

Multi-generational long-distance migration of the painted lady butterfly between Africa and Europe

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59 *Abstract.* Long-range, seasonal migration is a widespread phenomenon among insects,
60 allowing them to track and exploit abundant but ephemeral resources over vast geographical
61 areas. However, the basic patterns of how species shift across multiple locations and seasons
62 are unknown in most cases, even though migrant species comprise an important component of
63 the temperate-zone biota. The painted lady butterfly, *Vanessa cardui*, is such an example; a
64 cosmopolitan continuously-brooded species which migrates each year between Africa and
65 Europe, sometimes in enormous numbers. The migration of 2009 was one of the most
66 impressive recorded, and thousands of records were collected through citizen science
67 programmes and systematic entomological surveys, such as insect-monitoring radar and
68 butterfly monitoring schemes. In this pan-European collaborative study, we use these various
69 and complementary data sources to investigate the migration system of *V. cardui* in the
70 western Palaearctic. We found an annual poleward advance of the populations followed by an
71 equatorward return movement, encompassing a latitudinal shift of thousands of kilometres.
72 This migratory cycle involves six generations, some of which move seasonally from an area
73 of emergence to a breeding area located at a distance of hundreds of kilometers. We show, for
74 the first time, that summer and autumn European generations engage in return flights, with
75 returning individuals potentially moving thousands of kilometres. We also provide conclusive
76 evidence that many long-distance migrants take advantage of favourable winds, moving
77 downwind at high elevation (from some tens of metres from the ground to altitudes over
78 1,000 m), pointing at strong similarities in the strategies used by *V. cardui* and other migrant
79 Lepidoptera. *Vanessa cardui* undertakes a round-trip migration with major population
80 movement taking place over 5,000 to 15,000 km (up to 60 degrees of latitude and back) from
81 tropical Africa to northern Europe, maintaining direction and “population integrity” across
82 multiple generations.

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84

85 **Introduction**

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87 Large parts of the world are characterised by the seasonal abundance of resources,
88 interspersed by periods when resources are unavailable or when the physical environment is
89 inhospitable for survival. Most species exploit such resources *in situ* by means of diapausing
90 stages, including seed and egg banks, hibernation and aestivation (Tauber et al. 1986).
91 However, the evolution of hypometabolic or dormant states has only been achieved by a
92 relatively small subset of the world's species, the majority remaining at least partially active
93 throughout the year in relatively aseasonal regions (e.g. the moist tropics).

94 The alternative potential strategy to exploit temporary resources is by some form of
95 migration, breeding when temporary resources become available, and then retreating to
96 locations where survival is possible at other times of the year (Dingle 1996, Dingle and Drake
97 2007). This phenomenon is best studied in vertebrates and other long-lived animals (e.g.
98 Newton 2008), which have generation times comparable to or longer than the annual seasonal
99 cycle. Individuals of these species either migrate with conspecifics (often family groups) and
100 learn traditional routes, or immatures migrate in genetically-determined seasonal directions,
101 and then retrace their steps back to the breeding grounds in the following season or year.
102 Thus, individuals track suitable environments during their lifetimes.

103 Investigation of migration in species with generation times much shorter than the seasonal
104 cycle or year is generally more difficult, and this is the case for the majority of migratory
105 insects (Drake and Gatehouse 1995, Holland et al. 2006). Insects that track suitable
106 environments (arising from responses to spatially and temporally variable conditions) must
107 exhibit patterns of movement that encompass multiple generations. Inhabitants of arid/semi-
108 arid regions, such as desert locusts and African armyworm moths allow themselves to be
109 carried towards large-scale convergence zones where seasonal rains are likely to occur, and

110 hence survive by exploiting successive areas where the vegetation is temporally lush and
111 suitable for reproduction (Pedgley 1981, Pedgley et al. 1995). However, the precise means by
112 which the very large number of migratory insect individuals and species that occur in the
113 temperate zone survive throughout the course of the year is largely unknown. Most of these
114 species are in the northern hemisphere, given the distribution of land in the two hemispheres.
115 The only well-documented species is the monarch butterfly, *Danaus plexippus*, which is
116 highly atypical because it migrates southwards in the North American autumn and then enters
117 physiological diapause at specific sites, notably in Mexico. This species thus combines
118 migration and diapause (cf. Reppert et al. 2010). This leaves open the question of whether
119 other species also use (unknown) over-wintering sites, or whether they breed continuously
120 throughout the year, in a succession of migratory steps from south to north and back again.

121 In this study, we document the migration of the highly migratory painted lady butterfly,
122 *Vanessa cardui*, in Europe, concentrating on the exceptional events recorded in 2009. Each
123 year, this butterfly species colonizes the European continent from its African overwintering
124 quarters (Pollard et al. 1998, Stefanescu et al. 2011). However, the pattern and timing of the
125 whole migration system is poorly understood, and return migration back to Africa during
126 autumn remains largely hypothetical. The scarcity of records of southward return migrations
127 has even led to the suggestion that this species may regularly disperse beyond areas that are
128 favourable for long-term survival and reproduction, without any chance of a return movement
129 (i.e. the evolutionary paradox known as the ‘Pied-Piper phenomenon’; see discussion in
130 Nesbit et al. 2009).

131 In 2009, numbers of *V. cardui* migrating across Europe were so high that they raised
132 awareness among the general public, with the result that a large number of people contributed
133 to online surveys and made it possible to investigate with unprecedented detail the migration
134 system in this part of the range. Additional data were obtained through more systematic

135 surveys based on established protocols, such as the extensive network of butterfly recording
136 schemes operating in many European countries (van Swaay et al. 2008), and the continuous
137 monitoring of high-altitude insect migrations by radars operating in southern England and
138 Finland (e.g. Chapman et al. 2003, Leskinen et al. 2011).

139 Here we bring together a combination of ground and aerial (radar) observations to
140 evaluate the following hypotheses:

141

142 a) Does this species exhibit a succession of population shifts throughout the year, representing
143 a succession of breeding generations?

144 b) In Central and Northern Europe (for which the best data are available), does the species
145 show a clear reversal of migratory direction from early season (spring) to late season
146 (autumn) generations?

