σ_{xx} / σ_{yy}) gives an indication of the insect's body shape, with ratios close to 1 indicating an insect with a circular underside aspect (e.g. a ladybird), and larger values indicating longer and thinner-bodied insects. The mean ratio (9.2, range = 7.2 – 13.0) was typical for a relatively long-bodied species such as a vanessid butterfly, and smaller than would be expected for very long-bodied insects like dragonflies or green lacewings (Chapman et al. 2005, 2006). Based on these laboratory measurements, a size range of 100-250 mg was used to select day-flying insects detected by the radar during the spring, summer and autumn of 2009 that might correspond to *V. cardui*. The radar back-scattering terms of these targets were then examined, and it was found that the great majority of the targets had σ_{xx} / σ_{yy} values that would be expected for a butterfly like *V. cardui* (i.e. ratios falling between 5 and 15). A few targets with ratios that fell well outside the expected values were excluded from further analysis, and so we are confident that the majority of the selected radar signals were produced by insects that closely resembled *V. cardui* in both size and shape. Given the huge invasion of *V. cardui* that occurred in 2009, the very close association of radar peaks of abundance with visual observations of ground-level migrations (see results section of main paper), and the shortage of other likely candidate species of similar size and shape, we conclude that the majority of this data did indeed relate to high-flying *V. cardui*. For technical details of the vertical-looking entomological radar (VLR) operating procedures, see Chapman et al. (2002a, 2003, 2011). High-altitude wind directions were obtained from the UK Met Office's numerical weather prediction model, the 'Unified Model' (Wood et al. 2006).

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

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

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Table A1a. Number of 'ad-hoc' distribution records and the subset of observations of migratory flights (all years and 2009) obtained from different data sources.

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

Table A1b. Number of ‘ad-hoc’ distribution records obtained for 67 countries/regions in the study of the western Palaearctic-west African migratory system of *Vanessa cardui*. Most records were for year 2009 and gave only general information on adult abundance, but 10.5% records corresponded to observations of migrations and 3.2% to observations of immature stages. Also indicated are the countries/regions for which BMS and radar data were available.

country / region	latitude (ºN)	longitude (ºE)	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 (ºN)	longitude (ºE)	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

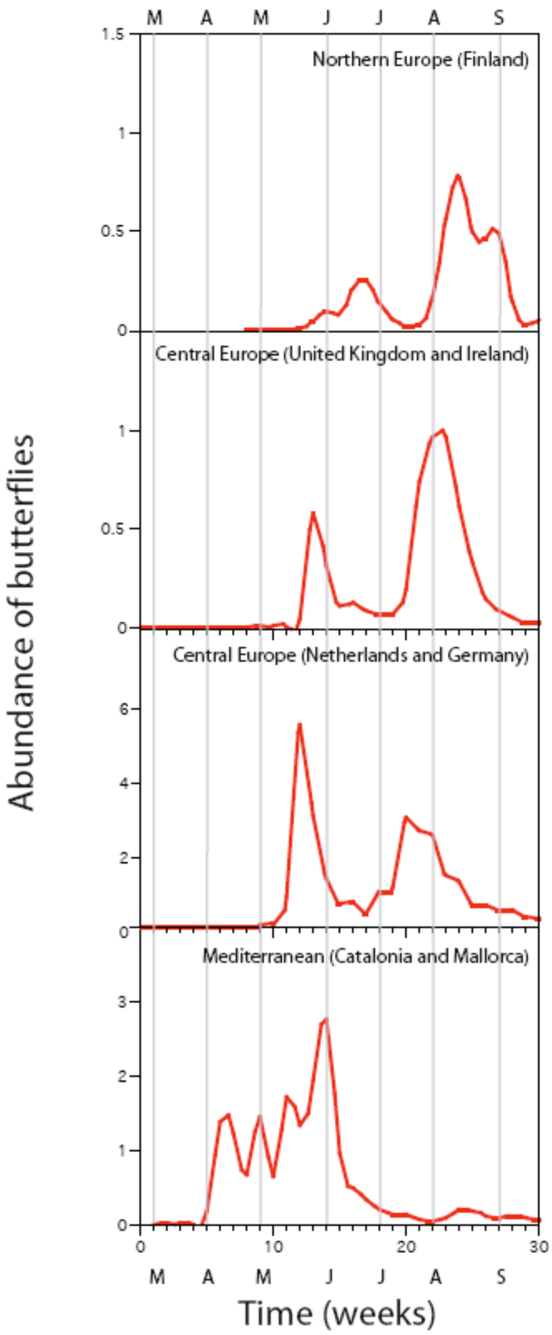
Table A1c. Number of records across the five latitudinal regions considered in our analysis, and at different longitudes within each region (all years and 2009).

