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

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

Introduction

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

Investigation of migration in species with generation times shorter than the seasonal cycle or year is generally more difficult, and this is the case for the majority of migratory insects (Drake and Gatehouse 1995, Holland et al. 2006). Insects that track suitable environments (arising from responses to spatially and temporally variable conditions) must exhibit patterns of movement that encompass multiple generations. Inhabitants of arid/semi-arid regions, such as desert locusts and African armyworm moths, *Spodoptera exempta*, allow themselves to be carried towards large-scale convergence zones where seasonal rains are likely to occur, and hence survive by exploiting successive areas where the vegetation is temporally lush and suitable for reproduction (Pedgley 1981, Pedgley et al. 1995). However, the precise means by which the very large number of migratory insect individuals and species that occur in the temperate zone survive throughout the course of the year is largely unknown. The only well-documented species is the monarch butterfly, *Danaus plexippus*, which is probably atypical of most other insect migrants because it migrates southwards in North America to enter diapause at specific over-wintering sites, notably in Mexico (Solensky 2004). By contrast, most other insect migrants probably have far more widely-distributed (but currently unknown) over-wintering sites, and breed continuously throughout the year, including during winter.

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

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

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

Material and methods

Study species

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

Study regions

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

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

Datasets

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

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

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

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

(3) *Radar observations of insect migrations*. Data were obtained from radars located in England and Finland (for 2009) and in Mauritania (for 2003 and 2004). English data were obtained from a vertical-looking entomological radar (VLR) situated in Chilbolton, Hampshire (51º8'40'' N, 1º26'13'' W), which provided information on the intensity of high-altitude flights (i.e. the number of butterflies actively migrating through a 1 km^2 'window' of the atmosphere), the altitude of flights, ground speed and direction of movements. Finnish data were obtained from three weather radars situated in southern Finland: Helsinki-Kumpula

(60°12'16" N, 24°57'47" E), Järvenpää (60°29'4" N, 25°4'55" E), and Kerava (60°23'17" N, 25°6'50" E). Mauritanian data were collected by two ornithological radars, running in either a fixed-beam mode or tracking mode, operated by the Swiss Ornithological Institute in 24 August-25 October 2003 and 15 March-10 May 2004 in central Mauritania, near the oasis of Ouadâne (20º 56' N, 11º35' W), and on the Mauritanian coast, near Nouakchott (18°6' N, 15°57' W).

Data analysis

Phenology and frequency of migrations

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

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

Migration directions

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

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

In the case of VLR radar data at Chilbolton, we analysed individual high-flying targets attributable to *V. cardui*, rather than daily means, because they are not subject to human measurement error. The number of individuals detected on most days was small (<20 per day), and butterflies were flying over a long period (8 hours) and wide altitude range (150-1,200 m above ground level (a.g.l.)), such that very few individuals will have been flying under the same wind conditions; thus the potential for pseudoreplication to skew the results is also very low in these data. We therefore carried out circular statistics on all individual radar-detected butterflies to find the mean seasonal migration directions, and in addition we calculated the mean daily direction for the two principal spring migration dates in the UK (25 and 29 May 2009), which together accounted for 43% of all spring radar-detected butterflies at Chilbolton during 2009.

Comparison of high-altitude and ground-level migrations

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

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

Results

Seasonal distribution of populations

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

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

Mating behaviour and egg-laying were observed as soon as migrants arrived in the Mediterranean, while larvae were recorded in large numbers soon after, giving rise to the emergence of a local adult generation from mid May to the beginning of June. The appearance of this new generation coincided with the second critical period of the expansion in Europe (Fig. 2, Supplementary material Appendix 3). The eastern part of Central Europe was colonized in a continuous succession of migratory waves between 10-25 May, while the western part had two distinct peaks of immigration, the first on 24-25 May and the second between 28 May and 1 June (Fig. 3). Butterflies from the first peak probably belonged to the same migrants colonising eastern Central Europe from the southern Mediterranean coast, part of which eventually progressed in a north-westward direction. Migrants from the second peak originated in the Iberian Peninsula and further south (e.g. northern Morocco and northwestern Algeria), as deduced from a mixture of worn and fresh butterflies in northward flights in coastal areas of Portugal, southern Spain and the Balearic Islands. In Northern Europe, migrants were not recorded in abundance until the third week of May, and secondary peaks of migration occurred during the second half of June (Fig. 3).

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

Data from 2009 and previous years show an increase in the number of records in the African continent in August and subsequent months, coincident with the disappearance of European populations (Fig. 2). The few systematic counts that have been carried out in the Sahel and further south in Western Africa confirm the sudden arrival of *V. cardui* from the end of August to early October (e.g. data from Mauritania, The Gambia and Sierra Leone). However, this population is apparently soon gone again, given its complete absence from extensive areas in the Sahel from December to March (e.g. comprehensive surveys in Senegal and Mali in 2009 and 2010). Immigrations into Northwestern Africa occurs mainly in October and early November (more rarely in late September), with the species being recorded at relatively low densities all through the winter months (Fig. 2).

Frequency and direction of migratory flights near the ground

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

Data from ground-level migratory flights in Africa were too scarce to draw any firm conclusion. In Northwestern Africa, northward flights precipitating the colonization of the Mediterranean region clearly predominate in the spring but the situation becomes more complex in the autumn, when southward and northward flights were equally recorded, which may genuinely represent immigration from both the south (Sahel) and north (Central Europe and Mediterranean). In Western Africa there were a few reports of southward and westward flights from August to November, while a single massive northward flight of several thousands of butterflies was observed in Mali in early November 2009.

Frequency and direction of high-altitude migratory flights

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

Migratory activity remained rather low through June and July, but increased again from the beginning of August to mid October, when it peaked on certain days, e.g. 7 August with ~1.2 million, 5 September with ~1.0 million, and 19 September with ~1.6 million high-flying butterflies passing southward (Fig. 5). Over the whole late-summer/autumn period (August–October), we estimate that ~25.9 million *V. cardui* engaged in high-altitude flights, but of these only 55% (~14.1 million) were transported in a generally southwards direction, i.e. between 90° and 270°. However, the overall mean direction of all butterflies was in a south-westward direction (mean migration direction: 236º, $n = 446$ individuals, $r = 0.16$, $p < 0.001$) and there was a distinct absence of flights close (± 20°) to north (Supplementary material Appendix 4). The mean migration direction was thus almost 180° opposite to the mean spring direction, albeit with a greater dispersion of individual tracks. The mean migration direction (towards the south-west) contrasts with the patterns of high-altitude winds (measured at 300 m) during the autumn migration period, which had a significant mean direction blowing from the WSW towards the ENE (wind from: 251°, $n = 63$ days, $r = 0.22$, $p = 0.048$), and a comparative shortage of northerly winds favourable for autumn return migration. Thus there is some evidence that butterflies preferentially migrated on winds with a northerly component (resulting in a significant tendency for southward displacement), even though many of the individuals were displaced in unfavourable directions (towards the north-west or north-east) due to the shortage of suitable tailwinds. The mean displacement speed during summer/autumn migrations was 12.7 m/s (~45 km/h).

