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MOROCCAN SOURCE AREAS OF THE PAINTED LADY BUTTERFLY *VANESSA CARDUI* (NYMPHALIDAE: NYMPHALINAE) MIGRATING INTO EUROPE IN SPRING

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ABSTRACT. Each spring, *Vanessa cardui* (Linnaeus) migrates into Europe, sometimes in huge numbers. Although it is widely accepted that migrants come from North Africa, there is currently a dearth of information on the source areas they originate from. However, in a recent study, a strong association between *V. cardui* arriving in spring in Catalonia (NE Spain) and synoptic-scale winds originating in North Africa was found, which allowed us to predict the most likely location for the source areas in the Maghreb. In March 2009 we organized an expedition to confirm *in situ* the occurrence of immature stages and/or emerging adults at one of the hypothetical breeding areas in Morocco. Immatures were found at virtually all the sampled sites, with the maximum abundance being recorded in the Souss valley. Breeding habitats with plenty of thistles and mallows were sufficiently common to permit populations of great density to build up. We found a massive emergence site of 1.8 ha with an estimated population of 170,000 larvae, of which 155,000 had successfully pupated, the rest having been parasitised by the wasp *Cotesia vanessae*. Bird predation of adults was also recorded at this site. Our observations, together with the typical patchy distribution of the ruderal habitats used for breeding, suggest that source populations most frequently originate in small habitat pockets with favourable conditions that allow for high patch occupancy and levels of oviposition.

Additional key words: hostplants, parasitoids, predation, population outbreak, Morocco

Undoubtedly, *Vanessa cardui* (Linnaeus) stands out as one of the best known and most popular butterfly migrants in the world. Its spectacular migrations have been recorded for at least the last two centuries, both in Europe and North America (see Williams 1930 for an excellent and comprehensive review of early data). Mass movements across extensive regions and continents have been analysed by several authors in an attempt to synthesise and understand different aspects related to this migratory process, as for example seasonality, flight paths, orientation behaviour and the causes underlying dramatic fluctuations in abundance. In North America, the works of Abbot (1951), Tilden (1962), Williams (1970), Myres (1985), Giuliani & Shields (1997a) and Vandenbosch (2003), and in Europe those of Williams (1951), Pollard (1982), Hansen (1997), Stefanescu (1997), Pollard *et al*. (1998), Stefanescu *et al*. (2007) and Nesbit *et al*. (2009) have all addressed these topics.

Despite all this research, some crucial aspects regarding this migratory system have remained elusive until now. For example, there is a dearth of information on the source areas where the migrants recorded in spring, particularly in Europe, originate from. However, the enormous numbers involved in northward migrations in 'outbreak' years means that there must be some areas where breeding occurs on a vast scale in spring. A few such areas have been localised in Sonora (Mexico), Baja California and California, and Abbot (1951) and, especially, Giuliani & Shields (1995, 1997a,b, 1998) have provided accurate and fascinating

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descriptions of huge concentrations of larvae and massive emergences of adults in April, May and early June. Breeding grounds consist of desert or semi-desert and chaparral areas, characterised by a short plant-growth season highly dependent on scant and irregular rainfall (Abbot 1951). Moreover, the observations made in consecutive years in Inyo County, California (Giuliani & Shields 1995, 1997a,b, 1998), strongly suggest that butterflies use regular migratory paths and the same areas to breed, although the numbers occurring will fluctuate enormously in terms of resource availability (linked to climatic conditions; cf. Myres 1985; Vandenbosch 2003).

Although it is widely accepted that *V. cardui* migrating into Europe are of African origin (e.g. Pollard *et al*. 1998), there are in fact very few observations of mass breeding in Africa. Skertchly (1879) and Egli (1950; quoted by Johnson 1969, p. 42) localised two such areas in Sudan (in March) and near Algiers, respectively. In both cases, thousands of butterflies were seen to emerge from pupae in the early morning and then take off within an hour or so and head towards the sea. More recently, Owen (1987, 1989) reported vast numbers of larvae in Lanzarote (Canary Islands) in late February and in Madeira in April, and suggested that these islands could act as source areas for European migrants recorded in spring. Other potential sources can be traced from the detailed account provided by Williams (1930) of remarkable concentrations of larvae and/or adults showing ovipositing behaviour in several areas of north Africa (e.g. Egypt).

It is most likely, however, that the sources of spring migrants vary according to the European region under consideration. For instance, observations in some Eastern Mediterranean islands and Turkey seem to indicate that migrants recorded in Eastern Europe mainly originate in the Arabian Peninsula (John 2001), where directional flights of *V. cardui* are a common sight (Wiltshire 1940; Larsen 1976, 1982; Pittaway 1981). Indeed, all the available data strongly suggest that European spring migrants originate from the band of desert crossing North Africa and the Arabian Peninsula in a wide latitudinal zone roughly distributed south of 35º N (Emmet & Heath 1989; Shields 1992).