147 c) Is migration wind-assisted and at least partly at high altitude (as suggested by Stefanescu et
148 al. 2007), or, in common with other migratory butterflies, largely restricted to within their
149 Flight Boundary Layer (i.e. the layer of the atmosphere close to the ground where the wind is
150 light enough for the insect to make progress in any direction; Srygley and Oliveira 2001)?

151

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

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159 **Material and methods**

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162 **Study species**

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

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179

180 **Study regions**

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182 The present analysis covers the western Palaearctic region (i.e. the biogeographical region
183 that includes the western part of the Eurasian landmass and northernmost Africa) and West

184 Africa (i.e. the region of western Africa between the Sahara Desert and the Gulf of Guinea).

185 We divided this geographical area into the following five subregions, which coincide with

186 broadly recognized biogeographic regions:

187 (1) Western Africa (5-25°N, 26°W-0°W),

188 (2) Northwestern Africa (26-35°N, 19°W-15°E),

189 (3) Western and Central Mediterranean (36-45°N, 10°W-15°E),

190 (4) Western and Central Europe (46-55°N, 11°W-25°E), and

191 (5) Northern Europe (56-71°N, 25°W-31°E) (Fig. 1).

192 For simplicity, subregions (3) and (4) are referred to as Mediterranean and Central Europe,

193 respectively. In order to document the European migration pattern in more detail, the last

194 three subregions have been further divided into a western and an eastern part along the 5°E

195 meridian (for the Mediterranean) or the 2°E meridian (for Central and Northern Europe) in

196 some analyses.

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199 **Datasets**

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201 We used three independent datasets:

202

203 (1) *Ad-hoc distribution records*. 30,002 observations of adults or immatures encompassing the

204 latitudinal range 5°-71° N and 67 countries/regions, obtained from a diversity of sources. Data

205 were gathered during 2009, except for a subset of 1,337 records (including some published

206 data) from earlier years. Records prior to 2009 have mainly been used to improve knowledge

207 of the timing and location of the species' breeding quarters in Africa. Each record contained

208 at least information on location and date of the observation. In many cases there was also

209 information on relative abundance, adult behaviour (e.g. reproductive and migratory
210 behaviours) and condition of butterflies (i.e. fresh, worn). We classified butterflies as
211 migrating within the Flight Boundary Layer (FBL) whenever they showed sustained and
212 undistracted low altitude flights (i.e. up to 20 m from the surface, generally within the 2 m)
213 (Dingle and Drake 2007). The main heading direction was classified into eight compass
214 directions (north, northeast, east, etc.).

215
216 (2) *Butterfly Monitoring Scheme (BMS) records*. 30,358 weekly estimates of adult densities
217 (butterflies seen on 100 m of line transect) were extracted from standardized transect counts
218 carried out between March and September 2009 in eight European countries/regions:
219 Andorra, Balearic Islands, Catalonia (NE Spain), Finland, Germany, Ireland, The Netherlands
220 and the UK. Data were pooled into three different latitudinal bands (Northern Europe, Central
221 Europe and Mediterranean), matching the geographical subregions defined above. For Central
222 Europe we distinguished two subsets of the data: that covering Britain and Ireland and the
223 Dutch-German data, respectively, as we had good evidence that migratory waves arriving into
224 these areas frequently had different origins and followed different routes.

225
226 (3) *Radar observations of insect migrations*. Data were obtained from radars located in
227 England and Finland (for 2009) and in Mauritania (for 2003 and 2004). Radar provided
228 information on migratory intensity (i.e. number of butterflies involved in migratory flights),
229 the altitude of flights, ground speed and direction of movements. English data were obtained
230 from a vertical-looking entomological radar (VLR) situated in Chilbolton, Hampshire
231 ($51^{\circ}8'40''$ N, $1^{\circ}26'13''$ W). Finnish data were obtained from three weather radars situated in
232 southern Finland: Helsinki-Kumpula ($60^{\circ}12'16''$ N, $24^{\circ}57'47''$ E), Järvenpää ($60^{\circ}29'4''$ N,
233 $25^{\circ}4'55''$ E), and Kerava ($60^{\circ}23'17''$ N, $25^{\circ}6'50''$ E). Mauritanian data were collected by two

234 ornithological radars, running in either a fixed-beam mode or tracking mode, operated by the
235 Swiss Ornithological Institute in 24 August-25 October 2003 and 15 March-10 May 2004 in
236 central Mauritania, near the oasis of Ouadâne (20° 56' N, 11°35' W), and on the Mauritanian
237 coast, near Nouakchott (18°6' N, 15°57' W).

238

239 For further details on these datasets see Supplementary material Appendix 1.

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241

242 **Data analysis**

243

244 *Phenology and frequency of migrations*

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

250 Phenological curves showing different generations and waves of migration were fitted
251 using the cubic spline method, using the JMP package (SAS Institute 1989-2002). This
252 method uses a set of third-degree polynomials spliced together such that the resulting curve is
253 continuous and smooth at the splices (knot points). The estimation is done by minimizing an
254 objective function composed by a combination of the sum of squares error and a penalty for
255 curvature integrated over the curve extent.

256 We used direct observations of migration within the FBL to calculate the frequency of
257 migratory events in different regions and to identify those days when peaks of ground-level
258 migration occurred across Europe.

259

260 ***Migration directions***

261 Standard circular statistical methods (Fisher 1993) were used to calculate and compare the
262 mean migration directions of butterflies flying at low altitude, and during different periods
263 and subregions. To estimate the relative number of butterflies migrating within their FBL on a
264 given date in each of the geographical subregions, each observation reporting more than 100
265 individuals was equated to 10 observations reporting 11-100 individuals and 100 observations
266 reporting 1-10 individuals.

267 For ground-based *ad-hoc* data (type 1 data, above), we aggregated data by date: all
268 migrations recorded on the same day in a given subregion were used to calculate the mean
269 track direction on that date (alleviating potential pseudoreplication issues caused by
270 individuals being recorded when they were experiencing the same local conditions; Alerstam
271 et al. 2011), and the Rayleigh test of uniformity for circular data was applied. We also only
272 used data from days with more than 20 individuals to reduce the likelihood of individual
273 recorder measurement error. The same procedure was used for the many thousands of
274 butterfly-like targets detected by the ornithological tracking radars deployed in Mauritania in
275 2003.

