1 # Migration of the Painted Lady butterfly *Vanessa cardui* to
2 # north-eastern Spain is aided by African wind currents

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22 Running headline: Windborne migration of *Vanessa cardui*

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26 **Summary**

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28 **1.** Thousands of records of migratory butterfly species such as *Vanessa cardui* flying
29 just above ground-level on fixed compass bearings have led to the common belief that
30 these insects migrate within the so-called 'flight boundary layer', where movements are
31 relatively independent of the wind.

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1   **2.** Given the selective advantages of windborne migration and the existence of a number

2   of observations of flights of *V. cardui* from the upper levels of the atmosphere, we

3   propose here to test the hypothesis that migration from North Africa to southern Europe

4   in this species is influenced by synoptic-scale wind currents.

5

6   **3.** Even with modern technology it is extremely difficult to observe high-altitude flights

7   directly and so we rely on an indirect approach that examines whether or not arrival

8   peaks in north-eastern Spain are associated with winds blowing from Africa.

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10   **4.** Arrivals of *V. cardui* were determined for the spring period (1 March – 27 June, from

11   1997 to 2006) at 79 sites in the Catalan Butterfly Monitoring Scheme. Wind patterns

12   were described on the basis of synoptic-scale maps, transport models and back

13   trajectories calculated for each day of the spring period.

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15   **5.** We found a strong association between migration and winds from North Africa, both

16   for the whole data set (1997-2006; $\chi^2 = 4.7$, $P = 0.03$) and for a restricted data set that

17   excludes years in which the species was very scarce ($\chi^2 = 7.26$, $P = 0.007$).

18

19   **6.** Episodes of massive northward migration within the species' flight boundary layer

20   also coincided with spells of winds from North Africa, suggesting a connection between

21   low-altitude (observational) and high-altitude flights (inferred from wind patterns).

22

23   **7.** Finally, on the assumption that migration in *V. cardui* is windborne, a source-receptor

24   transport model applied to spring-abundance data in north-eastern Spain enables us to

25   identify the most probable population source areas in North Africa.

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28   *Key-words*: Lepidoptera, migratory behaviour, Nymphalidae, population source areas,

29   synoptic–scale wind systems.

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1   **Introduction**

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4   Knowledge of insect migration has greatly increased over recent decades as a result of

5   intensive theoretical and applied research (Drake & Gatehouse 1995; Dingle 1996;

6   Dingle & Drake, 2007). For instance, the seminal contributions by Rainey (1951, 1963)

7   and Johnson (1969) have shown that long-distance movements of many insect species

8   are influenced by the high-altitude winds that blow several hundred meters above

9   ground-level. The development of new techniques, particularly the use of radar, has

10   greatly contributed to a deeper understanding of this phenomenon, albeit to date almost

11   exclusively in the field of insect pests (e.g. Reynolds & Riley 1997).

12   Although there are many examples of insects, including moths, whose migratory

13   movements depend on the external force of the wind (e.g. Johnson 1969; Drake 1985;

14   Reynolds & Riley 1997; Chapman *et al.* 2002), similar evidence is surprisingly rare for

15   butterflies. Since the pioneering work by Williams (1930, 1958), it has been widely

16   accepted that butterflies migrate mostly within the so-called 'flight boundary layer', that

17   is, the space within a few meters of the ground where the airspeed of the flying insect is

18   greater than the wind speed (Walker 1980; Drake & Farrow 1988; Pedgley, Reynolds &

19   Tatchell 1995). This conclusion is based on thousands of records of butterfly species

20   migrating at low altitudes on fixed compass bearings, their movements being relatively

21   independent of winds (e.g. Nielsen 1961; Baker 1978; Walker & Riordan 1981; Walker

22   1991; Srygley, Oliveira & Dudley 1996; Srygley 2001).

23   According to Johnson (1969), however, the range of data available for butterflies

24   is insufficient for drawing firm conclusions regarding the nature of the migratory

25   process. Johnson (1969) argued against the tendency to use records for relatively short

26   distances to extrapolate for very long distances. Such a practice would be misleading if

27   migration occurs for the most part in the upper air, as reported for both the Monarch,

28   *Danaus plexippus* (Linnaeus), and the Red Admiral butterfly, *Vanessa atalanta*

29   (Linnaeus). Monarch butterflies often ride the rising layers of warm air that precede the

30   arrival of cold air masses, thereby being able to take advantage of the northerly winds

31   that blow in association with such fronts (Calvert 2001). They rise on thermals up to

32   altitudes of over 1000 m and then glide while migrating to their wintering areas (Gibo &

33   Pallett 1979; Gibo 1981). The Red Admiral also uses northerly winds when migrating

34   from the north of Europe to its breeding areas in the Mediterranean (Mikkola 2003).