Much more detailed information comes from a recent study by Stefanescu *et al*. (2007), who analysed data from the Catalan Butterfly Monitoring Scheme (CBMS) for a period of over 10 years and found a strong association between *V. cardui* arriving in spring in Catalonia (NE Spain) and synoptic-scale winds originating in North Africa. This led these authors to suggest that significant butterfly migration was aided by African winds and occurred at several hundred metres above ground level. Meteorological trajectory analyses were then undertaken to identify probable source areas of migrants. According to a source-receptor model, migrants arriving in Catalonia in April–May mainly originate from three different areas in the Maghreb, located at a distance of 900–1,600 km: the Moroccan Anti-Atlas (and to a lesser extent in the equivalent area south of the Saharan Atlas in Algeria), the low plain of north-eastern Algeria stretching away across central Tunisia and up to the coast, and the coastal area of Tripolitania in Libya. If most migration is windborne and occurs at high altitudes butterflies would only need 20-36 hours to complete the journey with the help of tailwinds (Stefanescu *et al*. 2007). As the arrival of migratory waves in Catalonia follows a regular pattern and is concentrated in April and early May, this study provided, for the first time, testable predictions of the location and timing of source areas for *V. cardui* migrating into northern Spain in spring.

With this background information, in March 2009 we organized an expedition to one of the hypothetical breeding areas in Morocco to confirm *in situ* the occurrence of immature stages and/or emerging adults. In this article we describe the findings of the expedition and provide a full account of the biological observations that we gathered at one mass breeding site in western Morocco. For the first time, we present precise estimations of population density and mortality factors (viz. parasitism) at one source area of *V. cardui* in the African continent.

MATERIALS AND METHODS

Study species. The Painted Lady, *Vanessa cardui*, is one of the most widely distributed butterflies in the world, being absent only from tropical rain forests and parts of South America (Shields 1992). This cosmopolitan distribution is a consequence of its strong migratory behaviour coupled with the polyphagy of its larvae, two ecological traits that allow the species to thrive in virtually any kind of habitat.

Migratory phenology in the Palaearctic. In the Palaearctic, each spring the species arrives in Europe from northern Africa, spreading northwards from the Mediterranean in at least two successive generations (Williams 1970; Emmet & Heath 1989; Pollard *et al*. 1998). This poleward migration allows *V. cardui* to exploit resources that become available in spring and summer in the temperate zone, and to escape from the inhospitable environment of southern regions as the season advances.

In southern Europe, migratory waves are mainly recorded in April, May and early June (Stefanescu 1997; Pollard *et al*. 1998; Stefanescu *et al*. 2007). Migrants

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breed on a diversity of plants (see below) and give rise to a local generation at the start of summer. Newly emerged butterflies leave breeding areas quickly as they encounter the hot dry conditions typical of the Mediterranean summer and migrate northward in search of both nectar and egg-laying resources (Pollard *et al*. 1998). Adults arriving in Britain and Northern Europe in early summer are the progeny of the butterflies breeding in southern Europe; the few individuals regularly recorded there in the spring are thought to arrive directly from North Africa (Asher *et al*. 2001). Although adults emerging subsequently in northern Europe are forced to head for lower latitudes to escape increasingly unfavourable colder conditions at the end of the northern summer and early autumn, very few observations of southward movements exist (cf. Pollard *et al*. 1998). The lack of evidence of these return flights may be related to butterflies' use of alternative as yet unknown migratory routes: laboratory-reared autumn-generation butterflies flying in the UK displayed a highly significant mean orientation towards the SSW, consistent with a return migration to overwintering sites (Nesbit *et al*. 2009). Moreover, sudden appearances of huge numbers of worn adults in the Maghreb, the Canary Islands and the northern edge of the Sahel in September–October strongly support the existence of a return flight (C. Stefanescu & F. Páramo unpubl. data).

Larval hostplants and biological cycle. *V. cardui* is extremely polyphagous and many hostplants belonging to a number of plant families are known to be used in the wild (e.g. Ackery 1988; Whitebread 1988). However, in western Europe oviposition occurs mostly on thistles (many species in the tribe Cardueae, family Asteraceae) and common mallow, *Malva sylvestris* (Linnaeus) (e.g. Stefanescu 1997). Eggs are laid singly on the upper side of the leaves of the hostplant, each female potentially laying as many as 700 eggs (mean±SD: 507±57 eggs; Hammad & Raafat 1972). On hatching, larvae make a characteristic silken tent on the hostplant leaf. As it grows, the tent becomes very visible and may consist of the edges of one or more host leaves woven together. Excrements accumulate inside the tent, which remains highly conspicuous long after the larva has departed to pupate elsewhere.

V. cardui is a continuously–brooded species in which migration is used as an alternative to diapause as a means of surviving climatic extremes (Wiltshire 1949; Larsen, 1976). In laboratory-reared butterflies, Hammad & Raafat (1972) estimated a developmental time of ca. five days for the egg, 25 days for the five larval instars and 14 days for the pupa. The completion of the whole cycle in north-east Spain takes six to eight weeks, depending on temperatures (C. Stefanescu pers. obs.).

Natural enemies. Larvae and pupae are known to be attacked by several parasitoids (Shaw *et al*. 2009). Amongst those most frequently recorded is *Cotesia vanessa*e (Reinhard) (Hymenoptera: Braconidae: Microgastrinae), a gregarious larval parasitoid that parasitizes early instar larvae without killing them until they reach their fourth or, more usually, fifth instar. At that point, the larvae of the parasitoid erupt from the host to pupate in individual cocoons aggregated within a highly conspicuous mass of flocculent white silk. Cocoon masses are typically found close by the dead host larva. *Thyrateles camelinus* (Wesmael) (Hymenoptera: Ichneumonidae: Ichneumoninae) and several tachinids (Diptera: Tachinidae: Exoristinae) have also been reported as frequent larva-pupal parasitoids in the European (Linnaeus) range of *V. cardui*, as has the generalist *Pteromalus puparum* (Hymenoptera: Pteromalidae), which often parasitizes the pupae.