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

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

Appendix 2

Population abundance in various European regions as deduced from standardized BMS transect counts between March and September 2009. Abundance data are given as the weekly average of butterflies per 100 m in each region.



Appendix 3

Maps showing the expansion of *Vanessa cardui* across Europe during the two major periods of northward migration in 2009.

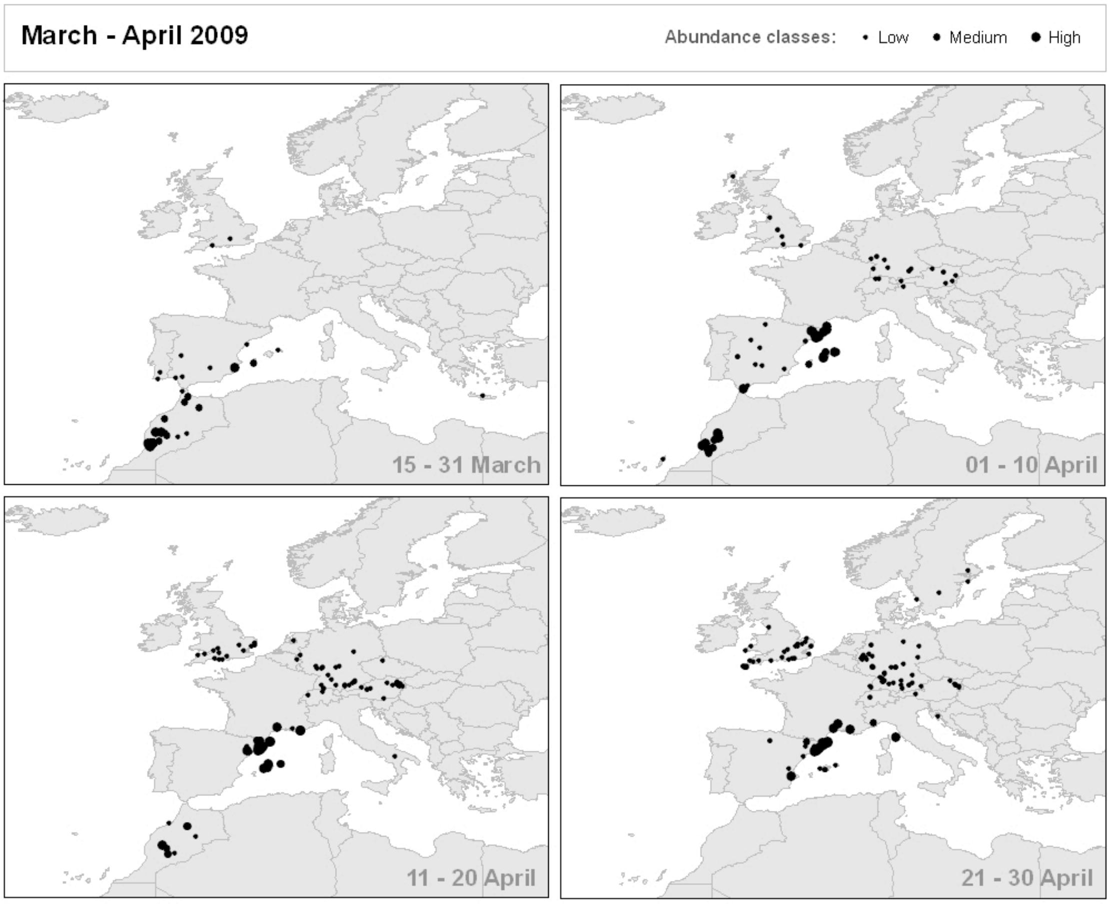


Figure A3a. Colonization of Europe by *Vanessa cardui* in March-April 2009. All European records during this period likely corresponded to migrants originating in western-central Morocco. Note that distributional data are biased due to higher sampling efforts in the UK, Central Europe (Austria, Germany and Switzerland), Sweden and Finland compared to the rest of Europe and North Africa.