1 Although butterflies have only ever been directly observed flying at heights of 20-100

2 m, radar data indicate that flights may occur as high as 1000-3000 m (Mikkola 2003). It

3 may well be the case, therefore, that the paucity of records of butterflies showing upper

4 level wind-borne migration is a consequence of the lack of appropriate methods for

5 detecting this phenomenon.

6   Here we return to the subject for one of the most well-known of all migratory

7 butterflies, the Painted Lady, *Vanessa cardui* (Linnaeus) (Nymphalidae), whose low-

8 altitude directional flights have been known all over the world for centuries (see

9 Williams (1930) for a comprehensive review of early data). However, previous

10 investigations have been strictly circumscribed to ground-level observations and flights

11 at higher levels have not as yet been studied.

12   The life history of *V. cardui* is shaped by long-distance migration (Wiltshire

13 1941; Larsen 1976). In the Palaearctic each spring the species arrives in Europe from

14 northern Africa (Williams 1970; Pollard *et al.* 1998) after journeys of several hundred

15 kilometres. In the Nearctic, such flights occur between desert areas in Mexico and Baja

16 California and latitudes between 35º-60º in the USA and southern Canada (e.g. Abbot

17 1951; Tilden 1962; Williams 1970; Myres 1985; Giuliani & Shields 1995). Taking into

18 account the selective advantages of windborne migration (e.g. allowing flight to be

19 more fuel-efficient and more rapid), it would be most surprising if *V. cardui* did not

20 make use of tailwinds to complete its migrations. Although a few observations of *V.

21 cardui* being carried by high altitude winds do exist (Giuliani & Shields 1997; Mikkola

22 2003), it is not known if these flights are a common strategy used on migratory

23 displacements to take advantage of wind currents.

24   We propose here to test the hypothesis that *V. cardui* migration from North

25 Africa to southern Europe occurs in the form of flights in the upper levels in the

26 atmosphere that benefit from synoptic winds. We examine this idea by testing whether

27 the peaks of individual arrival in north-eastern Spain are associated with winds blowing

28 from Africa. To describe wind patterns we use a variety of meteorological tools widely

29 employed for describing the transport of atmospheric chemicals (Stohl 1998).

30   Nevertheless, ground-level observations have also reported flight displacements

31 of *V. cardui* on fixed compass bearings, indicating that migration at surface level also

32 takes place. Given that a number of episodes of this kind have been observed, we have

33 also examined the specific meteorological conditions during these migratory episodes to

34 check whether this phenomenon contradicts or not our working hypothesis.

1   Previous work on atmospheric chemistry in eastern Spain has shown that winds

2   from North Africa, loaded with Saharan dust, are frequent in spring (Àvila, Queralt &

3   Alarcón 1997; Rodríguez *et al.* 2002; Àvila *et al.* 2007) and that back trajectories,

4   satellite images and transport models can be used to describe the provenance of the dust.

5   Therefore, a further task was to use these meteorological tools to identify the departure

6   areas of *V. cardui* in North Africa with a simple source-receptor transport model, as

7   there is little published data on potential source areas.

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11   **Material and Methods**

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14   <u>Migratory phenology of *Vanessa cardui* in the study area</u>

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16   In Catalonia, north-eastern Spain, spring migration of *V. cardui* is mainly recorded in

17   April, May and early June (Stefanescu 1997; Pollard *et al.* 1998). African migrants

18   breed throughout the region on a diversity of plants (mainly mallow, *Malva sylvestris*

19   (Linnaeus) and several thistle species), which are in full growth in this period

20   (Stefanescu 1997). At the start of the summer, newly emerged butterflies leave the area

21   quickly as they encounter the hot dry conditions typical of the Mediterranean summer

22   and migrate northward or towards higher mountains in search of both nectar and egg-

23   laying resources (Pollard *et al.* 1998). During the period of summer drought the species

24   is almost absent from lowland areas in Catalonia, although in the second fortnight of

25   August and in September moderate numbers are recorded again as part of autumn

26   migration. Small-scale breeding also occurs then and a new local generation is usually

27   detected in October. Although some of these late-summer butterflies may exceptionally

28   survive the winter in the region, virtually all the locally produced population flies

29   southward to Africa as shown by the sudden appearances of huge numbers of *V. cardui*

30   in the Maghreb, the Canary Islands and the northern edge of the Sahel in September-

31   October (C. Stefanescu, unpubl. data).

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34   <u>Migration peak characterization</u>

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2   For reasons as yet not fully understood, in Catalonia and elsewhere in Europe the

3 autumn migration of *V. cardui* remains relatively unnoticed in comparison with the

4 spring migration (e.g. Williams 1951; Pollard *et al.* 1998; but see Hansen 1997) and

5 thus it is dificult to identify any clear migratory waves during the return flight.