Data on predation of the adult stage are much scarcer. However, there are various observations of insectivorous birds (e.g. Spotted Flycatcher *Muscicapa striata* (Pallas) and European Bee-eater *Merops apiaster* (Linnaeus)) preying upon *V. cardui*, especially during migration (see Stefanescu & Julià 2002, for details).

Study area and sampling. The expedition was initially focussed on central western Morocco, at approximately latitudes 29º34'–31º15' N and longitudes 5º10'–8º10' W, one of the areas predicted as a source area for migrants arriving in north-eastern Spain in spring (see Stefanescu *et al*. 2007). We eventually extended our sampling area westwards to include the Souss valley. According to the timing of spring migration, we expected to find larvae in various developmental stages at the end of March and in early April (see above). Our data was complemented by additional observations made by several colleagues who had visited Morocco in February, March and April.

From 24 to 30 March 2009 we traveled across this region, performing detailed searches for eggs and larvae at different sites (Table 1). We chose those areas offering potential breeding grounds for *V. cardui* based on the presence of suitable hostplants (e.g. patches of thistles or mallows along road banks or in date plantations). We also carried out searches on other potential hostplants (e.g. *Echium* spp., *Forsskaolea tenacissima* (Linnaeus), *Plantago lanceolata* (Linnaeus), etc.) that have been recorded as hostplants in Morocco and the Canary Islands (C. Stefanescu pers. obs.). At each sampling site we spent a variable amount of time

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TABLE 1. Locations surveyed for *Vanessa cardui* immatures on central western Morocco in March 2009. Abundance of immatures follows a qualitative scale, from 0 (no egg, larva or pupa found) to 5 (>1,000 immatures). MDV gives the value representing the mean developmental stage of the breeding population, from 0 (egg) to 7 (freshly emerged adult). Also indicated is the presence (1) or absence (0) of the parasitoid *Cotesia vanessae* in samples of wild larvae reared in the laboratory.

Study site	Longitude (°W)	Latitude (°N)	Altitude (m)	Date	Immature abundance	MDV	Presence of *C. vanessae*
P3	-7.54	31.54	931	24-Mar-09	0	-	-
P4	-7.38	31.27	2149	24-Mar-09	0	-	-
P6	-6.58	31.03	1164	25-Mar-09	0	-	-
P7	-6.32	31.13	1298	25-Mar-09	0	-	-
P8	-5.82	31.37	1452	25-Mar-09	0	-	-
P9	-5.34	31.45	1151	26-Mar-09	2	4.3	1
P10	-5.34	31.44	1132	26-Mar-09	2	5.5	1
P11	-5.20	31.14	896	26-Mar-09	2	3.7	1
P12	-5.27	30.99	885	26-Mar-09	0	-	-
P13	-5.52	30.79	848	26-Mar-09	2	2.5	1
P14	-5.58	30.79	868	26-Mar-09	3	3.9	1
P15	-6.56	30.66	1039	27-Mar-09	3	4.7	1
P16	-6.90	30.53	1447	27-Mar-09	2	3.3	0
P17	-6.98	30.47	1062	27-Mar-09	1	2	0
P18	-6.92	30.43	995	27-Mar-09	1	2	0
P19	-6.93	30.43	1008	27-Mar-09	1	2	0
P20	-7.91	30.52	1015	27-Mar-09	3	4.5	1
P21	-8.18	30.62	655	28-Mar-09	3	6.9	0
P22	-8.75	30.49	287	28-Mar-09	2	6.4	1
P23	-8.79	30.49	254	28-Mar-09	2	5.8	1
P24	-8.85	30.49	255	28-Mar-09	5	6	1
P26	-8.90	30.43	204	29-Mar-09	3	6.6	1
P27	-9.07	30.06	780	29-Mar-09	2	5	1
P28	-9.03	29.99	1069	29-Mar-09	2	4.1	1
P29	-9.00	29.89	1213	29-Mar-09	2	3	0
P30	-9.15	30.07	564	30-Mar-09	3	6.8	1
P31	-9.25	30.17	209	30-Mar-09	4	6.5	1
P32	-8.86	31.28	659	30-Mar-09	2	2.8	0
P33	-8.67	31.58	334	30-Mar-09	-	-	-
P34	-8.58	31.58	361	30-Mar-09	3	4	1