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

Southward migration across the Gulf of Finland was also recorded by radars at Kerava and Kumpula between 3-6 August 2009 (Fig. 6a-b). On 5 August, the Kumpula radar vertical sections over the land and over the sea showed that these insects were flying mostly in the layer 500-700 m a.g.l. During the morning hours of 6 August, however, the wind direction changed from northerly to south-easterly and the insects drifted towards west and north-west to end up back on the Finnish coast and several nearby southern islands (Fig. 6c-d). Thousands of *V. cardui* were then recorded in this area, pointing towards a massive southward windborne flight that was interrupted by a sudden change in the formerly favourable weather conditions for migration. High-altitude southward migrations of large-sized insects across the Gulf of Finland were recorded again by Finnish radars throughout August (see details in www.helsinki.fi/~mleskine/vaellus/Vcar2009.html), suggesting the existence of regular return flights of *V. cardui* out of sight from ground-level observers.

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

Relationship between ground-level migrations and vertical looking radar data

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

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

Discussion

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

Although further details of the African legs of the migration are still needed, the basic pattern appears to be that of the successive displacement and reproduction of a population that in years of high abundance may attain a size of thousands of millions of individuals, through ca. six generations (see Supplementary material Appendix 6 for a full description of the migratory model). The extremities of the migration go from the Sahel region of Western Africa (at least for a large portion of the population) through North Africa, the Mediterranean, Central and Northern Europe, before retreating back to Africa in one or two steps. In addition, the predominant population movement described here meets additional populations in Eastern Europe and into Asia, and other populations apparently circulate within central and southern Africa (e.g. Williams 1930, Larsen 1976, John 2001). The extent to which there is gene flow between these different populations is unknown, although the low levels of genetic substructuring across continents (Wahlberg and Rubinoff 2011) suggests that it might be high. A strong gene flow leading to genetic homogeneity of populations has also been found in other migratory insects, and seems to be a common pattern in highly mobile species (Peterson and Denno 1998).

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

We believe that a key aspect for the whole migratory system to be maintained is the ability of *V. cardui* to use favourable high altitude winds to move rapidly in appropiate seasonal directions (see also Stefanescu et al. 2007). This would seem to be necessary particularly in the autumn given the distances that must be covered during this part of the annual cycle. Indeed, our results strongly suggest that butterflies leaving the European continent on their return flight travel far above the ground and mostly remain unnoticed by observers (Fig. 4). The radar data from southern England in autumn 2009 indicate that migrating *V. cardui* were not very successful at selecting suitable winds, given that only 55% of the radar-detected high-flying butterflies were displaced in a southwards direction. However, analysis of wind directions during this period indicated that there was a preponderance of winds blowing from the south-west and WSW, and relatively few days when winds blew from the north, and so presumably the shortage of suitable transport opportunities resulted in butterflies being forced to move on less than ideal winds. Radar observations from previous *V. cardui* invasions of the UK have shown much clearer southward return migrations (Chapman et al. 2010), and the Finnish radar data in the present study also demonstrate the ability of high-flying *V. cardui* to preferentially select suitable winds. We thus conclude that transport on fast-moving high-altitude winds is an essential part of the annual cycle, particularly during the autumn. Although windborne migration above the FBL has been widely described in insects showing long-range seasonal movements, particularly pest species (Chapman et al. 2011a,b), its presence had been questioned in some large day-flying insects such as butterflies and dragonflies (e.g. Baker 1978, Walker 1980, Walker and Riordan 1981). However, strong similarities in the strategies used by *V. cardui* and other migrant Lepidoptera, such as noctuids and hawk-moths (Chapman et al. 2010), raises the possibility that high-altitude windborne flights may be, in fact, much more widespread among migrant butterflies than has been assumed. The scarcity of records could be simply due to the difficulty of collecting data from the ground (see also Gibo 1981, Mikkola 2003). In this respect, radar technology is a useful complementary tool, as has been shown in our study.

However important high-altitude migration is, ground-level observations of movements along fixed compass bearings are very commonly reported in the spring, indicating that migration at ground level is still a major feature of *V. cardui*. The high synchrony that we found between high-altitude and ground-level migration shows that the two are linked. Whether higher and lower altitude flights represent distinct behaviours or phases of migration, as first suggested by Mikkola (1986), requires further work. This might be affected by both the prevailing weather conditions and individual physiological and reproductive characteristics (cf. Johnson 1969, McNeil et al. 1995).

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

In summary, we have documented a continuously-breeding migration path, in which a species undertakes a round-trip migration of up to 15,000 km (up to 60 degrees of latitude and back) from tropical Africa to northern Europe. This is close to double the latitudinal migration distance of the famed monarch butterfly (Solensky 2004), and potentially exceeds the distance achieved by the globe-skimmer dragonfly *Pantala flavescens* (Anderson 2009). The capacity of *V. cardui* to exploit winds and maintain migratory direction enables it to maintain this exceptionally long inter-generation migration route. We believe that our findings provide a useful framework for the study of insect migration in the temperate regions worldwide, especially for those species sharing common life-history traits with *V. cardui* (e.g. continuous breeding, strong polyphagy and habitat generalism) and predictable patterns of seasonal movements. Because these species include some of the most serious agricultural pests and may act as vectors of infections and diseases (Cannon 1998, Reynolds et al. 2006), understanding their migratory strategies is undoubtedly an essential issue.

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

Subregion	**Direction (º)**	***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

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 vertical looking radar), and the daily frequency of ground-level migratory flights in different subregions of Europe in spring (April-June) and summer/fall (July-November). OLS: ordinary least squares regression models; GLM: quasi-Poisson regression models. Med: Mediterranean, CEur: Central Europe, NEur: Northern Europe, All: all subregions pooled. Correlations were calculated with lags of one day for LagMed and LagNEur, under the hypothesis that windborne migrants passing over the Mediterranean would arrive one day later in southern England, and migrants passing over southern England would arrive one day later in Northern Europe. Significance levels: ** $p < 0.01$, *** $p < 0.001$.

			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**

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

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

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

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

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

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

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

Fig. 1.