6 Therefore, we have restricted our study to spring migration, that is, northward

7 migration from Africa.

8   We used data from 79 monitoring transects of the Catalan Butterfly Monitoring

9 Scheme (from now on CBMS; Stefanescu 2000), including three recording stations in

10 the Balearic Islands, for the period 1997-2006 (Fig. 1). Overall, the data set comprised

11 385 yearly transect counts. Counts (standardised to individuals/100 m of the recording

12 route) were made on a weekly basis from 1 March to 26 September, thus comprising the

13 whole period of northward migrations. *V. cardui* was recorded virtually at every

14 monitored site and its yearly frequency of appearance ranges from 0.96-1 (mean ± SD:

15 0.99 ± 0.02). The number of transects where it was observed varied each season in line

16 with the number of sites included in the scheme, from a minimum of 24 in 1998 to a

17 maximum of 51 in 2004 (38.80 ± 10.86).

18   To identify spring migratory waves, data from the first 17 weeks of the CBMS

19 calendar (1 March – 27 June) were used, the latter date being considered as the latest

20 date when northward migrations can still be detected, as indicated by exceptional

21 observations of poleward flights by African butterflies on 21 and 27 June 1996

22 (Stefanescu 1997). Mean abundance of the species was calculated for all the available

23 transects for each of these 17 weeks, each year being analysed separately. Abundance

24 estimates for every pair of consecutive weeks were carried out on the assumption that

25 any significant numerical increase would be the result of the arrival of a migratory

26 wave. One-tailed *t*-tests for paired comparisons were used for comparing abundance

27 between consecutive weeks. Data from each transect for one week were paired with data

28 from the same transect the following week to avoid biases in the butterfly abundance

29 estimates stemming from factors such as missing counts and spatial heterogeneity in

30 nectar and oviposition resources along transects.

31   Two different data sets were used: the whole data set (10 migratory periods

32 monitored between 1997 and 2006) and a subset excluding years with low abundance of

33 the species. Population levels of *V. cardui* were extremely low in 1997, 1998, 1999 and

34 2005 (Fig. 2), which meant that chances of detecting increases in abundance were

1 greatly reduced (1997 and 2005) and made estimates of migration less reliable (in 1998

2 and 1999, when two out of three increases in abundance in very late June might have

3 been caused by local emergence).

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6 <u>Meteorological data and air-mass trajectories</u>

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8 We investigated the possible association between the arrival of waves of migratory

9 butterflies and the occurrence of high-altitude African winds originating from synoptic-

10 scale systems, that is, from a succession of low and high pressure cells approaching the

11 region from the west or south. A positive association would be expected if spring

12 migration were mainly wind-borne at high altitude.

13   The possible source region of an air mass was determined with backward in time

14 trajectories. A single 96-hour back trajectory arriving in Catalonia at 00 UTC was

15 calculated for each day between 1 March and 27 June during the 10-year period 1997-

16 2006 (i.e. a total of 1190 back trajectories). Trajectories were run at 1500 m above sea

17 level (asl) using the Hybrid Single-Particle Lagrangian Integrated Trajectory

18 (HYSPLIT-4) model of the National Oceanic and Atmospheric Administration (NOAA)

19 (available at http://www.arl.noaa.gov/ready/hysplit4.html; Draxler & Rolph 2003). The

20 HYSPLIT model calculates isentropic trajectories from the gridded meteorological

21 fields of the FNL archive data. A height of 1500 m, corresponding to 850 hPa standard

22 pressure level, was selected as being the most representative for transport in the lower

23 troposphere. This layer is typically sensitive to cyclonic-wave features and is the

24 approximate boundary between the surface-wind regime and the free troposphere (Artz,

25 Pielke & Galloway 1985). Moreover, a relationship between the 850 hPa wind direction

26 and the prevailing weather patterns associated with the passage of cyclonic waves is

27 well established (Dayan & Lamb 2003). For each recording week an incursion of

28 African winds was considered to have taken place when at least one of the seven daily

29 back trajectories crossed the shaded area in figure 4b.