276 In the case of VLR radar data at Chilbolton, we analysed individual high-flying targets
277 attributable to *V. cardui*, rather than daily means, because they are not subject to human
278 measurement error. The number of individuals detected on most days were small (<20 per
279 day), and butterflies were flying over a long period (8 hours) and wide altitude range (150-
280 1,200 m), such that very few individuals will have been flying under the same wind
281 conditions; thus the potential for pseudoreplication to skew the results is also very low in
282 these data. We therefore carried out circular statistics on all individual radar-detected
283 butterflies to find the mean seasonal migration directions, in addition to calculating the mean

284 daily direction for the two principal spring migration dates (25 and 29 May 2009), which
285 together accounted for 43% of all spring radar-detected butterflies at Chilbolton during 2009.

286

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

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

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

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304 **Results**

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307 **Seasonal distribution of populations**

308

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

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

323 Mating behaviour and egg-laying were observed as soon as migrants arrived in the
324 Mediterranean, while larvae were recorded in large numbers soon after, giving rise to the
325 emergence of a local adult generation from mid May to the beginning of June. The
326 appearance of this new generation coincided with the second critical period of the expansion
327 of *V. cardui* in Europe (Fig. 2, Supplementary material Appendix 3). The eastern part of
328 Central Europe was colonized in a continuous succession of migratory waves between 10-25
329 May, while the western part had two distinct peaks of immigration, the first on 24-25 May
330 and the second between 28 May and 1 June (Fig. 3). Butterflies from the first peak probably
331 belonged to the same migrants colonising eastern Central Europe from the southern
332 Mediterranean coast, part of which eventually progressed in a north-westward direction. On
333 the other hand, migrants from the second peak originated in the Iberian Peninsula and further

334 south (e.g. northern Morocco and north-western Algeria), as deduced from a mixture of worn
335 and fresh butterflies in northward flights in coastal areas of Portugal, southern Spain and the
336 Balearic Islands. In Northern Europe, migrants were not recorded in abundance until the third
337 week of May, and secondary peaks of migration occurred during the second half of June (Fig.
338 3).

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

353 Data from 2009 and previous years show an increase in the number of records in the
354 African continent in August and subsequent months, coincident with the disappearance of
355 European populations (Fig. 2). The few systematic counts that have been carried out in the
356 Sahel and further south in Western Africa confirm the sudden arrival of *V. cardui* from the
357 end of August to early October (e.g. data from Mauritania, The Gambia and Sierra Leone).
358 However, this population is apparently soon gone again, given its complete absence from

359 extensive areas in the Sahel from December to March (e.g. comprehensive surveys in Senegal
360 and Mali in 2009 and 2010). Immigrations into Northwestern Africa occurs mainly in October
361 and early November (more rarely in late September), with the species being recorded at
362 relatively low densities all through the winter months (Fig. 2).

363

364

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

366

367 We compiled a total of 3,174 observations of ground-level migratory flights, of which 2,894
368 were from Europe in 2009 (Supplementary material Appendix 1). Notably, ground-level
369 spring migration was observed much more commonly than summer/autumn migration in
370 Europe (Fig. 4). Migrations showed a very clear seasonal pattern for direction, with spring
371 flights being essentially northward and summer/autumn flights being southward (Table 1,
372 Supplementary material Appendix 4). The change in the direction of migrations occurred by
373 mid July: the few flights recorded in the Mediterranean in the first fortnight of July (1.4% of
374 the flights in the region; Fig. 4) still showed northward direction, while those recorded in
375 Central and Northern Europe during the second fortnight of July (3.5% of the flights in both
376 regions) were predominantly southward. Overall mean directions in spring were very similar
377 across subregions, although in the western part of Central Europe there was a distinct
378 westward tendency which contrasted with a slight eastward tendency in the eastern part
379 (Table 1). The two distributions were found to be significantly different (mean directions of
380 329° and 18° respectively; test for a common mean direction: $Y_r = 24.5$, $p < 0.0001$).

381 Data from ground-level migratory flights in Africa were too scarce to draw any firm
382 conclusion. In Northwestern Africa, northward flights precipitating the colonization of the
383 Mediterranean region clearly predominate in the spring but the situation becomes more

384 complex in the autumn, when southward and northward flights were equally recorded, which
385 may genuinely represent immigration from both the south (Sahel) and north (Central Europe
386 and Mediterranean). In Western Africa there were a few reports of southward and westward
387 flights from August to November, while a single massive northward flight of several
388 thousands of butterflies was observed in Mali in early November 2009.

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390

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

392

393 High-altitude migration of *V. cardui* was recorded by the Swiss Ornithological Institute's
394 radar group in Mauritania between 25 August and 25 October 2003: large numbers of high-
395 flying, radar-detected insects were present at the radar site on the coast moving generally
396 towards the south (mean migration direction: 188°, n = 20 days, r = 0.33, p = 0.107), on
397 northerly winds (wind from: 35°, n = 1,250, r = 0.48, p < 0.001). Although other insects were
398 also present, *V. cardui* was the most abundant insect at ground-level, as indicated by periodic
399 transect counts (Swiss Ornithological Institute unpubl. data). A similar abundance of ground-
400 level *V. cardui* was recorded 500 km inland, at Ouadâne, although there the high-flying
401 insects were displaced westward (mean migration direction: 283°, n = 49 days, r = 0.61, p <
402 0.001), on easterly winds (wind from: 85°, n = 2,680, r = 0.43, p < 0.001). On 18 October it
403 was possible to demonstrate unequivocally that most insects detected by the radar from
404 ground level up to 2,000 m were *V. cardui*. Observations at high altitude were confirmed by
405 using telescopes trained on the radar 'sensed-volume'. A ground speed of 25.1 ± 3.8 km/h
406 (mean \pm sd) was estimated for a subset of 7 individuals flying at 241 ± 62 m, but speeds at
407 higher altitude were not recorded.