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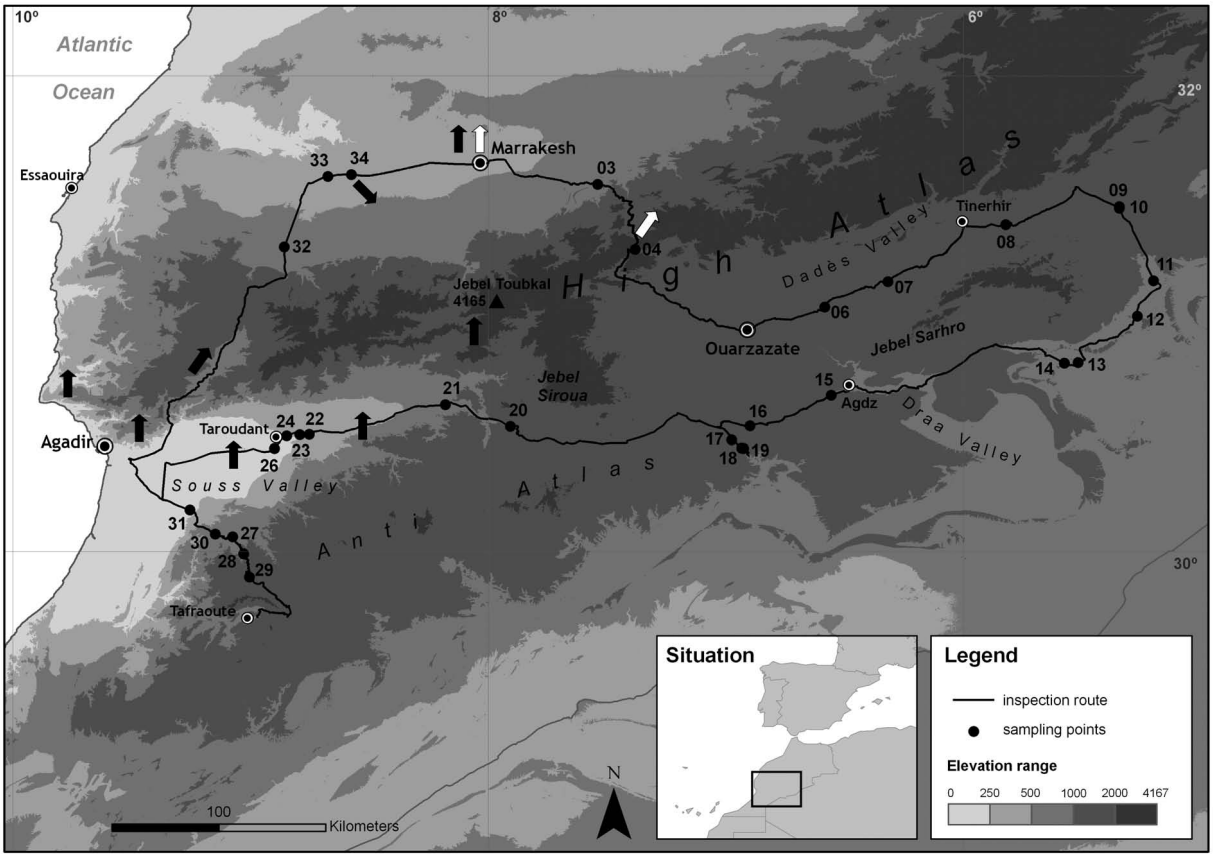


FIG. 1. Area surveyed in Morocco, with indication of sampling sites for immatures and adult migratory flights (black arrows: migrations of freshly emerged adults; white arrows: migrations of worn adults).

(between 15–60 min) that was proportional to the number of potential hostplants present. Although the resulting data was not strictly comparable, we believe that we spent enough time at each site to provide an accurate estimate of the breeding population, as expressed in the following qualitative scale: 0 = no immatures found (egg, larva or pupa), 1 = 1 immature, 2 = 2–10 immatures, 3 = 11–100 immatures, 4 = 101–1,000 immatures, 5 = >1,000 immatures. The presence of adults, their wing wear and behaviour were also recorded. Freshly emerged adults can be easily distinguished from immigrants by their bright colours and perfect wing condition.

At the sampling sites, each larval nest found was inspected to determine larval instar according to cephalic size. Large empty nests with accumulated frass were considered to correspond to final-instar larvae that had left to pupate elsewhere. We then calculated, for each sample, a value representing the mean developmental stage of the breeding population according to the scale: 0 = egg, 1–5 = larval instars, 6 = empty nest corresponding to the last larval instar or pupa; 7 = freshly emerged adults.

At site P24 (see Results) we localised an exceptional and perfectly delimited small area of 1.8 ha where pupae were hanging from the low vegetation in enormous densities and adult emergence was taking place. To estimate population density at this site we carried out a belt transect survey, consisting of pupal counts along 10 random replicated belt transects of 10 × 1 m. Starting at the centre of the patch, we used random numbers to determine the position and orientation of each of the 10 belt transects.

Parasitoids attacking the immature stages were also investigated. Wild caterpillars of any instar were collected whenever found at field sites and reared in the laboratory until they produced either parasitoids or adult butterflies. Cocoon masses of *Cotesia vanessa*e found directly on hostplants were also used to record its presence in a breeding population. In addition, the incidence of *C. vanessae* was estimated at site P24 by counting the cocoon masses found along the belt transects established for pupal counts. A sample of 50 wild pupae was also collected at this site to investigate pupal parasitoids.

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RESULTS

Distribution of immatures. During the trip, we searched for immatures of *V. cardui* at 29 sites in an area of ca. 30,000 km^2 (Table 1; Fig. 1). Immatures were found at 23 sites, only being absent from the north-easternmost area, that is, the High Atlas and the high plateau situated between Ourzazate and the valley of Dadès. Past Tinerhir, immatures started to appear on a variety of hostplants, becoming commoner as we moved towards lowland areas near the Atlantic coast. This is clearly shown by the strong tendency of immatures to increase their abundance with decreasing altitude ($r = -0.65$, $P < 0.001$) and as we moved westwards ($r = -0.45$, $P = 0.014$). This increase in abundance was paralleled by an increase in the mean developmental stage of the breeding population, which showed the same trends as altitude ($r = -0.64$, $P = 0.001$) and longitude ($r = -0.44$, $P = 0.037$).