30   We also investigated which meteorological scenarios were responsible for the

31 synoptic-scale wind systems associated with the arrival of migrants. Weather charts

32 from the NOAA (http://www.arl.noaa.gov/ready.html) showing mean pressure at sea-

33 level and the geopotential height at 850 hPa and 700 hPa were used. The classification

34 by Escudero *et al.* (2005) of dust mobilisation and transport from North Africa to the

Iberian Peninsula was applied with slight modifications and the following three scenarios of transport were defined: (1) Atlantic Depression (AD), characterised by a deep low pressure situated west or south-west of Portugal and often associated with a ridge over the central Mediterranean; source areas under these conditions were mostly from the western Sahara. (2) Depression over North Africa or the Iberian Peninsula (thereafter named PD); this situation favours the transport of African air masses across the Mediterranean to the Iberian Peninsula and in these cases dust mostly originates from Algeria and Tunisia. (3) A high pressure system at higher levels (NAH-H) appearing in summer, when intense heating over the Sahara induces the development of the North African thermal low and the uplift of dust to around 5000 m. Then, dust is transported to the Iberian Peninsula by the western branch of the high situated at upper levels.

Low-altitude migratory flights

Several episodes of low-altitude migratory flights were recorded in the CBMS during the study period. We investigated a possible connection between low-altitude (observational) and high-altitude flights (inferred from the wind pattern) for a selected set of six episodes during which intensive northward flights were reported during butterfly counts. We also included observations from April-May 2003 and 2004 by bird-ringers on L'Illa de l'Aire (a small islet off the south-east coast of Menorca in the Balearic Islands). All six episodes coincided with a strong increase in *V. cardui* abundance in the region (CBMS data). Details on the nature of the wind regime prevailing during these major migratory events were obtained from back trajectories at 1500 m asl and from the DREAM Model (Dust Regional Atmospheric Model: http://www.bsc.es/projects/earthscience/DREAM), which provides information on dust load, wet and dry dust deposition, dust concentration and the vertical dust concentration profile over the city of Barcelona.

Source-receptor models

1   A final analysis was made to identify the most likely source regions of butterflies under

2   the assumption that migration was aided by winds from Africa. Source-receptor models

3   were applied to estimate the relationship between a receptor point and the probable

4   source areas connecting receptor recorded data with the regions crossed by the

5   trajectory pathways. For more clarity in the results, only the restricted data set was used.

6   714 (17 weeks x 7 days x 6 years) daily trajectories at 1500 m were computed using

7   HYSPLIT-4, whose segment end-points correspond to 60-min time steps (a total of

8   68544 end points). Each trajectory was associated with a corresponding value of

9   butterfly abundance, which was the mean abundance averaged for each 7-day period. A

10 grid with 2601 cells of 1° x 1° latitude and longitude was then superimposed on the

11 integration region of the trajectories. The Concentration Field Function (CFF; Seibert *et*

12 *al.* 1994) was used to identify the source regions. This model associates an abundance

13 value to each cell based on the residence time of the trajectories in the cells. If C_l is the

14 abundance associated with trajectory l and n_{ijl} the number of end points of the trajectory

15 l in the ij cell, then:

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17 $$\log C_{ij} = \frac{\sum_l n_{ijl} \log C_l}{\sum_l n_{ijl}}$$

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19 where C_{ij} is the computed abundance in the ij cell. The abundance field map obtained in

20 this manner reflects the contribution of each cell to the abundance at the receptor point.

21 To minimise the uncertainty of the trajectories smoothing was applied and the value of

22 each cell was replaced by the average between the cell and the eight neighbouring cells.

23 A final filter excluded cells with less than five time-steps.

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27 **Results**

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30 Phenology of the spring migration

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1   Between 1997-2006, 21 episodes of significant increase in the mean abundance of *V.*

2   *cardui* between consecutive pairs of recording weeks were identified, attributable to the

3   arrival of migratory waves (Table 1, Fig. 3). This number increased to 32 if significantly

4   marginal results ($0.05 < P < 0.1$) were also considered. April (weeks 5-9 of the CBMS

5   calendar) was the month with the most significant increases (47.6%), followed by May

6   (weeks 10-13: 28.6%), June (weeks 14-17: 19.0%) and March (weeks 1-4: 4.8%). Only

7   two significant increases (9.5%) occurred in the second fortnight of June. The number

8   of recording transects was uncorrelated with the number of yearly migrations ($P =$

9   0.48), thus indicating that the method used for detecting migratory waves was not

10   biased against this variable.