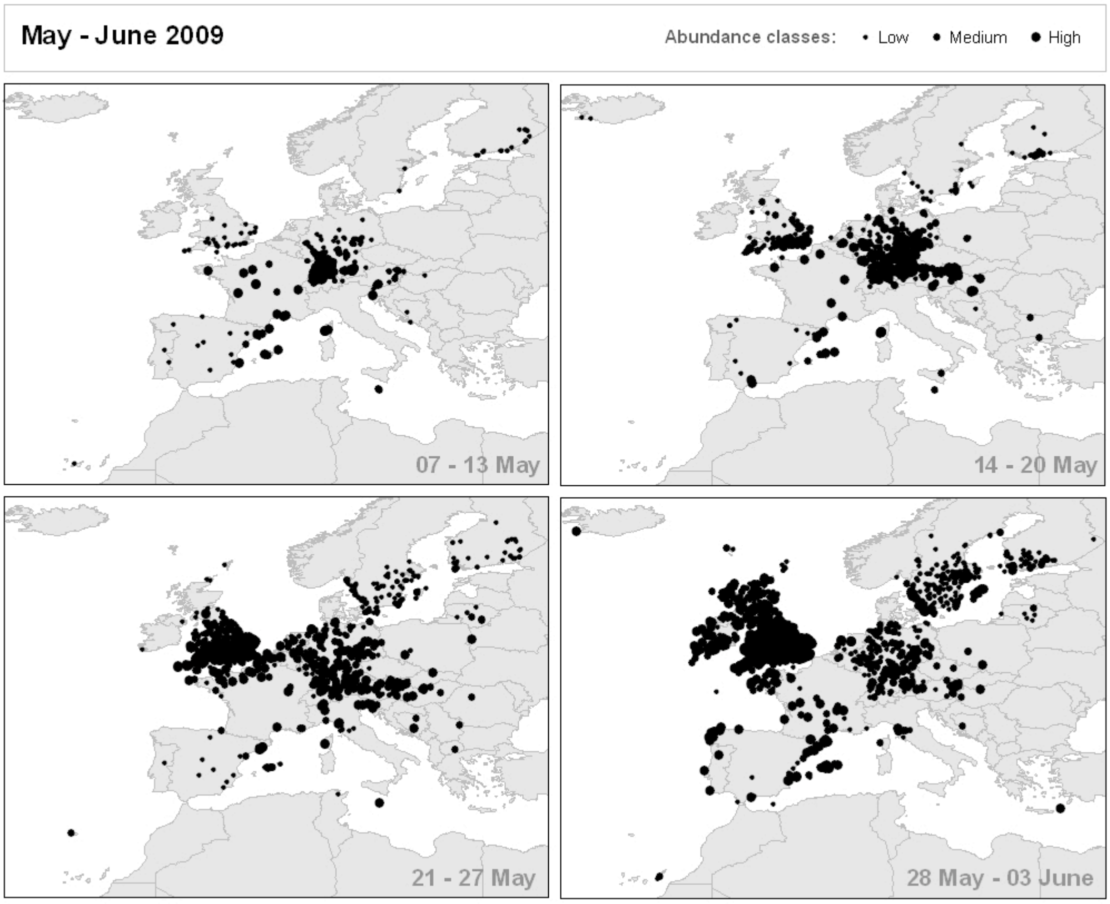