408 Further records of high-altitude migration were obtained by European radars in 2009. At
409 Chilbolton in England, the VLR detected large numbers of *V. cardui*-like targets moving
410 mostly in a northward direction between ~150-1,200 m above ground level (a.g.l.) from April
411 to June, with two major influxes occurring on 25 and 29 May (Fig. 5). Extrapolating from the
412 radar sensed volume, it was estimated that ~2.3 million and ~1.7 million high-flying
413 butterflies would have crossed a 300-km stretch of the English coast on those two days
414 respectively (mean migration direction on 25 May: 76°, n = 64 individuals, r = 0.70, p <
415 0.001; mean migration direction on 29 May: 0°, n = 37 individuals, r = 0.77, p < 0.001,
416 Supplementary material Appendix 4). During the whole of May and June, we estimate that
417 ~11.1 million high-flying *V. cardui* passed through southern UK, and of these 65% (~7.2
418 million) moved generally towards the north, i.e. between 270° and 90° (mean migration
419 direction: 52°, n = 202 individuals, r = 0.33, p < 0.001). The mean ground speed of the
420 windborne high-flying *V. cardui* in the spring migrations was 13.3 m/s (~50 km/h).

421 Migratory activity remained rather low through June and July, but increased again from
422 the beginning of August to mid October, when it peaked on certain days, e.g. 7 August with
423 ~1.2 million, 5 September with ~1.0 million, and 19 September with ~1.6 million high-flying
424 butterflies passing southward (Fig. 5).

425 Over the whole late-summer/autumn period (August–October), we estimate that ~25.9
426 million *V. cardui* engaged in high-altitude flights, but of these only 55% (~14.1 million) were
427 transported in a generally southwards direction, i.e. between 90° and 270°. However, the
428 overall mean direction of all butterflies was in a south-westward direction (mean migration
429 direction: 236°, n = 446 individuals, r = 0.16, p < 0.001) and there was a distinct absence of
430 flights close ($\pm 20^\circ$) to north (Supplementary material Appendix 4). The mean migration
431 direction was thus almost 180° opposite to the mean spring direction, albeit with a greater
432 dispersion of individual tracks. The mean migration direction (towards the south-west)

433 contrasts with the patterns of high-altitude winds (measured at 300 m) during the autumn
434 migration period, which had a significant mean direction blowing from the WSW towards the
435 ENE (wind from: 251° , $n = 63$ days, $r = 0.22$, $p = 0.048$), and a comparative shortage of
436 northerly winds favourable for autumn return migration. Thus there is some evidence that
437 butterflies preferentially migrated on winds with a northerly component (resulting in a
438 significant tendency for southward displacement), even though many of the individuals were
439 displaced in unfavourable directions (towards the north-west or north-east) due to the shortage
440 of suitable tailwinds. The mean displacement speed during summer/autumn migrations was
441 12.7 m/s (~45 km/h).

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

449 Southward migration across the Gulf of Finland was also recorded by radars at Kerava
450 and Kumpula between 3-6 August 2009. Coinciding with a sudden change in the wind
451 direction, which started to blow from the north, and the emergence of the local generation of
452 *V. cardui* in Finland in early August, a strong migration of large day-flying insects moving
453 southward was apparent from 3 to 5 August (Fig. 6a-b). On 5 August, the Kumpula radar
454 vertical sections over the land and over the sea showed that these insects were flying mostly
455 in the layer 500-700 m a.g.l., where air temperature (as recorded in atmospheric soundings at
456 Jokioinen and Visby meteorological stations) was above 15°C . During the morning hours of 6
457 August, however, the wind direction changed from northerly to south-easterly and the insects

458 drifted towards west and north-west to end up back on the Finnish coast and several nearby
459 southern islands (Fig. 6c-d). Direct observations of this event were made in the island of Örö,
460 in the western tip of the Gulf of Finland, when thousands of *V. cardui* arrived from the south
461 while flying north-westward on tailwinds and landed on the island (J. Kullberg pers. obs.).
462 Extremely high numbers of *V. cardui* were recorded on the southern Finnish coast and other
463 islands as well during the same period, pointing towards a massive southward windborne
464 flight that was interrupted by a sudden change in the formerly favourable weather conditions
465 for migration. High-altitude southward migrations of large-sized insects across the Gulf of
466 Finland were recorded again by Finnish radars throughout August (see details in
467 www.helsinki.fi/~mleskine/vaellus/Vcar2009.html), suggesting the existence of regular return
468 flights of *V. cardui* out of sight from ground-level observers.

469

470

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

472

473 A comparison between the temporal distribution of daily high-altitude and ground-level
474 migratory flights in 2009 is provided in Table 2. In the spring, high-altitude flights in south
475 England were positively correlated with ground-level flights across all western Europe ($p <$
476 0.001 , 1,398 flights). The correlation was significant for the Central Europe subregion ($p <$
477 0.001 , 1,213 flights), but not for the Mediterranean (148 flights) and Northern Europe (37
478 flights) subregions. High-altitude flights were also correlated with ground-level flights across
479 all of eastern Europe ($p < 0.001$, 1,020 flights), as well as with particular subregions
480 (Mediterranean: 46 flights; Central Europe: 910 flights; Northern Europe: 64 flights).
481 Interestingly, the correlations were stronger if it was assumed that the peak of windborne
482 flight would occur one day earlier in the Mediterranean than in southern England, which in

483 turn would be one day behind the flight peak in Northern Europe (Table 2). In the
484 summer/autumn, high altitude flights were only correlated with ground-level flights across all
485 eastern Europe ($p < 0.01$, 557 flights) and the eastern Central Europe subregion ($p < 0.01$, 534
486 flights), probably because of the very low number of records of ground-level migrations in
487 this part of the season (Fig. 4).

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

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498 **Discussion**

499

500 The results of this study show a succession of generations of *V. cardui* populations, exhibiting
501 a northwards spread out of Africa into a warming European continent, as spring develops,
502 followed by a southwards reversal in late summer and autumn. Like in some migrant moths
503 (Chapman et al. 2008a,b, 2010), the reversal of direction appears to involve complex
504 behaviour, including both the adoption of seasonally-favourable headings (see also Nesbit et
505 al. 2009) and the selection of favourable tailwinds when available. Exodus from each region
506 takes place before the environment becomes directly inhospitable, in anticipation of the
507 arrival of conditions unsuitable for continued breeding in the location of adult emergence.

508 Adverse seasonal conditions not only include extreme temperatures and the decreasing
509 availability of ephemeral resources for larvae and adults, but also increasing levels of natural
510 enemies such as specialist parasitoids (Stefanescu et al. 2012).