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13   <u>Back trajectories associated with migratory waves</u>

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15   There was an association between migratory waves and incursions of winds from North

16   Africa at 1500 m asl in 16 out of 21 cases (76.2%) (Table 2). While African winds also

17   occurred in 76 of the 149 weeks (51.0%) in which no migration was detected,

18   contingency table tests indicate a significant association between migration and African

19   winds for the complete data set ($\chi^2 = 4.70$, d.f. = 1, $P = 0.03$). When the analysis was

20   repeated with the restricted data set the significance of the association increased ($\chi^2 =$

21   7.26, d.f. = 1, $P = 0.007$), with 14 out of 16 migrations (87.5%) coinciding with African

22   winds (Table 2). Very similar results were obtained when the significance level for

23   accepting an increase in the abundance of *V. cardui* was lowered to $P < 0.1$ (Table 2;

24   complete data set: $\chi^2 = 5.01$, d.f. = 1, $P = 0.025$; restricted data set: $\chi^2 = 7.23$, d.f. = 1, P

25   = 0.007). These additional analyses were made because northward low-altitude

26   migratory flights were observed in some of the weeks that showed an increase in

27   abundance at the $P < 0.1$ but not at the $P < 0.05$ level (thus suggesting that a type II

28   error was being committed for a 5% significance level).

29   Of the different meteorological scenarios responsible for an increase in the

30   abundance of *V. cardui*, the Peninsular Depression and the Atlantic Depression were

31   equally common (37.5%) while the North African High at Upper levels (NAH-H) only

32   accounted for 25% of the cases. Source areas under PD conditions are mostly from

33   Algeria and Tunisia, whereas under AD conditions they are from the western Sahara

34   (Mauritania, West Sahara, West Morocco).

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3   <u>Low-altitude migratory flights and winds from Africa</u>

4

5   All six episodes recording intensive low-altitude northward flights and giving rise to

6   dramatic increases in *V. cardui* abundance in the CBMS coincided with an incursion of

7   winds from Africa, either on the same day or between one to four days before the

8   migration was observed (Table 3). The origin of winds was confirmed by the DREAM

9   model, which forecasted abnormally high levels of African dust over Barcelona during

10   these same periods. Thus, despite the limited number of episodes reporting massive

11   low-altitude northward flights, the evidence provided here indicates a strong link

12   between such phenomena and spells of winds from Africa.

13   As an example, Fig. 4 shows the situation for the migratory wave arriving in the

14   region in mid-May 2004 that was especially conspicuous in week 11 of the CBMS (10-

15   16 May) (Fig. 4a). At least four different recorders reported massive low-altitude

16   northward flights of *V. cardui* on 14 and 15 May, while other independent observations

17   were made during the same period at places as distant as the Pyrenees (at 2000 m, on 16

18   May) and L'Illa de l'Aire (Menorca, 11-14 May).

19   As deduced from back trajectories at 1500 m, African winds originating around

20   Algeria reached the Balearic Islands and approached the coast of north-eastern Spain on

21   11 May (Fig. 4b). The most accurate representation provided by the NAAPS model

22   (Navy Aerosol Analysis and Prediction System; http://www.nrlmry.navy.mil/aerosol/)

23   shows how a cloud of African dust was displaced at high atmospheric levels from

24   central Algeria to the Balearic islands and the north-eastern Spanish coast on that day

25   (Fig. 4c). This dust intrusion was recorded over the city of Barcelona on 12 May, with a

26   maximum level of 340 $\mu g/m^3$ at 4500 m and abnormally high levels also evident at

27   heights of 100-2000 m (Fig. 4d). These southerly African winds were provoked by the

28   passage of a Peninsular Depression over northern Algeria on 12 May (Table 1). As soon

29   as the low pressure cell had moved eastwards, a fierce northerly wind began to blow

30   over Menorca and L'Illa de l'Aire on 13 May and, especially, on 14 and 15 May (when

31   this wind –the *tramuntana*- reached a force of 4-5 on the Beaufort scale). This can be

32   seen in figure 4b, which shows how the direction of the back trajectories changed from

33   south to north between 11and 12 May (11 May back trajectory in black).

1   Although some migrating butterflies were recorded on Menorca on 11 May, it
2   was only on 13, 14 and 15 May that numbers increased dramatically (transects counts
3   on 11, 12, 13, 14 and 15 May: 1, 3, 16, 113 and 81 individuals, respectively), most
4   probably because butterflies were forced to fly closer to the ground in the face of
5   unfavourable head winds.

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8   <u>Source of migrants</u>

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10   The CFF source-receptor model applied to the restricted data set enabled several sources
11   for spring migrants to be identified, most of which are located along a vast area reaching
12   between 30-35ºN and 15ºW to 20ºE within the bioclimatic limit of the Mediterranean
13   region in North Africa (Fig. 5). The three main sources were all located in the Maghreb
14   around the Moroccan Anti-Atlas (and to a lesser extent in the equivalent area south of
15   the Saharan Atlas in Algeria), in the low plain of north-eastern Algeria stretching away
16   across central Tunisia and up to the coast, and in the coastal area of Tripolitania in
17   Libya. A fourth smaller but apparently still important source area was located much
18   farther south, at the northern limit of the Sahel, between Western Sahara and Mauritania
19   (approximately at 21-22ºN and 13-15ºW). Moreover, although incorrectly situated too
20   far north, the model also indicated the presence of a secondary source area in the Canary
21   Islands.