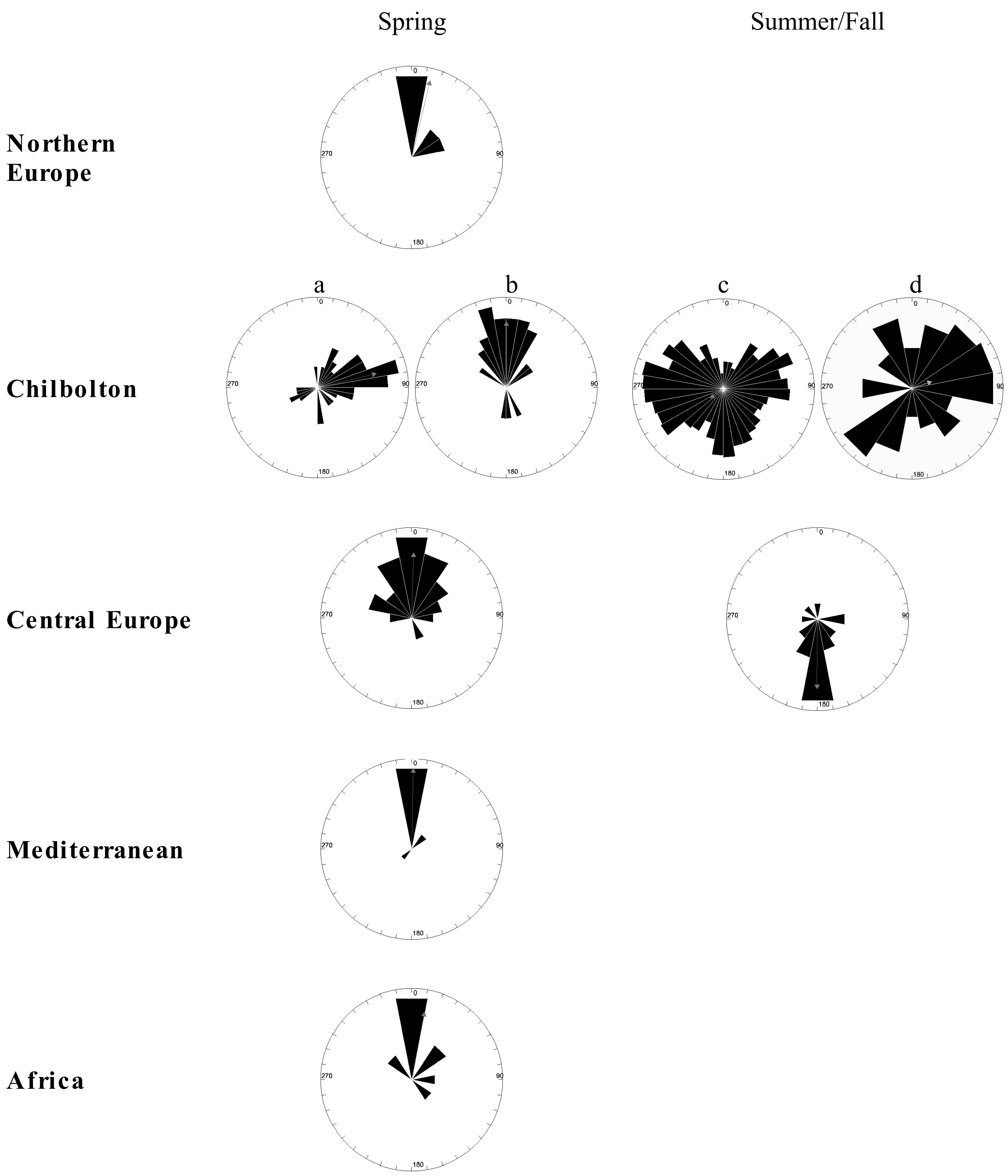