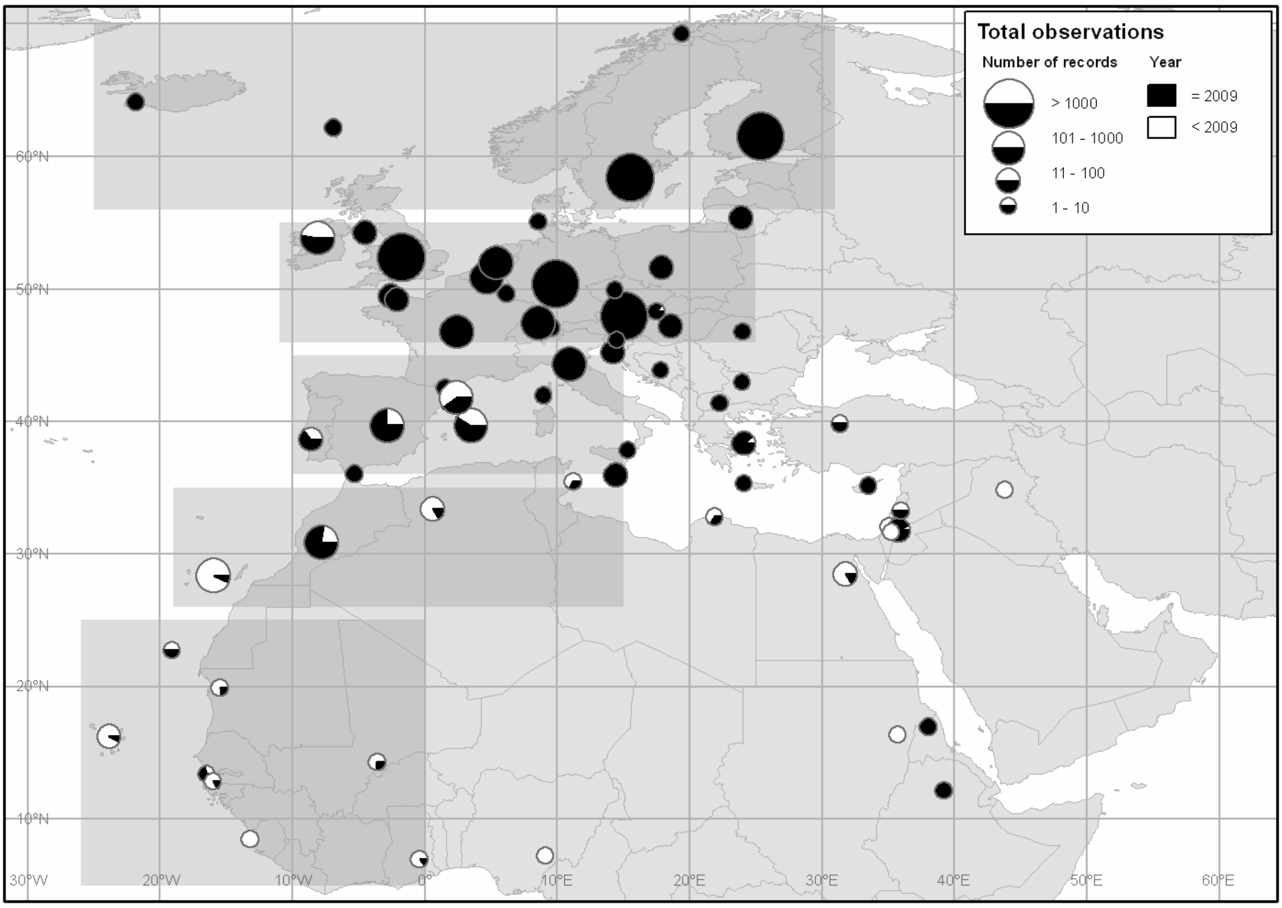

Total observations
Number of records
> 1000
101 - 1000
11 - 100
1 - 10
Year
= 2009
< 2009
60°N
50°N
40°N
30°N
20°N
10°N
30°W
20°W
10°W
0°
10°E
20°E
30°E
40°E
50°E
60°E

Fig. 2.

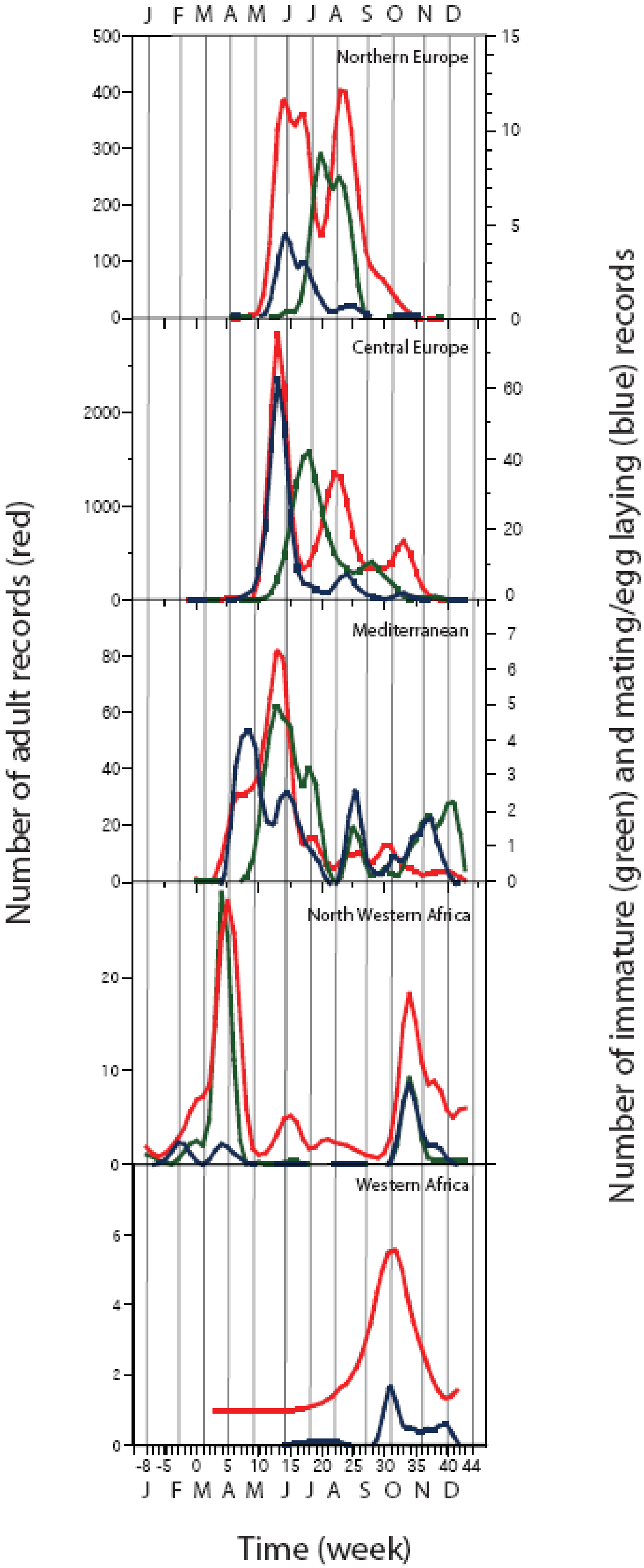

J F M A M J J A S O N D
Northern Europe
Central Europe
Mediterranean
North Western Africa
Western Africa
500
400
300
200
100
0
2000
1000
80
60
40
20
10
6
4
2
15
10
5
60
40
20
7
6
5
4
3
2
1
-8 -5 0 5 10 15 20 25 30 35 40 44
Number of adult records (red)
Number of immature (green) and mating/egg laying (blue) records
Time (week)

Fig. 3.