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

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

533 We believe that a key aspect for the whole migratory system to be maintained is the
534 ability of *V. cardui* to use favourable high altitude winds to move rapidly in appropriate
535 seasonal directions. This would seem to be necessary particularly in the autumn given the
536 distances that must be covered during this part of the annual cycle. Indeed, our results
537 strongly suggest that butterflies leaving the European continent on their return flight travel far
538 above the ground and mostly remain unnoticed by observers (Fig. 4). The radar data from
539 southern England in autumn 2009 would seem to indicate that migrating *V. cardui* were not
540 very successful at selecting suitable winds, given that only 55% of the radar-detected high-
541 flying butterflies were displaced in a southwards direction. However, analysis of wind
542 directions during this period indicated that there was a preponderance of winds blowing from
543 the south-west and WSW, and relatively few days when winds blew from the north, and so
544 presumably the shortage of suitable transport opportunities resulted in butterflies being forced
545 to move on less than ideal winds. Radar observations from previous *V. cardui* invasions of the
546 UK have shown much clearer southward return migrations (Chapman et al. 2010), and the
547 Finnish radar data in the present study also demonstrate the ability of high-flying *V. cardui* to
548 preferentially select suitable winds. We thus conclude that transport on fast-moving high-
549 altitude winds is an essential part of the annual cycle, particularly during the autumn.

550 Although windborne migration above the FBL has been widely described in insects showing
551 long-range seasonal movements, particularly pest species (Chapman et al. 2011), its presence
552 had been questioned in some large day-flying insects such as butterflies and dragonflies (e.g.
553 Baker 1978, Walker 1980, Walker and Riordan 1981). However, strong similarities in the
554 strategies used by *V. cardui* and other migrant Lepidoptera, such as noctuids and hawk-moths
555 (Chapman et al. 2010), raises the possibility that high-altitude windborne flights may be, in
556 fact, much more widespread among migrant butterflies than has been assumed. The scarcity
557 of records could be simply due to the difficulty of collecting data from the ground (see also

558 Gibo 1981, Mikkola 2003). In this respect, radar technology is a useful complementary tool,
559 as has been shown in our study.

560 However important high-altitude migration is, ground-level observations of flight
561 displacements on fixed compass bearings are very commonly reported in the spring,
562 indicating that migration at surface level is still one of the main features in the ecology of *V.*
563 *cardui*. The high synchrony that we found between high-altitude and ground-level migration
564 shows that the two are linked. Whether higher and lower altitude flights represent distinct
565 behaviours or phases of migration, as first suggested by Mikkola (1986), requires further
566 work. This might be affected by both the prevailing weather conditions and individual
567 physiological and reproductive characteristics (cf. Johnson 1969, McNeil et al. 1995).

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

582 In summary, we have documented a continuously-breeding migration path, in which a
583 species undertakes a round-trip migration of up to 15,000 km (up to 60 degrees of latitude and
584 back) from tropical Africa to northern Europe. This is close to double the latitudinal migration
585 distance of the famed monarch butterfly (Solensky 2004), and potentially exceeds the distance
586 achieved by the globe-skimmer dragonfly *Pantala flavescens* (Anderson 2009). The capacity
587 of the species to exploit winds and maintain migratory direction enables it to maintain this
588 exceptionally long inter-generation migration route.

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

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Subregion	Direction (°)	<i>r</i>	N	Rayleigh <i>P</i> -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

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

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			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**

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826 Fig. 1. Geographical extent of the *ad-hoc* distribution records used for the analysis of
827 migrations of *Vanessa cardui* in the western Palaearctic-West African regions (see
828 Supplementary material Appendix 1 for details on country records). For analytical
829 purposes, the area has been divided into five different subregions: Western Africa,
830 Northwestern Africa, Mediterranean, Central Europe, and Northern Europe. Another
831 30,000 records (not shown) from BMS networks in European countries were also used
832 to better define phenological patterns between March-September 2009. Additional
833 information was provided by radar sites in Mauritania, southern England and southern
834 Finland.

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837 Fig. 2. Phenology of the *ad-hoc* distribution records in the five geographical subregions
838 considered in the analysis. Records unequivocally showing reproductive behaviour
839 (courtship by males and egg-laying females) have been distinguished from the rest of
840 the adult data. Records from immatures (i.e. larvae and pupae) are also presented
841 separately from the rest. Red line: adult records; blue line: records of adults showing
842 reproductive behaviour; green line: records of immatures.

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844

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

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850

851 Fig. 4. Temporal distribution of 2,894 records of ground-level migrations in Europe in
852 2009, classified according to three categories of relative abundance: low abundance (1-
853 10 individuals recorded), medium abundance (11-100 individuals recorded), high
854 abundance (more than 100 individuals recorded).

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

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868 Fig. 6. Southern migration of *Vanessa cardui* recorded in the Gulf of Finland on 5 and 6
869 August 2009. a-d, Kerava radar images. Kerava is about 25 km north of the coastline
870 (NNE from the Helsinki city centre), and the map overlay shows the coastline of the
871 Gulf of Finland that lies between Finland (north) and Estonia (south). (a) 5 August,
872 05:00 UTC. Insects get airborne at the Finnish coastline, but not farther inland – cooler
873 air after the night before accompanied by low level clouds or fog over the land areas
874 delayed take-off. A few rain showers are seen over the Estonian coast (the strongest

875 reflectivity corresponds to these rain cells, and to birds near the radar in Finland). (b)
876 09:03 UTC. Insects flying over the land area causing most of the widespread echoes.
877 The intensity is lower over the sea because no take-off occurs there, and because short-
878 range migrants rarely fly over the water from land. However, long-range migration
879 continues over the sea, especially in the SW and SE, where many insects are seen flying
880 over the Gulf of Finland southward. Rain showers have developed over Estonia, south
881 of the coastline, and over Finland (125 km to the WNW, and 110-120 km to the NNE).
882 M. Leivo observed *V. cardui* on the outer islands 70-80 km ESE of the radar, with some
883 flying southward higher up in the air. (c) 6 August, 09:45 UTC. Strong and wide spread
884 echoes are caused by insects, and especially over the land areas both in Finland and in
885 Estonia. Line convection causes bands (called convective rolls) of stronger reflectivity
886 oriented along the air flow from NE-ENE over the land, because the low level
887 convergence in the air is gathering insects together and lifting them higher up in these
888 bands. Many insects are flying over the sea towards SW, especially in the SW sector.
889 (d) 12:46 UTC. Only a few insects are now flying over the sea, after a sea-breeze has
890 started to blow from SE in the coastal region. The sea-breeze front convergence is
891 gathering a maximum of insects to form a stronger echo band over the land following
892 the Finnish coastline. Insects flying below about 500 m are carried back to the land by
893 the sea-breeze. J. Kullberg observed hundreds of *V. cardui* coming from SE on the
894 island of Öro, about 150 km WSW from the radar.