22   It should be noted that the other areas in Fig. 5 which seem to be associated with
23   a high abundance of *V. cardui* do not correspond to true migrant sources. For instance,
24   the area located to the north-east of the British Isles represents an artefact of the model
25   caused by the fact that quite commonly African winds associated with migrants are
26   immediately succeeded by northerly winds originating in Iceland and to the north of the
27   British Isles following the eastwards passage of a low pressure cell. The migrants are
28   presumably forced down to low-levels when they encounter a switch to northerly winds,
29   and so will become visible at ground-level, as previously shown for the episode of
30   massive migration on 10-16 May 2004. Likewise, the uniform area of high abundances
31   recorded over the south-western Mediterranean represents the main route followed by
32   migrants from their source areas in Africa.

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2 **Discussion**

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5 Seasonal poleward movements allow a great variety of organisms to exploit resources

6 that become available in spring and summer in the temperate zone and to escape from

7 the increasingly inhospitable environments of southern regions as the season advances.

8 The large number of species showing such springtime movements suggests that there is

9 strong selection pressure for migratory behaviour (Johnson 1995) and, not surprisingly,

10 many of the organisms involved in this phenomenon have evolved a set of specific

11 attributes aimed at facilitating migratory journeys (Dingle 1996). One such adaptation is

12 the use of winds associated with the passage of fronts, which has been reported for birds

13 (Gauthreaux 1991) and many insects migrating in the temperate zone (reviews in

14 Pedgley 1982; Drake & Farrow 1988; Johnson 1995; Pedgley, Reynolds & Tatchell

15 1995).

16 Most migratory butterflies, however, do not seem to conform to this pattern, as

17 they reportedly stay within their flight boundary layer and exert some control over their

18 direction of displacement (Walker 1980; Walker & Riordan 1981). One particular good

19 example is provided by *V. cardui*, a highly mobile species which would be expected to

20 have evolved behavioural adaptations such as wind-borne migration. In spite of this,

21 numerous observations of poleward migration flights occurring near the ground,

22 surprisingly often against northerly winds (e.g. Williams 1930; Abbot 1951; Tilden

23 1962; Stefanescu 1997), would seem to contradict this assertion. One possible

24 explanation for this apparent maladaptive behaviour in this and other butterfly species

25 was advanced by Johnson (1969), who indicated that most observations simply recorded

26 individual tracks over relatively short distances that are difficult to interpret. He even

27 suggested that records of low-altitude directional movements may correspond to

28 situations of relatively unfavourable weather for flying, representing only a part of a

29 process that also involves flight at much higher altitude. He eventually concluded that

30 tracking the whole population displacement in relation to large-scale weather systems

31 would provide the key to the question.

32 Although most of these criticisms are fully applicable to the bulk of existing data

33 of *V. cardui* migration, recent systematic butterfly recording (e.g. in the form of the

34 Butterfly Monitoring Scheme; Pollard & Yates 1993) has provided a tool for further

1   exploring the nature of migrations of this and other butterfly species. In our study, we

2   have used more than 20000 individual records obtained from weekly CBMS counts in

3   north-eastern Spain to identify reliable peaks of *V. cardui* migration. The possibility that

4   spring migrants use synoptic wind systems was tested by backtracking air trajectories at

5   1500 m asl on days with and without associated migration, and comparing their

6   frequencies in relation to the occurrence of winds of African origin. We consistently

7   found a significant association between spring migrations and African winds, strongly

8   suggesting that migrants were carried on the moving air-masses above their flight

9   boundary layer. These air masses were related to meteorological scenarios involving the

10   passage of depressions approaching the Mediterranean region from the west or south.

11   Interestingly, a close association between migrants and winds from North Africa

12   was also found during the six episodes in which massive low-altitude northward flights

13   were recorded in the region. In some cases, directional flights occurred with time-lags

14   of 1-4 days with respect to the incursions of African winds. A possible explanation is

15   that butterflies undertake high-altitudinal wind-borne migration for most of the distance

16   travelled from source areas, but descend to ground levels and then continue migrating

17   within their flight boundary layer on fixed compass bearings for a period of time,

18   perhaps even for days. As noted by Gatehouse & Zhang (1995), this change in

19   behaviour would presumably commence with the transition from an initial phase of

20   truly migratory behaviour to a second phase in which the migrants regain

21   responsiveness to stimuli associated with favourable habitats. A similar explanation was

22   provided by Mikkola (1986), who suggested that the migration of several butterflies

23   (including *V. cardui*) and moths into Finland consisted of two phases, the first one

24   involving wind-borne flights over long distances, and the second one much shorter

25   displacements near the ground. Physiological studies coupled with behavioural

26   laboratory experiments (e.g. flight tests using tethered butterflies) may help to elucidate

27   these aspects.