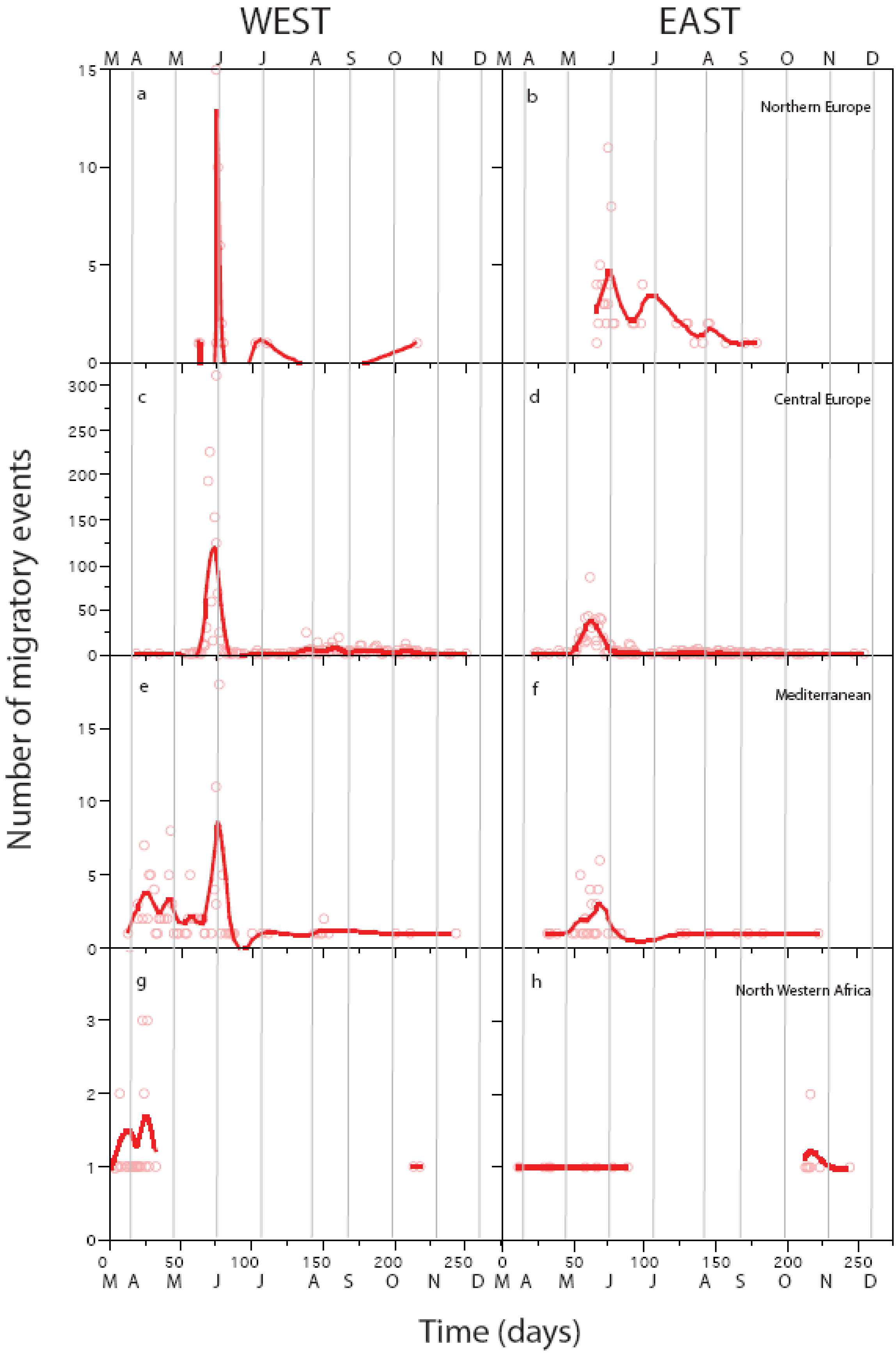

WEST
EAST
M A M J J A S O N D
M A M J J A S O N D
a
b
Northern Europe
c
d
Central Europe
e
f
Mediterranean
g
h
North Western Africa
0 5 10 15
0 50 100 150 200 250 300
0 5 10 15
0 1 2 3
0 50 100 150 200 250
0 50 100 150 200 250
Number of migratory events
Time (days)

Fig. 4.

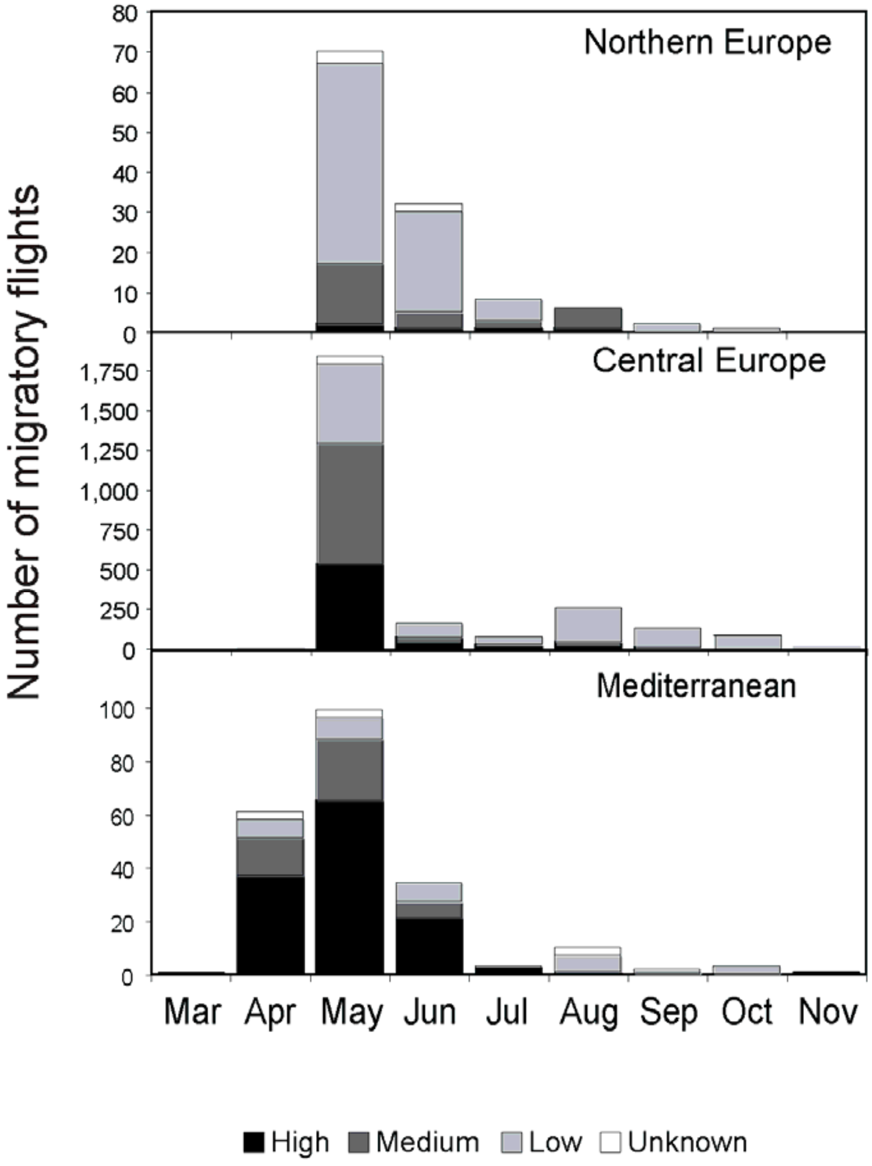

Number of migratory flights
Northern Europe
80
70
60
50
40
30
20
10
0
Central Europe
1,750
1,500
1,250
1,000
750
500
250
0
Mediterranean
100
80
60
40
20
0
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
■ High
▨ Medium
▨ Low
☐ Unknown

Fig. 5.