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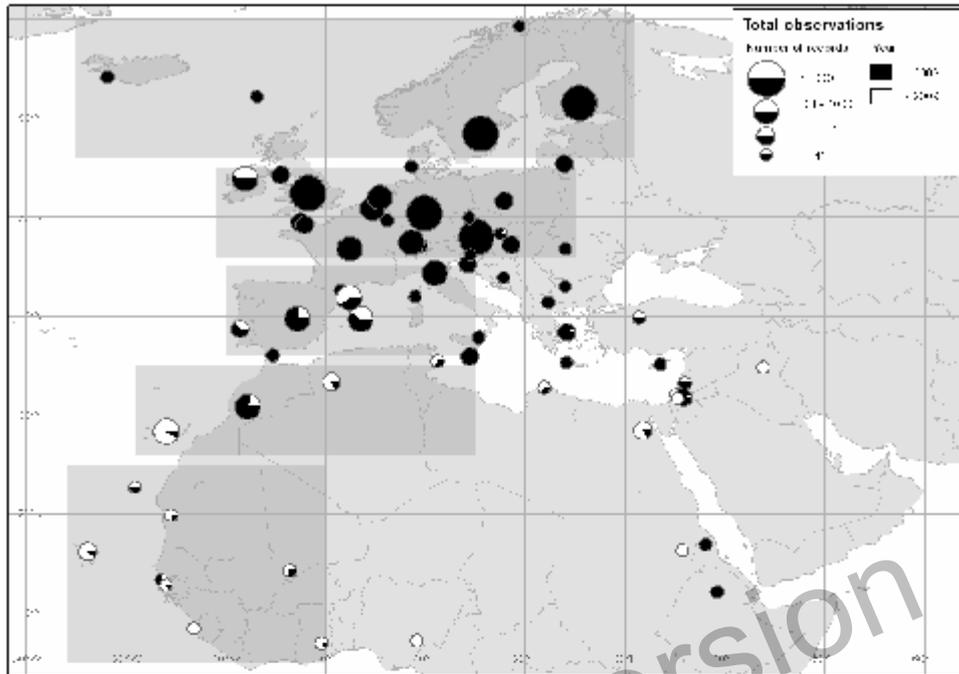
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Fig. 1.