Figure A3b. Colonization of Europe by *Vanessa cardui* in May-early June 2009. Eastern-central Europe was colonized by mid May by migrants likely originating in the southern Mediterranean shore (e.g. eastern Algeria, Tunisia and Libya). By 24-25 May part of these migrants had moved in a north-westward direction and reached the UK in great numbers. From 28 May to 2 June a new wave of massive migrations was recorded in western Europe, with migrants most likely originating in the Iberian Peninsula, northern Morocco and northwestern Algeria. As in Fig. S3a, note that distributional data are biased due to higher sampling efforts in the UK, Central Europe (Austria, Germany and Switzerland), Sweden and Finland compared to the rest of Europe and North Africa.

Appendix 4

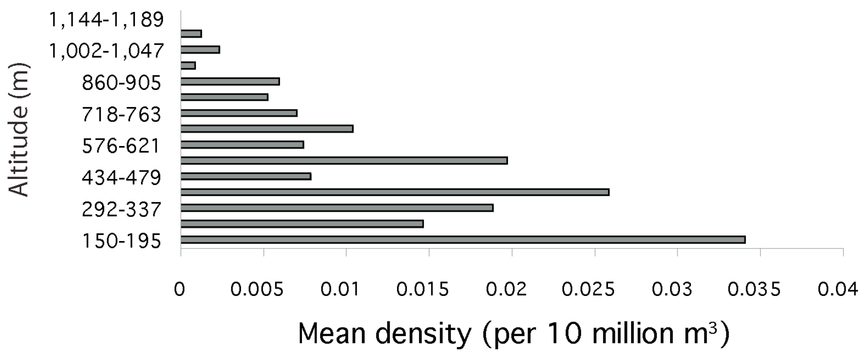
Circular histograms of migratory directions for ground-level flights in different subregions during spring (March-June) and summer/fall (July-November). The area of the black segments is proportional to the number of individual dates within each 22.5º bin (see text for details, and Table 1 for results of Rayleigh tests). The mean displacement direction of the daily migrations, and the degree of clustering of the data set about the mean are given in Table 1. Circular histograms of high-altitude migration (for individual butterflies) recorded by the Chilbolton vertical looking radar in 2009 are also shown for the two principal spring dates for migration into England (a) 25 May, and (b) 29 May, and all summer/fall days (c). The mean migration direction in summer/fall (236º) contrasted with the patterns of high-altitude winds (measured at 300 m) for the same period, which had a significant mean downwind direction of 71º (d). This suggests that butterflies actively selected favourable winds with a northerly component when migrating southwards.


Spring
Summer/Fall
Northern Europe
a
b
c
d
Chilbolton
Central Europe
Mediterranean
Africa
0
90
180
270

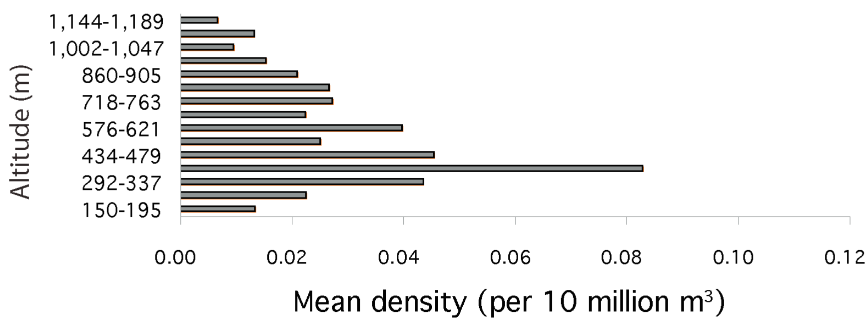
Appendix 5

The density-height profile of *Vanessa cardui*-like targets detected by the Chilbolton vertical looking radar in (a) spring (May-June), and (b) summer/fall (August-September) 2009. Data expressed as mean density of butterflies per 10 million m^3. Flying insects were sampled in each of 15 altitude range gates between 150-195 m a.g.l. (gate 1) and 1,144-1,189 m a.g.l. (gate 15).

(a)



(b)



Appendix 6

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

Sources of variation and uncertainties of the model

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

The most serious uncertainties of our model refer to the part of the cycle occurring in the African continent. Firstly, there is a lack of detail about the extremely long-distance migration between the European continent and West Africa for generation 3 in our scheme (Fig. S6). Several lines of evidence point at a main migratory route occurring over the Atlantic ocean, favoured by the prevailing northerly winds (Dubief 1979, Newell and Kidson 1979). Vertical looking radar data at Chilbolton in August-October were correlated with ground-level flights in eastern Central Europe (Table 2), and showed a predominant south-westward direction of butterflies flying over south England. Both observations seem to indicate a general westward movement of local European populations by the end of summer and fall, which would seemingly result in arrival on the Atlantic shores and the start of an 'oceanic' southward movement to West Africa. This would also explain the low number of butterflies appearing in the Mediterranean once the local generations disappear from Central and Northern Europe (Figs 2, 4 and Appendix 2). Moreover, this possibility is in agreement with reports of massive invasions of the Canary and Cape Verde islands in late summer and early fall (compiled in the present study), and the frequent sightings of butterflies in southward flights over the sea and along the African coast during this same period (e.g. observations in Cape Blanc, in Mauritania, in different years, and radar data at Nouakchott in 2003; see also Schouten 1988). In fact, this same idea was previously suggested by Williams (1958), after his observation, in September 1943, of a steady southward movement of *V. cardui* fifty miles at sea off the west coast of Africa, from "the mouth of the Mediterranean to as far as Sierra Leone". As with other large Lepidoptera, migrant *V. cardui* finding themselves over large expanses of water will continue in flight for very long distances and well outside their normal diel flight period. Nonetheless, alternative routes cannot be discarded, given the great dispersion of individual tracks in the migratory flights in summer and fall (Appendix D).