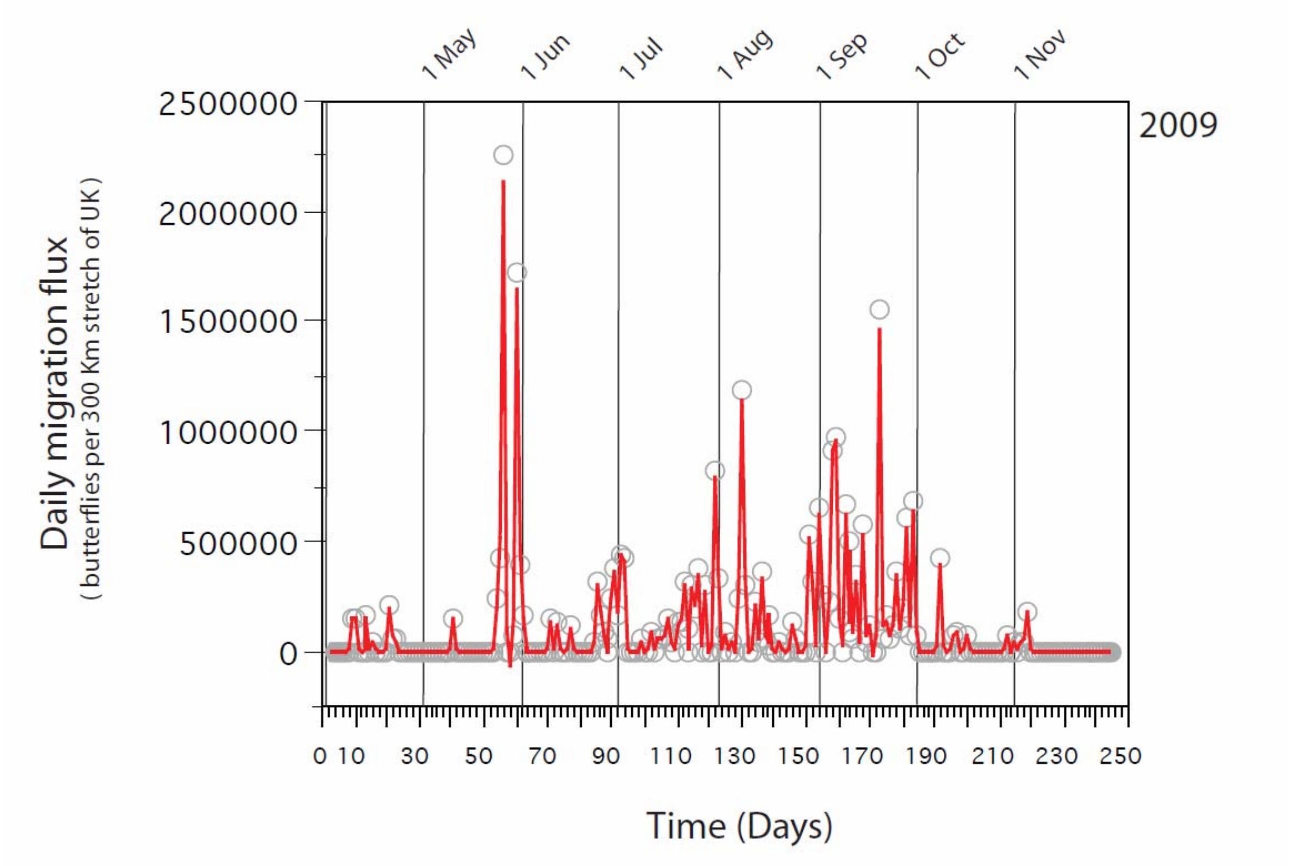
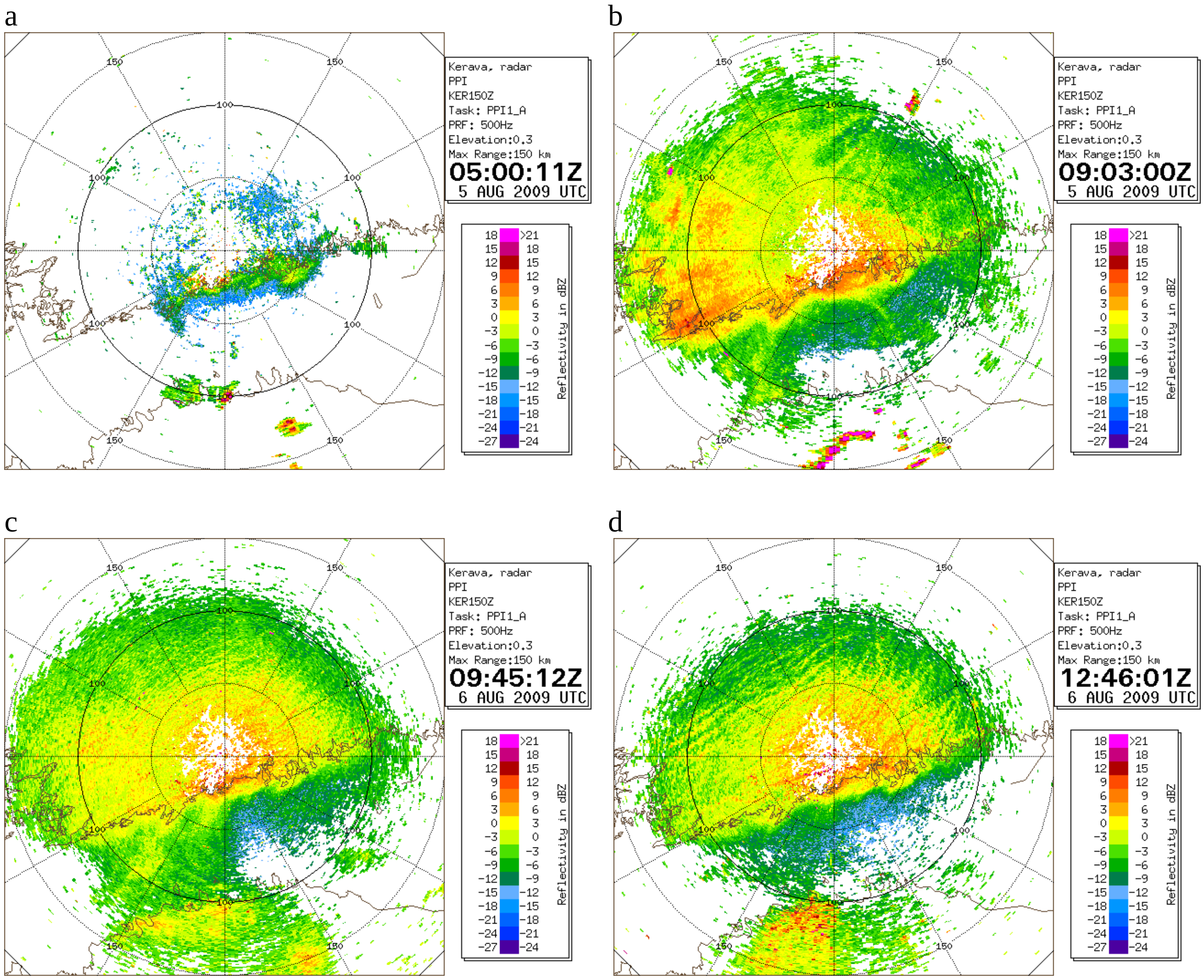