28   Some reports of high-level flights in *V. cardui* provide additional clues that

29   wind-borne migration could indeed be a common phenomenon in this species. Giuliani

30   & Shields (1997) recorded two large spring migrations in California extending up to at

31   least 100-300 m above ground-level. Most butterflies appeared to be drifting, allowing

32   themselves to be carried by the wind; in one instance migrants were seen on top of a

33   2315 m ridge, hence the displacement was actually taking place at approximately 2500

34   m asl. Mikkola (2003) also reported a few individuals of *V. cardui* on autumn migration

1   at a Finnish site flying south on tail winds at around 20-100 m above ground-level

2   amongst large numbers of *V. atalanta*, and radar observations at a nearby site indicated

3   that many unidentified insects were moving south at heights of up to 3000 m. Likewise,

4   unusual records of *V. cardui* at sea, far from any continental source, and data on the

5   daily rate of advance have been interpreted as indirect evidence of wind-borne

6   migration (Bowden & Johnson 1976; Mikkola 1986). All in all, the evidence gathered

7   so far leads us to believe that the scarcity of records for *V. cardui* of high-altitude flights

8   mainly responds to the practical difficulties of observing butterflies far above the

9   ground. In this sense, the use of alternative techniques, as for example the vertical-

10   looking radar described by Chapman, Reynolds & Smith (2003), could add crucial data

11   for understanding the mechanistic basis of this migratory system.

12   Although it is widely accepted that *V. cardui* migrating into Europe are of

13   African origin (e.g. Pollard *et al.* 1998), there are in fact very few observations of mass

14   emergence of adults of this species in Africa (Skertchly 1879; Egli 1950, quoted by

15   Johnson 1969, p. 42). Our study is the first to use testable predictions of the location of

16   these source areas. According to our source-receptor model, migrants arriving in north-

17   east Spain come mainly from three different areas in the Maghreb, roughly 900, 1300

18   and 1600 km away (Fig. 5). If we assume that migration is mainly wind-borne and that

19   it takes place mostly at altitudes of 500-1500 m asl (where air masses move at a mean

20   speed of 30 km/h and usually have temperatures in the range of 10-20ºC in the spring),

21   the journey from the Maghreb may take 30-53 hours with a tailwind. If we also include

22   in the estimate the speed of the insect's flight (15 km/h; cf. Abbot 1951), these figures

23   drop to 20-36 hours. Of course this would imply that part of the migration is done at

24   night, a supposition that seems to be supported by fairly frequent records of *V. cardui*

25   being attracted to electric lights during favourable migration periods (Ryrholm &

26   Källander 1986).

27   Source areas in Africa could be confirmed by direct observations of massive

28   concentrations of larvae or adult emergences at predicted times or, alternatively, by the

29   application of such techniques as the analysis of isotopes in migrants (Wassenaar &

30   Hobson 1998). In addition, BMS data on population levels in the spring could be used

31   for testing forecasted breeding success in the hypothetical source areas, according to

32   particular environmental conditions (e.g. rainfall levels or a combination of several

33   climatic variables; e.g. Myres 1985; Vandenbosch 2003). Of further interest would be

34   the use of data from different BMS networks to obtain a comprehensive picture of the

1 progress of *V. cardui* across Europe each season, as well as the identification of possible

2 source areas which may vary from one European country to another.

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32

1   Table 1. Weeks with significant increases in *Vanessa cardui* in the CBMS between

2   1997 and 2006. In italics, significance at *P* < 0.1; otherwise, *P* < 0.05. Also shown are

3   the presence of winds of African origin during the same dates (indicated by the sign '+')

4   and the meteorological scenarios prevailing at that time: Atlantic Depression (AD),