Hostplant use. Larvae were recorded on a variety of hostplants belonging to the families Asteraceae, Urticaceae, Boraginaceae, Malvaceae and Arecaceae (Table 2; Fig. 2). In general, thistles (tribe Cardueae) were the most commonly used hostplants, particularly *Onopordon* spp. (up to three different species) growing in habitats such as road banks and fallow land near cultivated areas and villages. Other hostplants commonly recorded were *Echium* spp. and *Forsskaolea tenacissima* (mostly in the Anti Atlas), and common mallow (especially near the coast). Moreover, at site P24, where we found massive numbers of larvae, an unidentified species of *Centaurea*, as well as other thistles and common mallow, were being used. Finally, a subsequent visit to site P3 in April 12 produced a surprising record of a 4th instar larva feeding on *Chamaerops humilis* (Linnaeus), a palm belonging to the family Arecaceae.

Parasitoids. *Cotesia vanessa*e was recorded at 16 of the 23 sites (70%) visited, from where we collected immature stages. It was widely distributed throughout the region, from the western lowland areas of the Souss valley to the eastern high plateau situated between Tinerhir and Agdz. Its apparent absence from sites P16–19, P29 and P32 was probably an artefact of the very small number of larvae collected for rearing at these sites (only 1–5 larvae).

Apart from *C. vanessa*e, the only recorded larval parasitoids were the solitary wasp *Cotesia vestalis* (Haliday) (Hymenoptera: Braconidae: Microgastrinae), reared from a single larva collected at site P20, and one unidentified Ichneumonidae Campopleginae and one unidentified Braconidae Microgastrinae, reared from two larvae collected at P15. On the other hand, several ichneumonid and chalcidoidea wasps were recorded as pseudohyperparasitoids of *C. vanessae* cocoons (cf. Shaw *et al*. 2009). Details of this parasitoid complex will be presented elsewhere (C. Stefanescu, M.R. Shaw & R.R. Askew in prep.).

In total, 17 out of 50 pupae collected at site P24 turned out to be parasitized by *Pteromalus puparum*. No larva-pupal parasitoids (e.g. either ichneumonid wasps or tachinid flies) were recorded from this sample. Neither did we record any dead pupae in the transect counts exhibiting the characteristic proteinaceous strands left by tachinid larvae when vacating their host pupa (Baumgart *et al*. 2003).

The population outbreak at site P24. Population densities were especially high in the Souss valley, the vast flat area extending around *oued* Souss immediately south of Agadir (Fig. 1). In the dry riverbed of the *oued* there were large concentrations of thistles, on which larvae from later instars and empty nests were very common. High densities were also recorded on thistles and *Echium* spp. growing on the margins of wheat fields and Argan, *Argania spinosa* (L.) Skeels, woodland, but also in dry sandy areas with sparse vegetation (e.g. with bushes of the Asclepiadaceae *Calotropis procera* (Aiton)). However, the highest density was found in the outskirts of the city of Taroudant (site P24, Fig. 1). Attracted by an unusual concentration of butterflies flying low over the ground, we located an emergence area consisting of a small patch of waste land of 1.8 ha, perfectly delimited by the main road, a river bank, and several buildings and crops, where there were huge numbers of fresh adults and pupae hanging in their thousands from the herbs and bushes (Fig. 2).

Pupal density in the patch was estimated at 85.8±27.8 pupae/10 m^2 (95% confidence interval), which gives a total number of 154,440±50,109 pupae for the whole patch (Table 3). Pupae were found on all types of vegetation, but were especially abundant on bushes of *Launaea arborescens*, a spiny Asteraceae that was likely selected as a pupation site due to the mechanical protection it affords against predators. In some bushes we counted up to 200–300 pupae (Fig. 2). Butterflies had already emerged from most of the pupae (94% of the pupae were empty). Of the remaining 6%, 1.5% of the pupae bore characteristic signs that could be attributed to invertebrate predation (e.g. lateral holes in the pupal case; see Frank 1967), 1.7% were parasitized by *Pteromalus puparum* (as estimated from our rearing sample), and 2.8% were healthy (Table 3).

Cocoons of *C. vanessae* (each one corresponding to a larva that had been parasitized) were also very common among the vegetation. From the transect counts, we estimated a density of 9.5±6.8 cocoon masses/10 m^2,