1 May
1 Jun
1 Jul
1 Aug
1 Sep
1 Oct
1 Nov
2009
Daily migration flux
(butterflies per 300 Km stretch of UK)
2500000
2000000
1500000
1000000
500000
0
0
10
30
50
70
90
110
130
150
170
190
210
230
250
Time (Days)

Fig. 6.


a
Kerava, radar
PPI
KER150Z
Task: PPI1_A
PRF: 500Hz
Elevation:0.3
Max Range:150 km
05:00:11Z
5 AUG 2009 UTC
b
Kerava, radar
PPI
KER150Z
Task: PPI1_A
PRF: 500Hz
Elevation:0.3
Max Range:150 km
09:03:00Z
5 AUG 2009 UTC
c
Kerava, radar
PPI
KER150Z
Task: PPI1_A
PRF: 500Hz
Elevation:0.3
Max Range:150 km
09:45:12Z
6 AUG 2009 UTC
d
Kerava, radar
PPI
KER150Z
Task: PPI1_A
PRF: 500Hz
Elevation:0.3
Max Range:150 km
12:46:01Z
6 AUG 2009 UTC
150
100
18 >21
15 18
12 15
9 12
6 9
3 6
0 3
-3 0
-6 -3
-9 -6
-12 -9
-15 -12
-18 -15
-21 -18
-24 -21
-27 -24
Reflectivity in dBZ

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 S1a. 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 S1b. 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

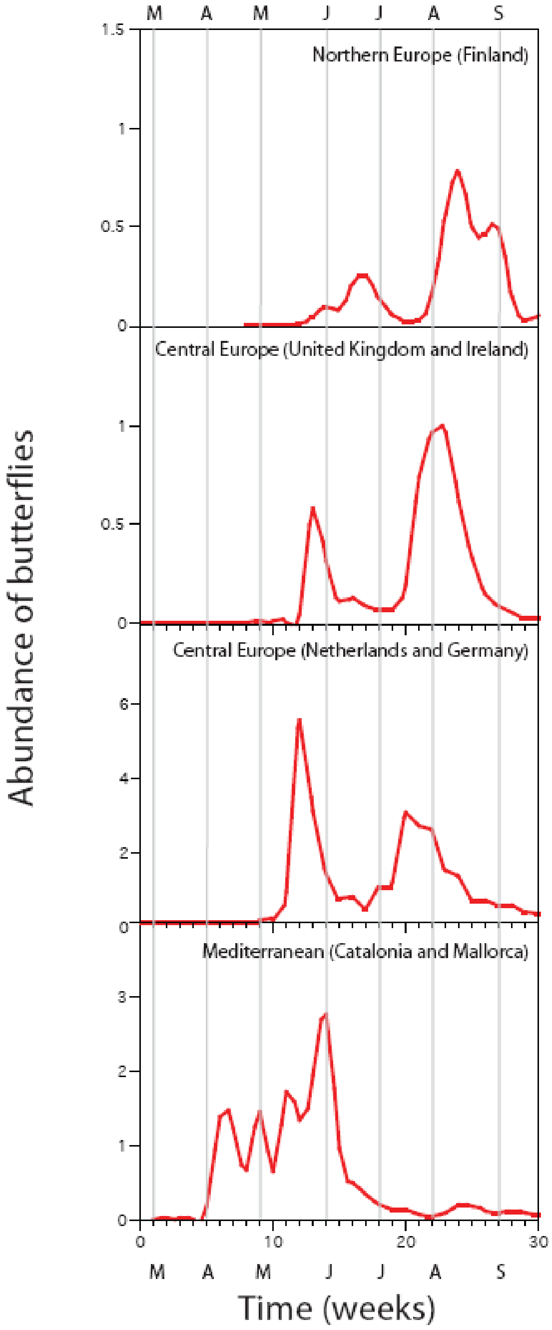
Table S1c. Number of records across the five latitudinal regions considered in our analysis, and at different longitudes within each region (all years and 2009).

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.