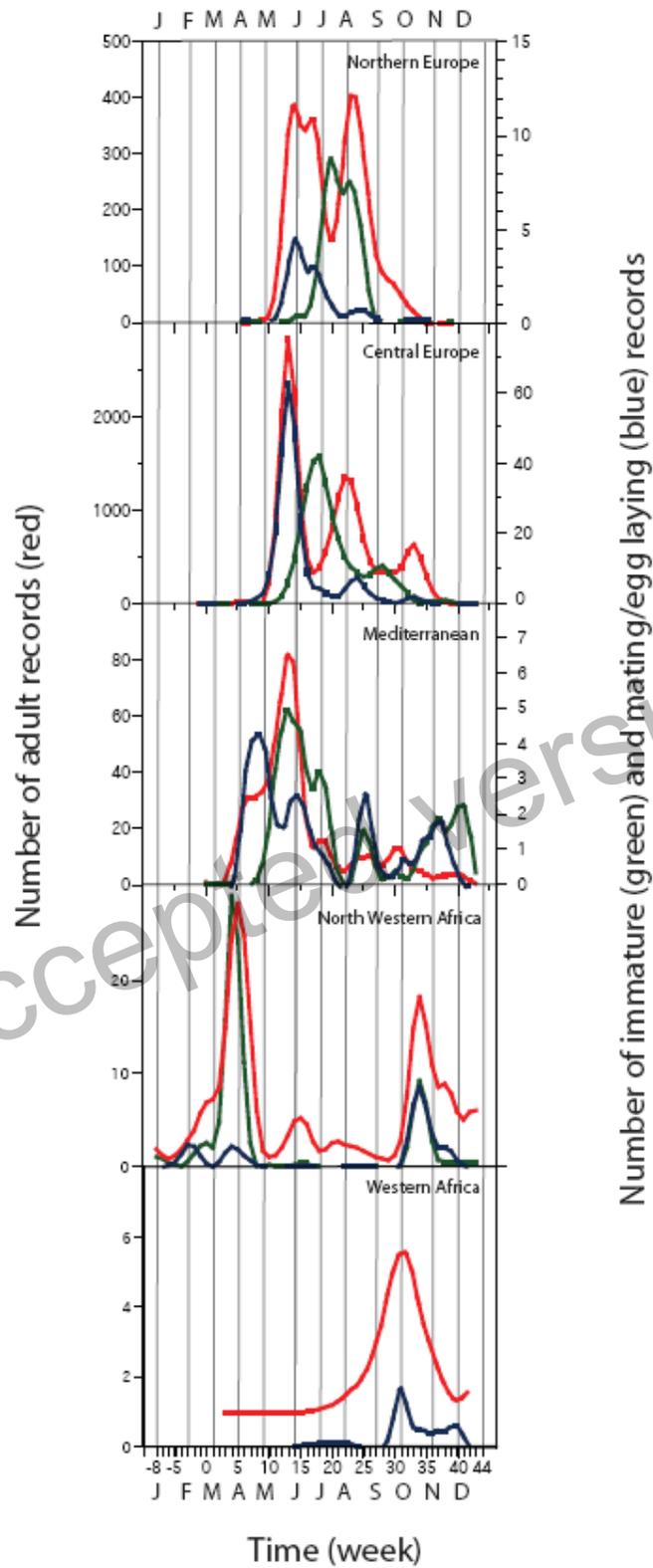


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903 Fig. 2

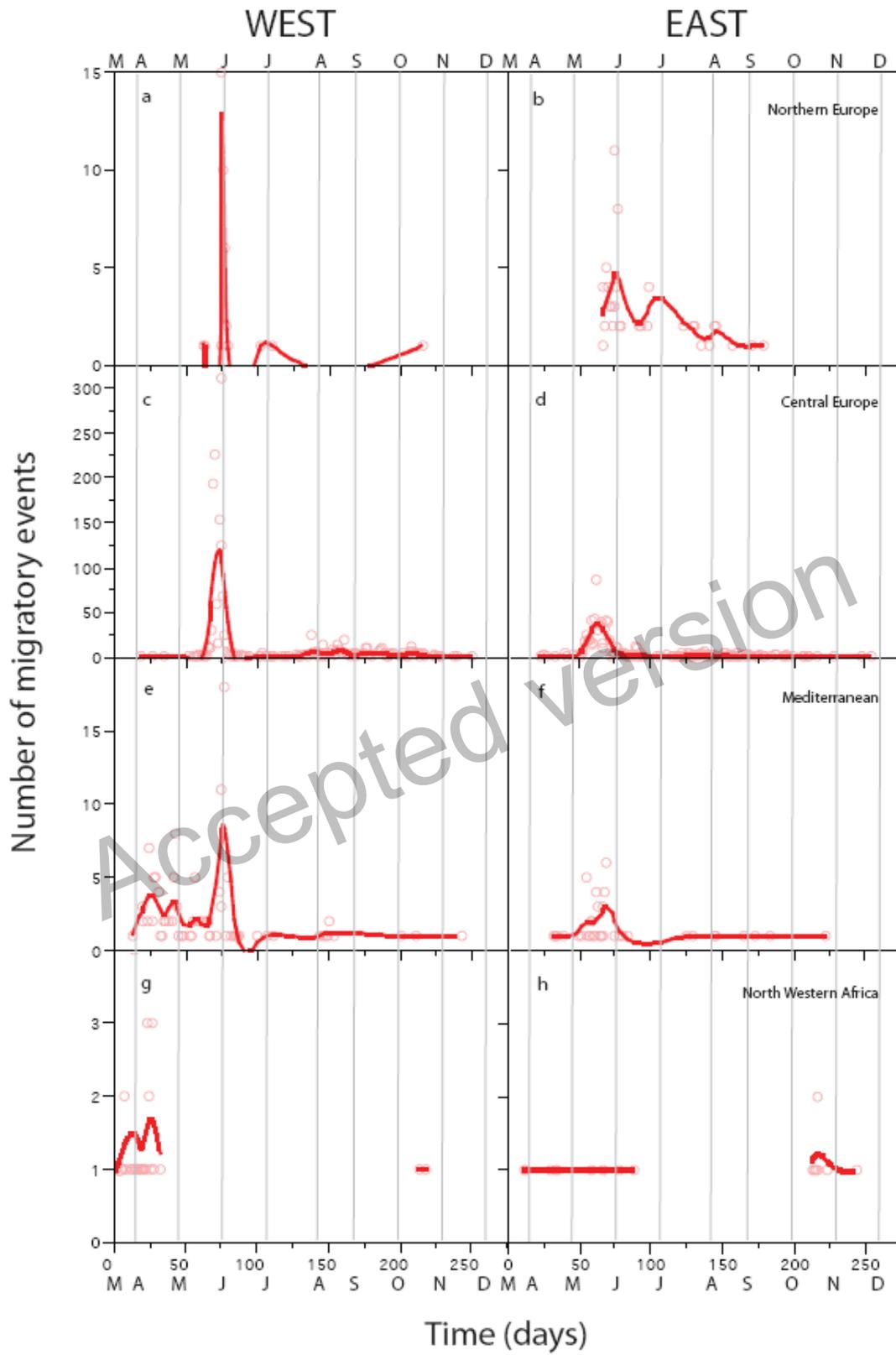


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907 Fig. 3

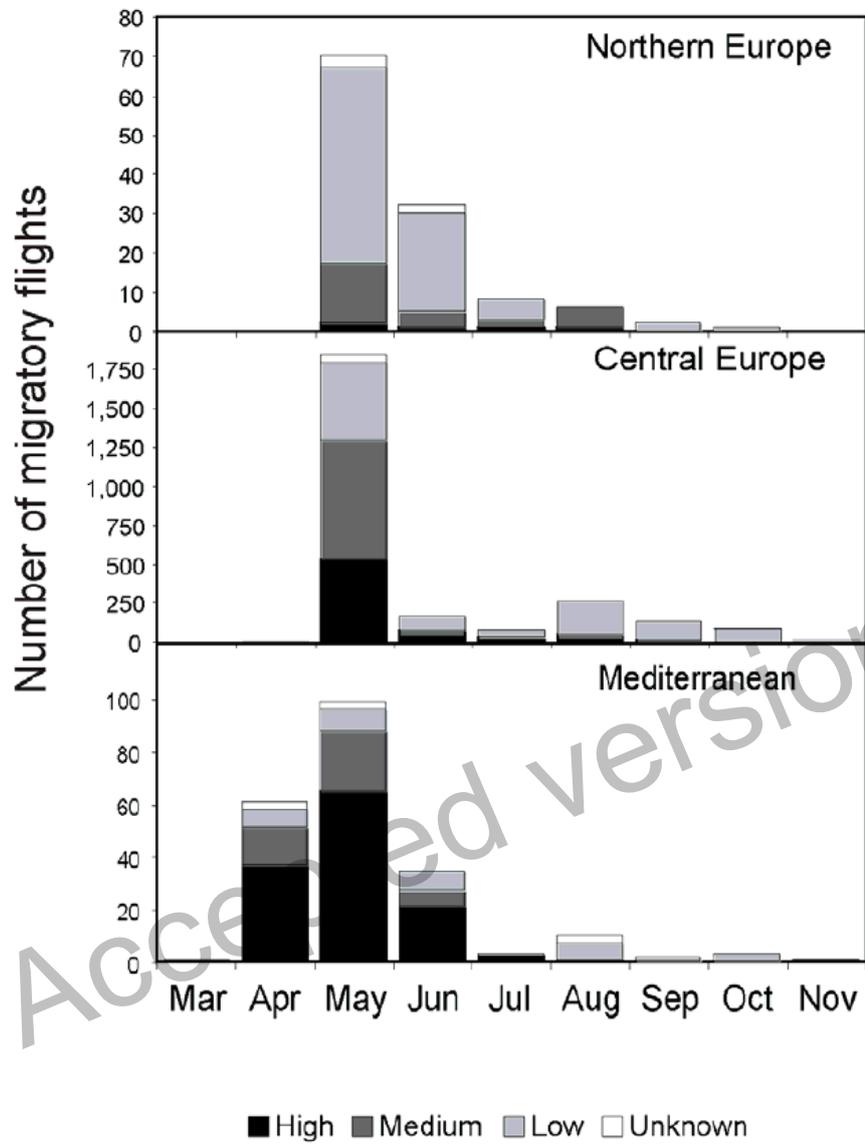


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911 Fig. 4



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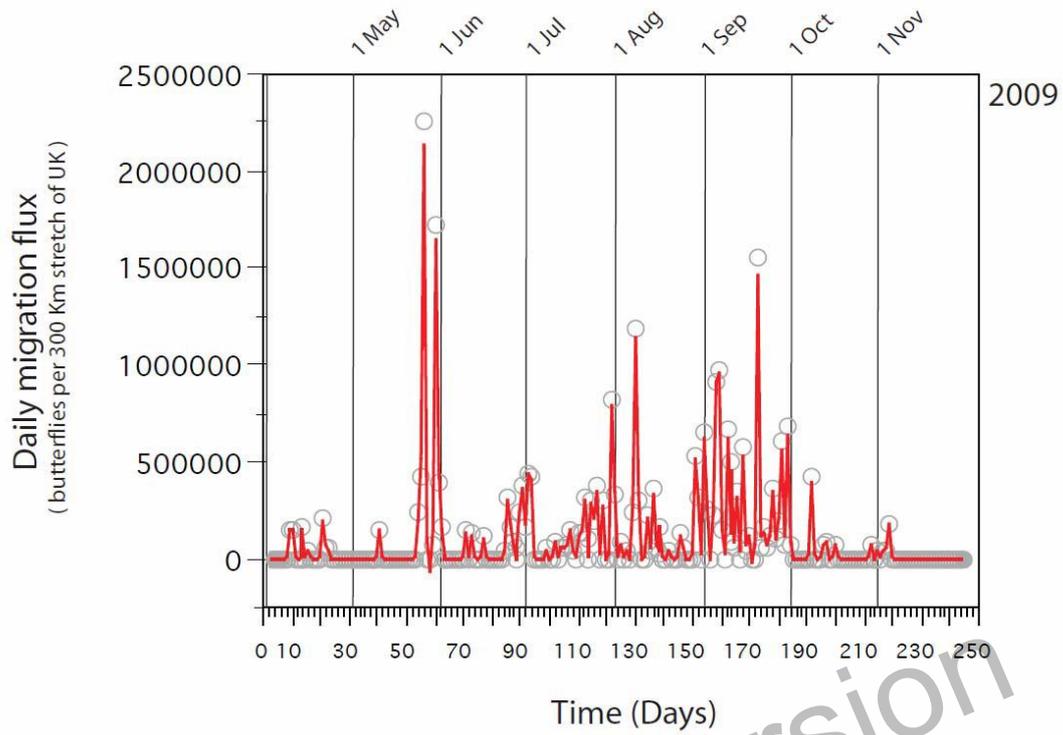