5   Peninsular Depression (PD) and North African High located at Upper levels (NAH-H).

6

Year	Week	African winds	Meteorological scenario
1997	*10-16 May*	+	PD
1998	12-18 April	-	AD
1998	14-20 June	-	NAH-H
1999	26 April - 2 May	+	PD
1999	24-30 May	+	AD
1999	*7-13 June*	-	PD
1999	14-20 June	-	NAH-H
2000	15-21 March	-	PD
2000	19-25 April	+	AD
2000	*7-13 June*	+	AD
2001	26 April - 2 May	+	PD
2001	*10-16 May*	+	AD
2001	*31 May - 6 June*	-	NAH-H
2001	*14-20 June*	+	AD
2002	26 April - 2 May	-	AD
2002	3-9 May	+	PD
2002	17-23 May	+	AD
2002	*31 May - 6 June*	+	NAH-H
2003	12-18 April	+	PD
2003	26 April - 2 May	+	AD
2003	31 May - 6 June	+	AD
2004	12-18 April	+	PD
2004	26 April - 2 May	+	PD
2004	10-16 May	+	PD
2004	*21-27 June*	-	NAH-H
2006	*5-11 April*	-	AD
2006	12-18 April	+	NAH-H
2006	*19-25 April*	+	PD
2006	*26 April - 2 May*	+	AD
2006	3-9 May	+	PD
2006	10-16 May	+	NAH-H
2006	7-13 June	+	NAH-H

7

8

1 Table 2. Contingency tables for testing the independence of *Vanessa cardui* migrations

2 and the entrance of African winds at 1500 m asl. Figures are shown for both the

3 complete data set and for a restricted data set that excludes years in which the species

4 was very scarce, and for migrations identified both at $P < 0.05$ and at $P < 0.1$ (see text

5 for details).

6

	Weeks with migration	Weeks without migration		Weeks with migration	Weeks without migration
Complete data set; $P < 0.05$			Complete data set; $P < 0.1$		
African trajectories	16	76		23	69
Non African trajectories	5	73		9	69
Restricted data set; $P < 0.05$			Restricted data set; $P < 0.1$		
African trajectories	14	44		20	38
Non African trajectories	2	42		5	39

7

8

1 Table 3. Dates for the six episodes with intensive northward migration within the

2 butterfly's flight boundary-layer as reported by CBMS recorders and bird-ringers (see

3 text for details).

Episode	African winds	# days	Dust concentration (mg/m3)[1]	Observations
19-25 April 2000	+	1 (22 April)	Not available	Northward flights on 22 and 24 April - CBMS
17-23 May 2002	+	1 (17 May)	265 at 4500 m (17 May)	Northward flights on 18 and 19 April - CBMS
26 April-2 May 2003	+	3 (28-29 April, 2 May)	60 at 4000 m (29 April)	Very strong northward passage in Illa de l'Aire on 26-30 April (butterflies resting on sea objects between Menorca and Mallorca)
31 May-6 June 2003	+	3 (3-5 June)	100 at 3500 (5 June)	Very strong northward passage on 5 June - CBMS
10-16 May 2004	+	1 (11 May)	340 at 4500 m (12 May)	Very strong northward passage on 13-16 May - CBMS and Illa de l'Aire
10-16 May 2006	+	3 (13, 15-16 May)	100 at 1800 (15 May) 550 at 4000 m (16 May)	Very strong northward passage on 14-15 May - CBMS

4

5 [1]Dust concentration from the DREAM model

6

7

8

1 Fig. 1. Location of the 79 recording transects in the CBMS used for monitoring *Vanessa*

2 *cardui* populations in Catalonia (north-eastern Spain) and the Balearic Islands (two

3 transects in Menorca and one transect in Ibiza, not shown in the figure) in 1997-2006.

4 The size of each circle is proportional to the number of recording years.

5

6

7 Fig. 2. Average spring abundance (1 March to 27 June) of *Vanessa cardui* in the study

8 sites from 1994 to 2006. Population levels were estimated using the methodology of

9 Moss & Pollard (1993).

10

11

12 Fig. 3. Significant increases in *Vanessa cardui* abundance from consecutive weeks in

13 spring (1 March to 27 June) from 1997 to 2006.

14

15

16 Fig. 4. Case study: peak migration on 10-16 May 2004. (a) Increase in abundance

17 detected in the CBMS; (b) back trajectories at 1500 m asl for the seven days of the

18 period (labelled next to each trajectory is the arrival date in Catalonia); the shaded area

19 corresponds to the region over which a trajectory was considered to be of African

20 origin; (c) displacement of a dust cloud (at 3000 m asl) originating in central Algeria on

21 11 May 2004, from the DREAM model; and (d) vertical profile of the dust

22 concentration ($\mu g/m^3$) over Barcelona on 12 May 2004, from the DREAM model.

23

24

25 Fig. 5. Abundance of *Vanessa cardui* (in individuals/100 m transect) computed with a

26 source-receptor model (Concentration Field Function; Seibert *et al.*, 1994) applied to

27 spring counts for the period March-June 2000-2004 and 2006. For more details, see

28 text.