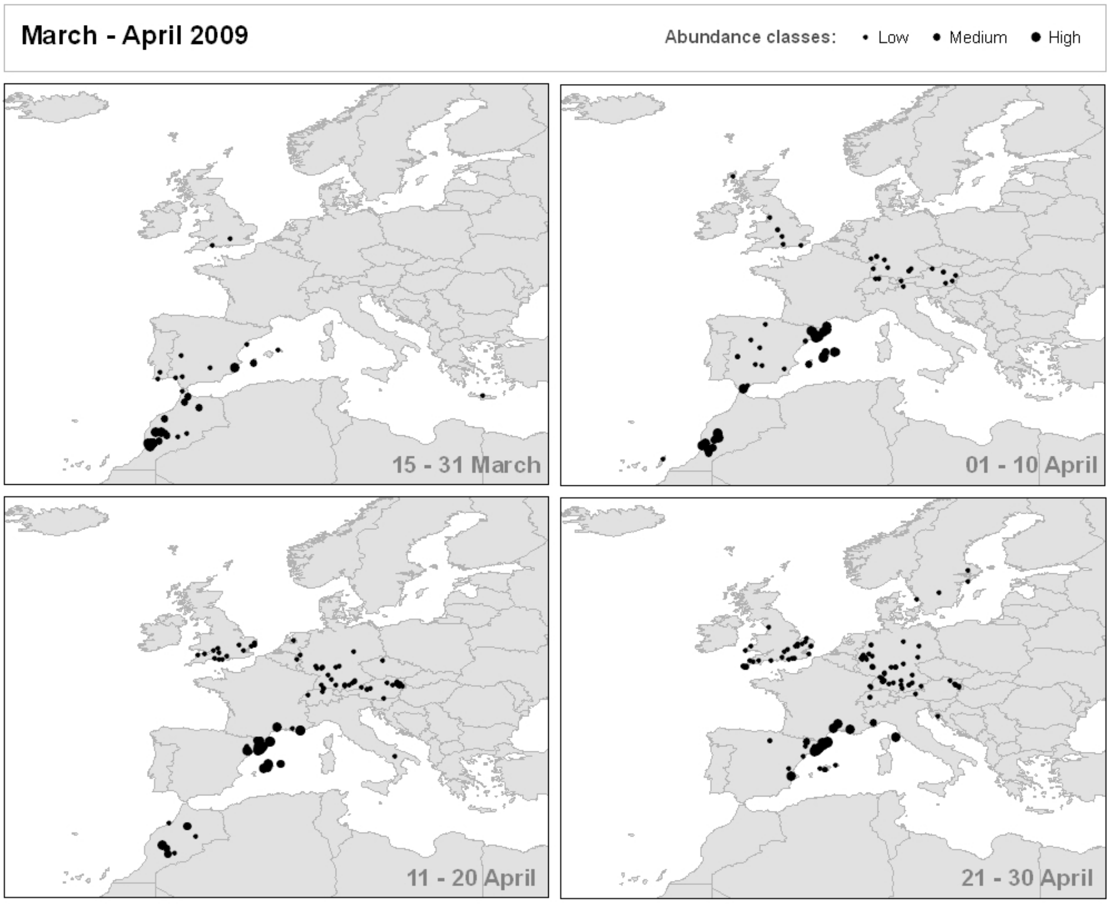


Fig. S3a. Colonization of Europe by *Vanessa cardui* in March-April 2009. All European records during this period likely corresponded to migrants originating in western-central Morocco. Note that distributional data are biased due to higher sampling efforts in the UK, Central Europe (Austria, Germany and Switzerland), Sweden and Finland compared to the rest of Europe and North Africa.

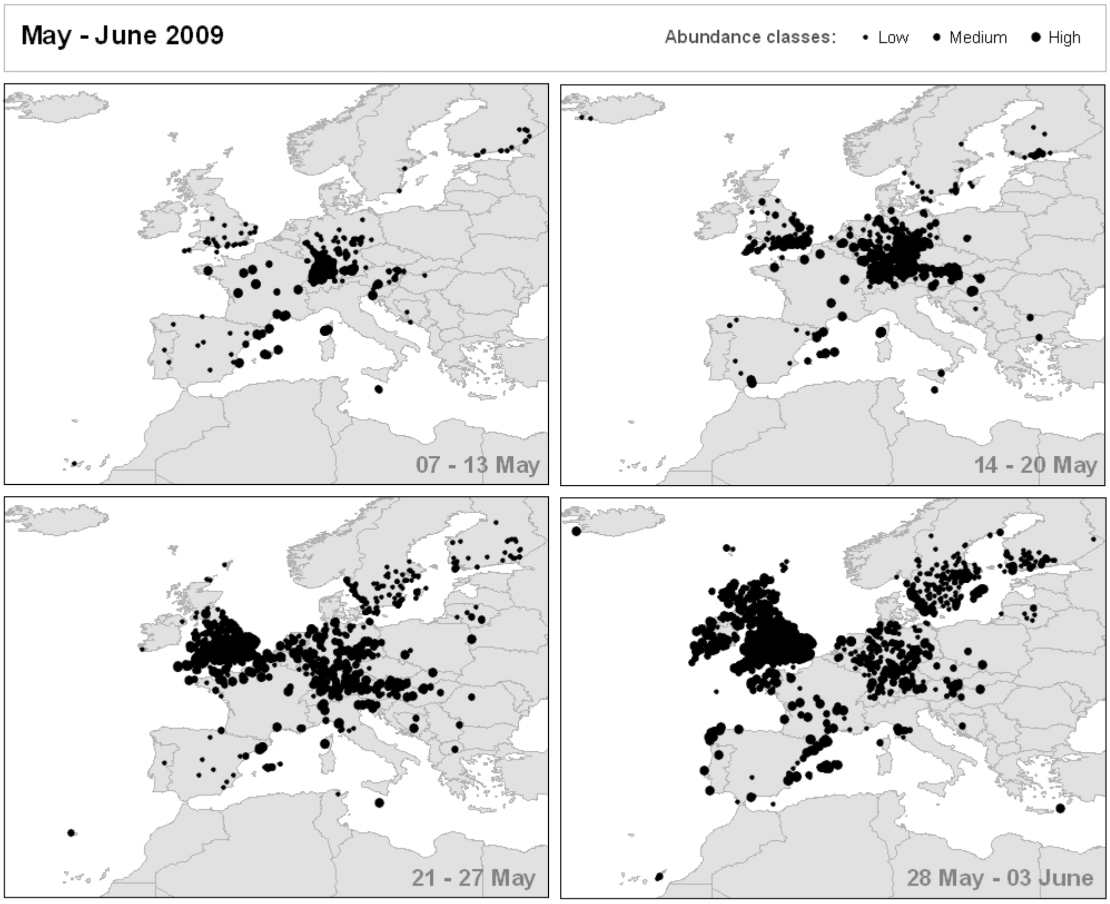
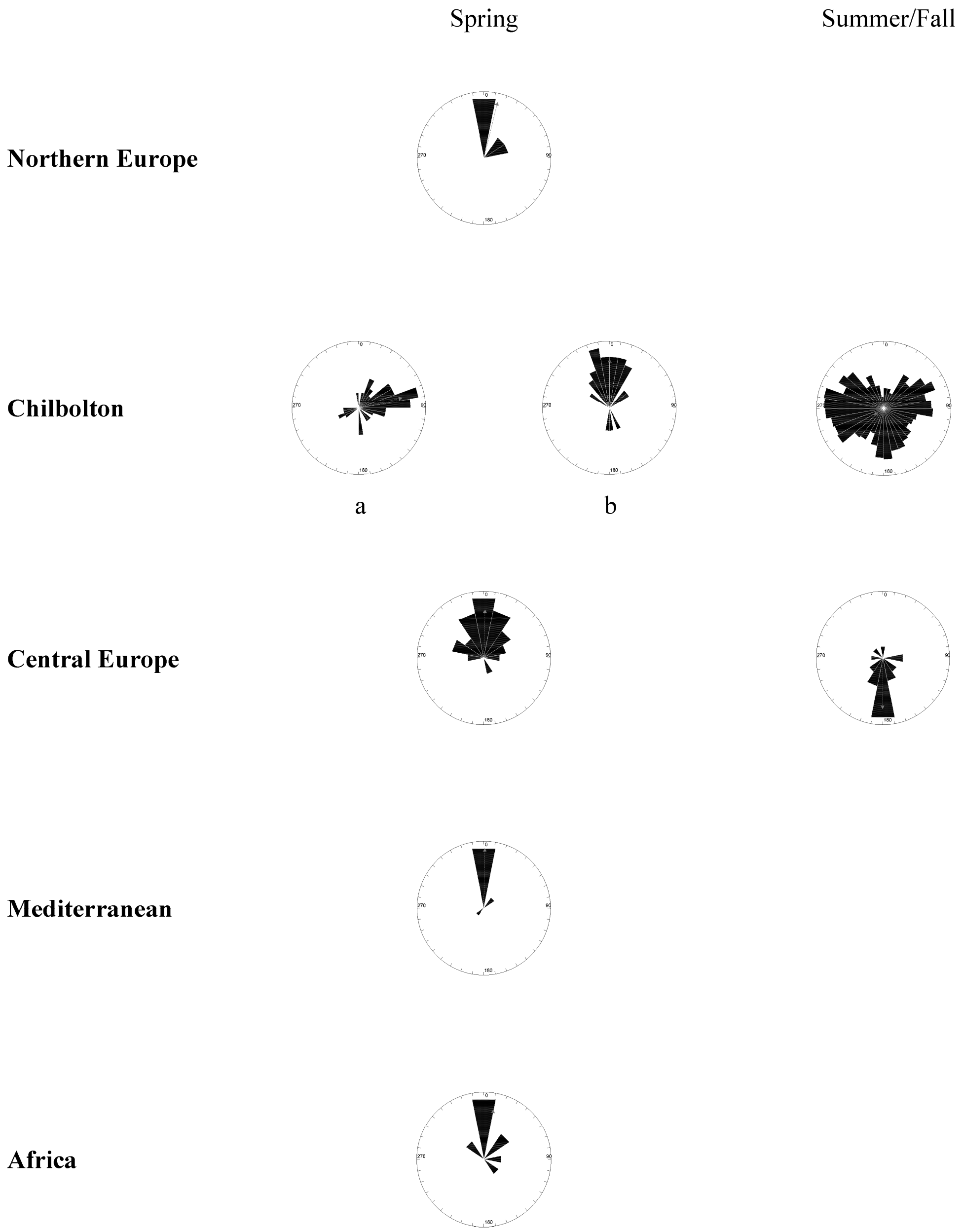