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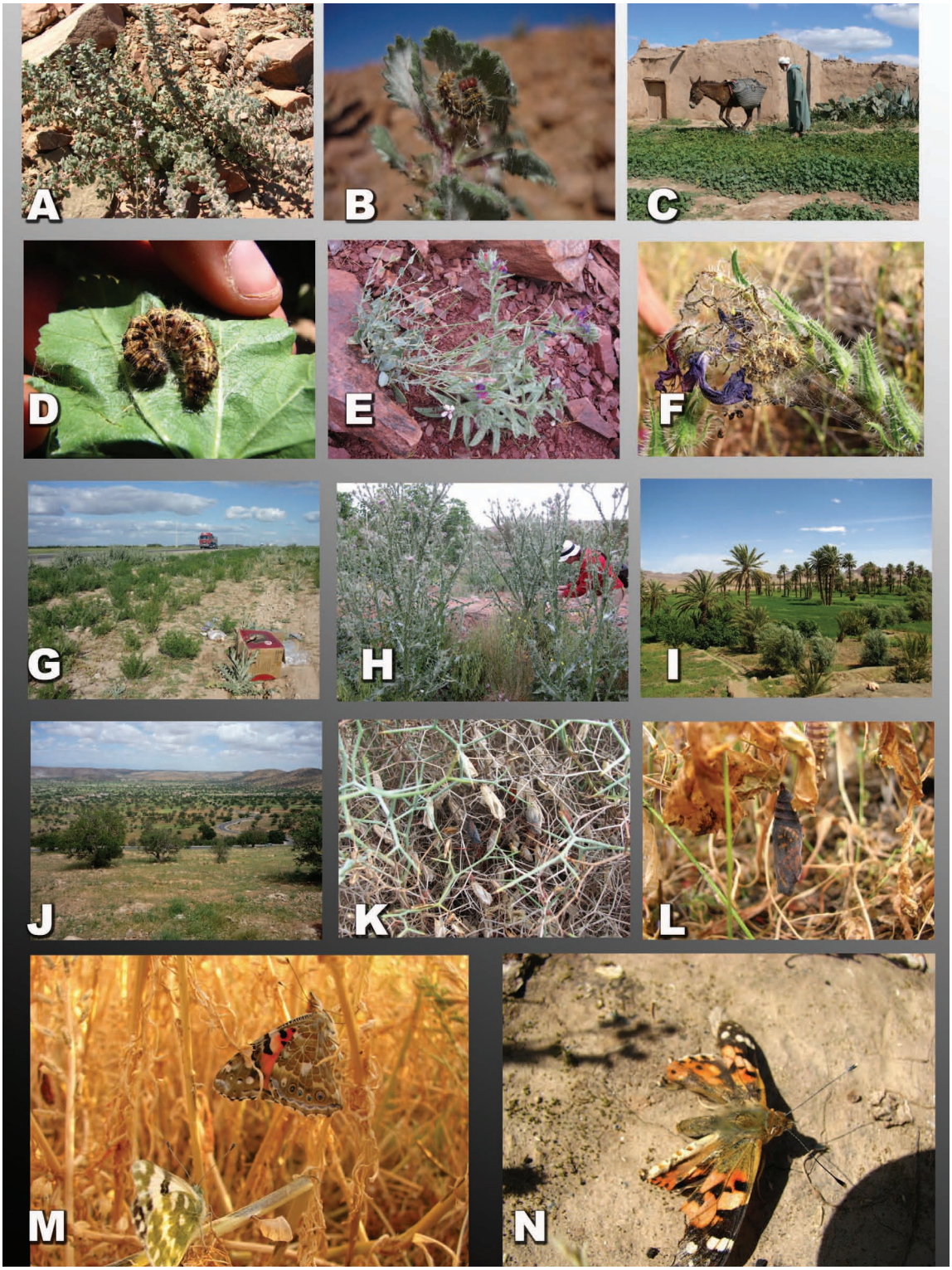


FIG. 2. Main hostplants of *Vanessa cardui* and explored landscapes in Morocco, March 2009. **A,** General aspect of *Forsskaolea tenacissima*; **B,** and plant with a 5th instar larva; **C,** patch of *Malva sylvestris* in a village; **D,** and plant with a 5th instar larva; **E,** *Echium* spp.; **F**, and plant with a 5th instar larva; **G,** road bank plenty of *Onopordon* sp.; **H,** and plants bearing larval nests; **I,** site P11, palm plantation in the Jebel Sarhro near Alnif; **J,** the Souss valley; **K–L,** concentration of pupae in the outbreak population at site P24; **M,** roosting of *V. cardui* and *Pontia daplidice* at site P24; **N,** a crippled adult at site P24, as a result of a heavy downpour at the time of emergence.

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TABLE 2. Hostplants of *Vanessa cardui* recorded during the expedition to central western Morocco in March 2009.

Hostplants	**Sites**
Malvaceae	
Malva sylvestris	P11, P20, P24, P30, P32
Urticaceae	
Forsskaolea tenacissima	P17, P18, P19, P30
Boraginaceae	
Echium spp.	P16, P21, P27, P29, P30
Asteraceae	
Centaurea sp.	P24
Echinops spinosus bovei	P10, P13, P28
Onopordon spp.	P9, P10, P11, P13, P14, P15, P21, P22, P23, P24, P26, P28, P31, P34
Unidentified thistle	P16
Arecaceae	
Chamaerops humilis	P3*

* observation in a later visit, on 12 April 2009

which gives a total number of 15,120±12,188 cocoons for the whole breeding patch. The total population can therefore be estimated as consisting of 169,560±59,984 larvae of *V. cardui* (i.e. pupae plus cocoon masses), of which ca. 10% were parasitized by *C. vanessae* (Table 3).

Observations of adult behavior were obtained on two consecutive days, on the afternoon of 28 and the morning of 29 March. There was no sign of sexual behaviour (i.e. no males showed territorial or courtship behaviour; cf. Brown & Alcock 1991). Instead, butterflies spent most of their time looking for nectar sources. We recorded many butterflies nectaring on *Eucalyptus* sp. and, to a lesser extent, on *Nerium oleander* (Linnaeus) around the breeding patch. Other nectar sources included *Asphodelus fistulosus* (Linnaeus), *Peganum harmala* (Linnaeus), *Reseda alba* (Linnaeus) and the few larval hostplants that had not been completely consumed by the larvae (e.g. *Onopordon* sp., *Centaurea* sp. and *Echium* sp.). On the morning of March 29 we also saw numerous interacting pairs behaving in the manner described by Giuliani & Shields (1995): butterflies on the ground rose up to join butterflies flying above them, the two interacting butterflies then continuing flying together for a certain distance before resettling again or departing northward.