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921 Fig. 5



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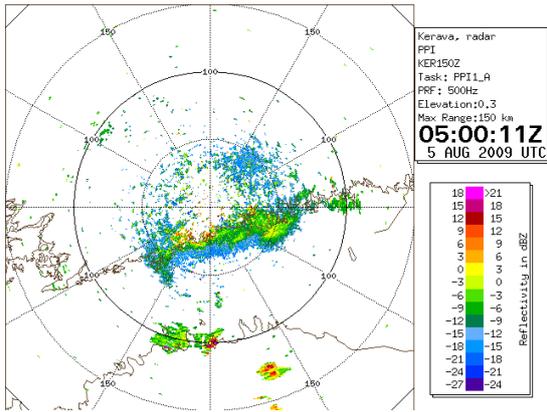
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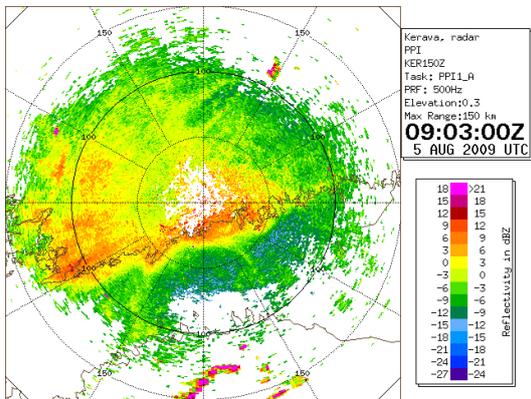
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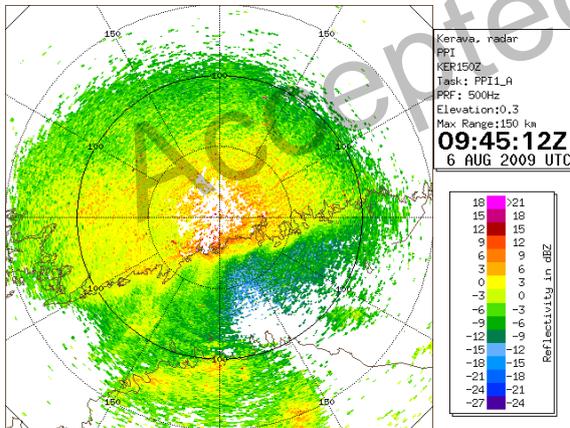
936 Fig. 6



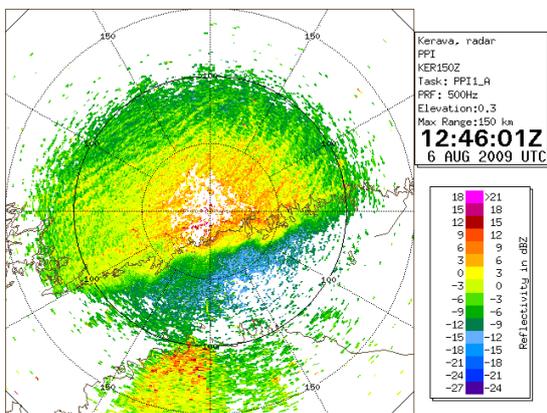
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