A second aspect that remains speculative at present is the fate of the generation locally produced in the Sahel in the fall (generation 4; Fig. S6). Based on theoretical considerations but also on empirical evidence, it is clear that this generation must immediately leave the region, as it dries up very quickly after the rainy season (Zwarts et al. 2009). However, whether these butterflies engage in regular ‘directed’ migrations or just adopt a nomadic strategy and move according to the prevailing winds is not known. Limited evidence (e.g. radar observations of northeast/eastward movements from Ouadâne in October 2003, and ground-level observations of northward migration in central Morocco in October 2003 and 2009) suggests that at least some of these butterflies will move approximately northward by flying at high altitude under favourable conditions – thus avoiding the prevailing northeasterly Harmattan winds – to end up eventually in Northwestern Africa. Similar seasonal windborne migration between the Sahel and Northwestern Africa has been described in other insects, and is part of a typical seasonal circuit in the desert locust, *Schistocerca gregaria* (Pedgley 1981). We do not know, however, how regular this phenomenon might be in *V. cardui*, nor if a variable fraction of the Sahelian population is carried downwind to the south-west, ending up in the savanna zone of West Africa and thus potentially moving out of the North Africa-European migration circuit as defined in this study.

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

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

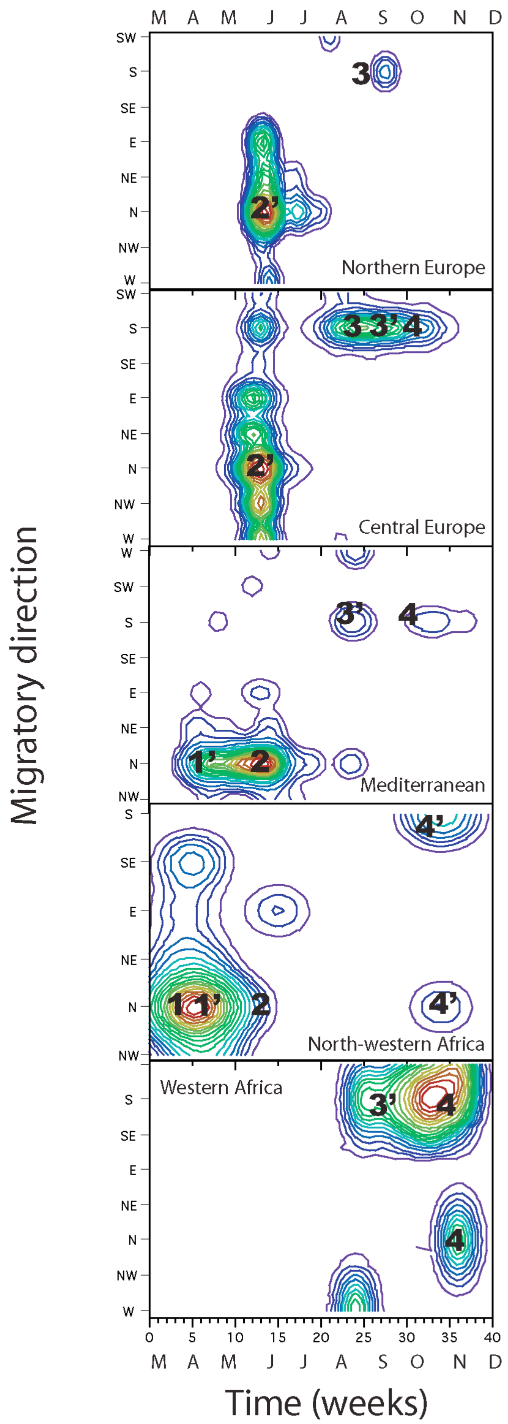


Fig. S6. A conceptual model for migration of *Vanessa cardui* in the western Palaearctic and West African regions. Smooth surfaces show density of records of migration in five latitudinal bands, together with observed heading directions. Red contour lines indicate maximum point density. Numbers indicate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

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