Butterfly emergence was also commonly recorded both in the afternoon and in the morning. In the afternoon of March 28 there were a couple of heavy downpours that lasted for several minutes. As a consequence, some of the emerging butterflies were unable to extend their wings successfully and were found dead on the ground the following day (Fig. 2). By late afternoon we observed many butterflies roosting in the patch itself. They mainly selected high dry twigs of *Reseda alba*, which was the most abundant plant in the area. It was not unusual to find groups of two or three Painted Ladies roosting together on the same plant, sometimes side by side with *Pontia daplidice* (Linnaeus) (Pieridae), the second most common butterfly at the site (Fig. 2).

By the time butterflies started to look for a roosting site, barn swallows, *Hirundo rustica* (Linnaeus), from a colony in a nearby building were attracted by the butterfly swarm. The birds started to hunt the butterflies, mainly chasing them while in flight but sometimes also by picking them off the vegetation. We recorded at least ten birds (including one Red-rumped Swallow, *Cecropis daurica* (Laxmann)) successfully capturing butterflies and taking them to their nests to feed their chicks.

Migratory flights. A migratory wave was detected on the afternoon of 24 March near Col du Tichka (2,250 m), at site P4. Worn adults were seen flying at 0.5–1 m above the ground in ENE direction, in singles or in pairs at an estimated density of 45 butterflies/15 min (as visible to a recorder on the ground). Several old females engaged in searching behaviour at P3 a couple of hours before were probably also part of the same migratory wave (see Fig. 1).

Except for two butterflies found at sites P7 and P10, adults were not detected again until the Souss valley. On

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TABLE 3. Estimations of population density and mortality factors in the outbreak population of *Vanessa cardui* occurring at site P24 on the outskirts of Taroudant.

	Mean	± 95% CI
Density of pupae/10m²		
Already emerged	80.3	25.5
Not emerged yet	4.2	2.9
Dead with signs of predation	1.3	0.9
Total density	85.8	27.8
Density of cocoon masses of Cotesia vanessae/10m²	9.5	6.8
Number of pupae in the patch[1]		
Already emerged	144,540	45,865
Not emerged yet	7,560	5,143
Dead with signs of predation	2,340	1,612
Total number	154,440	50,109
Number of cocoon masses of *Cotesia vanessae* in the patch[1]	15,120	12,188
Total number of larvae in the patch[2]	169,560	59,984

[1]Patch area of 1.8 ha
[2]Number of pupae plus number of larvae parasitized by *Cotesia vanessae*

the other hand, from site P21 westwards, fresh adults were commonly recorded all along the route. Although at some sites only a few butterflies exhibited migratory behaviour (see the previous section), in the mornings and early afternoons of 28, 29 and 30 March we recorded several spectacular mass movements along the main roads between Taroudant and Agadir, Aït–Baha and Agadir, and Agadir and Chichaoua (Fig. 1). Many thousands (if not millions) of newly emerged butterflies were flying in a northward direction, 0.5–2 m above the ground. Many butterflies were knocked down by vehicles when crossing roads and on several occasions we saw house sparrows, *Passer domesticus* (Linnaeus), waiting on road banks to eat the butterflies killed by cars. Interestingly, all the migratory flights coincided with southerly winds, except for one abnormal southward movement (recorded at P34 at 1630 h), when the wind had also veered towards the south (Fig. 1). Fresh adults migrating northwards were also recorded in Marrakech and at a high mountain pass at 3,000 m near the summit of Toubkal during the first week of April (G. Muñoa pers. com.).

Other northward flights consisting of worn individuals were reported by ornithologists working at a bird-ringing station near Merzouga in the second week of March (M. Anton pers. com.). In contrast with the migratory flights recorded in the Souss valley, movements of worn individuals in early March (and also in the High Atlas on 24 March) may correspond to populations originating further south (e.g. in the Canary Islands). In other words, they may involve the progenitors of the butterflies that later emerged in our studied source areas.

DISCUSSION

Our expedition to Morocco was organized to test in situ for the presence of high numbers of immature *V. cardui* in one of the source areas predicted by Stefanescu *et al*. (2007) of the migrants arriving in north-east Spain in April–May. Our predictions were essentially correct, as we did find immatures at virtually all the sampled sites except from the north-easternmost explored region and the central High Atlas, at altitudes of over 1,000 m, which lie on the edge of the predicted source region. The maximum abundance was found in the Souss valley, slightly more to the west than predicted by the model, although it must be stressed that our modelling approach should be regarded more as a useful tool for approximating the most likely source areas than a method for determining their exact locations.

It is also important to note that spring migrations in north-east Spain typically last for a period of nearly two and a half months, from early April to mid-June (see Fig. 3 in Stefanescu *et al*. 2007). Thus, the exact location of the source areas probably varies over time and the first migrants arriving in Spain are predictably those that develop in warmer areas earlier in the season. By late March, for instance, the abundance of immatures in the source region increased towards the west and at lower altitudes, that is, in those areas that fulfilled the right climatic conditions for larval and pupal development. Similarly, the mean stage of development of the breeding populations increased along the same variables, so that in the Souss valley butterflies were emerging. This coastal plain is characterised by its mild climate, with average minimum temperatures for January (the coldest month) ranging between 3ºC and 7ºC, in comparison with a range of 0ºC to 3ºC in the neighbouring mountain and inland areas (Sauvage 1963). As the season advances, it is very likely that other more northern and higher areas become favourable for breeding and therefore act as the main sources of migrants later in the spring. A clear example is provided by site P3 on the northern slope of the central High Atlas, where on March 24 we found no immatures but recorded several egg-laying females. A visit to the same

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site on 12 April, revealed the presence of many mid-aged larvae, from which adults would emerge by late April or early May. This example shows how the breeding area progressed northwards over the course of a period of three weeks.