Fig. S3b. Colonization of Europe by *Vanessa cardui* in May-early June 2009. Eastern-central Europe was colonized by mid May by migrants likely originating in the southern Mediterranean shore (e.g. eastern Algeria, Tunisia and Libya). By 24-25 May part of these migrants had moved in a north-westward 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.

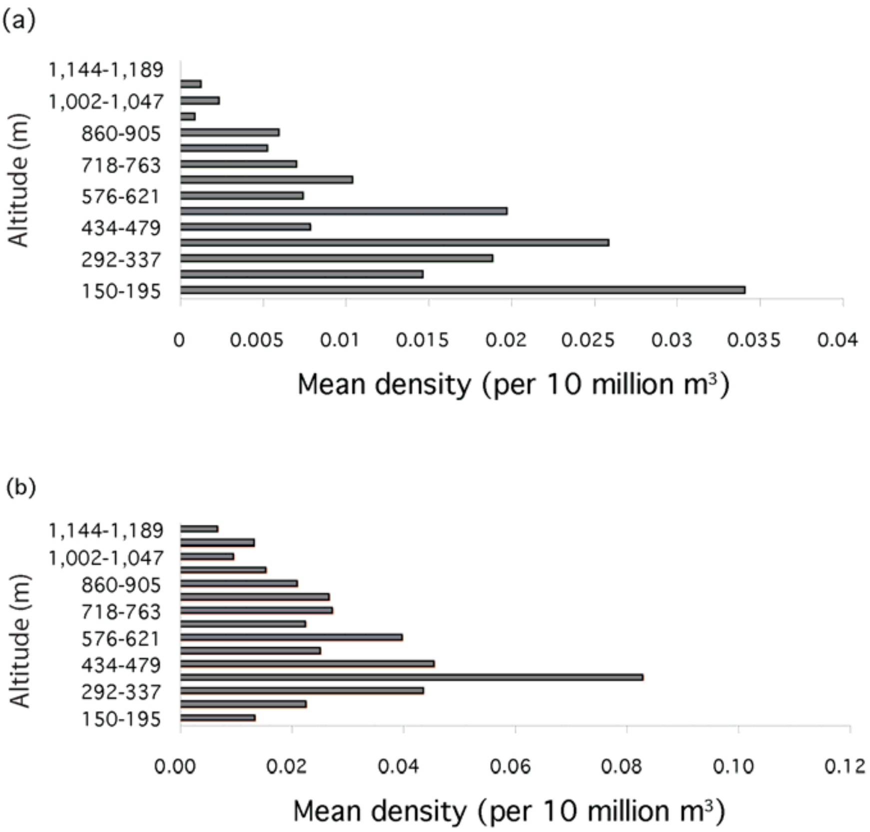
Appendix 4

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.


Spring
Summer/Fall
Northern Europe
Chilbolton
a
b
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).



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.

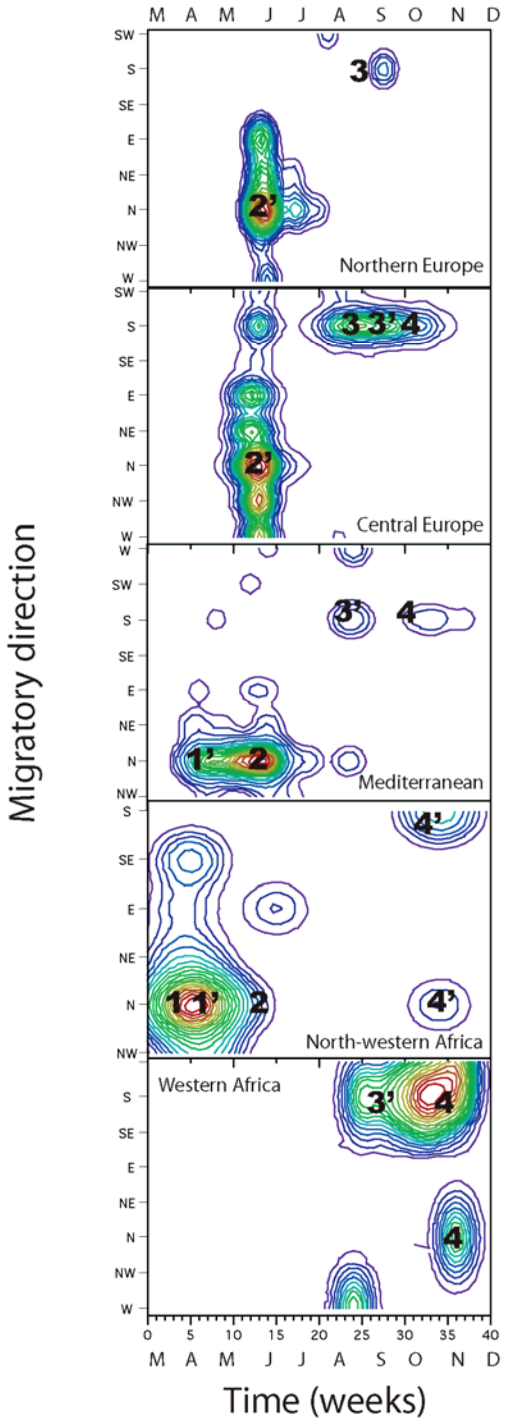


Fig. S6. A conceptual model for migration of *Vanessa cardui* in the western Palaearctic and West African regions. Smooth surfaces show density of records of migration in five latitudinal bands, together with observed heading directions. Red contour lines indicate maximum point density. Numbers indicate 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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