Field work also allowed us to confirm that breeding habitats were suitable and common enough in the region to permit population densities to build up into the high numbers that are periodically recorded in Europe. Because *V. cardui* is a highly opportunistic species that uses a diversity of hostplants growing in ruderal areas (e.g. derelict land, road banks, field margins, etc.; see Fig. 2), there is no shortage of hostplants or habitats for reproduction. In this respect, the use of *F. tenacissima* in the Anti Atlas (confirming previous unpublished observations) is remarkable, especially because this plant can be very abundant, offering an alternative to the plants typically used in more ruderal habitats. Likewise, the unusual record of a larva feeding on *C. humilis* provides further evidence of the extremely polyphagous nature of *V. cardui* (Ackery 1988). Another crucial aspect of the field work was that we were able to confirm that hostplant quality was optimal in early spring, thus allowing larvae to exploit a highly temporal resource that deteriorates rapidly as the growing season advances in this semi-desert region (e.g. Pedgley *et al*. 1995).

Our observations, together with the typical patchy distribution of the ruderal habitats used for breeding, lead us to suggest that source populations in this Moroccan region do not stem from large continuous areas, but most frequently originate in small pockets hosting the most favourable conditions. Only under certain circumstances, that is when abundant larval resources coincide with abundant nectar sources and lead to higher patch occupancy and levels of oviposition (Janz 2005), will outbreak populations occur. An example of such a situation was provided by the single small patch of waste land near Taroudant of little over 1.5 ha, where more than 150,000 larvae had completed their development. Countless comparable sites occur all over the Souss valley, but also along many roads and near human settlements elsewhere, making the whole region a potential source area for the butterflies colonising Europe every year.

The finding of the massive emergence site together with the observation of vast numbers (probably several millions) of fresh butterflies migrating nearby, clearly indicates that outbreak populations originating in the Souss valley immediately depart to colonize regions situated to the north. This pattern agrees well with earlier reports of mass exodus soon after emergence (Skertchly 1879; Egli 1950; Giuliani & Shields 1995). Interestingly, we also frequently noted that pairs formed as individuals on the ground rose up to interact with those flying above them, before departing in a northward direction. These pairs with one butterfly pursuing another may last for the whole migratory journey, as they are a very common sight in *V. cardui* mass movements (e.g. Myres 1985; C. Stefanescu pers. obs.). Giuliani & Shields (1995) even suggested that this kind of behaviour could trigger the start of a migratory wave, a possibility that deserves further investigation.

If, as posited by Stefanescu *et al*. (2007), long-distance migration of *V. cardui* is associated with synoptic wind masses and occurs mostly at high elevation, we would expect the butterflies that departed from the Souss valley on 28–30 March to arrive in north-east Spain in the first week of April after a non-stop flight of only a couple of days. This prediction agrees well with data from the CBMS in 2009, which indicates that the first noticeable wave of migrants arrived in Catalonia around 4–5 April. On the contrary, if migration were restricted to the flight boundary layer close to the ground and was essentially non-wind assisted, butterflies would have arrived in Catalonia no earlier than 20 April at the earliest (taking into account a total distance of 1,500 km, a flight speed of 15 km/h and an average of five hours of migratory flight per day; cf. Abbot 1951). This is, in fact, a highly optimistic estimation, since bad weather would likely stop migration for long periods and energetic demands would lead to stops of various days for refuelling (e.g. Davis & Garland 2004). In this respect, it is interesting to note the negative effect of the southward wind that we recorded at site P34, which seemed to reverse the direction of the migratory movement. Therefore, although considerable uncertainty remains regarding the migratory process (e.g. the actual altitude at which butterflies fly), there is now strong evidence pointing to the selection of favourable tailwinds by migratory *V. cardui* (see also Myres 1985). This strategy, which minimizes energy consumption and travelling time and would be expected to evolve in an organism whose life history is shaped by long-distance migration, has indeed been confirmed in some other related species (e.g. *Vanessa atalanta* (Linnaeus) (Nymphalidae: Nymphalinae) and *Danaus plexippus* (Linnaeus) (Nymphalidae: Danainae); Gibo & Pallett 1979; Mikkola 2003; Brower *et al*. 2006; Brattström *et al*. 2008).

Finally, as far as we know, the present work is the first to provide a quantification of the population size and the impact of parasitoids in an outbreak area (but see the interesting descriptions by Giuliani & Shields (1995, 1997a,b, 1998), for outbreak populations in California).

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Population density was assessed at 94,200±33,324.4 larvae/ha, which gives an idea of the huge number of butterflies that can be produced in such a vast region at the right phenological time. Likewise, we estimated that 8.9% of the larvae died as a result of the impact of the main parasitoid, *C. vanessa*e, while 1.7% of the pupae were attacked by *P. puparum*. Although the impact is moderate, the parasitoid populations will build up to enormous numbers on this single butterfly generation: taking into account that each butterfly larva produced 38.9±25.4 wasps (±SE; n = 28), a population of 588,637 *C. vanessae* can be estimated to have emerged from this single patch (without pseudohyperparasitism). This means that the impact of *C. vanessae* on a hypothetical second butterfly generation occurring in the same area would be extremely high. Therefore, our data give further support to Owen's (1987) hypothesis that migration in *V. cardui* is at least partly adaptive to reduce parasitoid load.

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