



Discovery of mass migration and breeding of the painted lady butterfly *Vanessa cardui* in the Sub-Saharan: the Europe–Africa migration revisited

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Migratory behaviour has repeatedly evolved across taxa as an adaptation to heterogeneity in space and time. However, insect migration is still poorly understood, partly because of the lack of field data. The painted lady butterfly *Vanessa cardui* undertakes a long-distance annual migration between Europe and Africa. While spring flights from the Maghreb to Europe are well characterized, it is not known how far the European autumn migrants travel into Africa and whether they massively cross the Sahara Desert. We conducted fieldwork in four African countries (Chad, Benin, Senegal, and Ethiopia) in autumn and documented southward migrants in central Chad and abundant breeding sites across the tropical savannah as far south as the Niger River in the west and the Ethiopian highlands in the east. Given directionality and timing, these migrants probably originated in Europe and crossed the Mediterranean, the Sahara and the Sahel, a hypothesis that implies the longest (>4000 km) migratory flight recorded for a butterfly in a single generation. In the light of the new evidence, we revise the prevailing spatiotemporal model for the annual migration of *V. cardui* to incorporate tropical Africa, which could potentially be regarded as the missing geographic link between autumn (southwards) and spring (northwards) movements. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, 00, 000–000.

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INTRODUCTION

Animal migration is an evolutionary response to heterogeneity in both space and time, since it functions as a strategy for exploiting temporary resources associated with non-permanent habitats (Southwood, 1962, 1977; Dingle, 2014). Migratory strategies have evolved independently on a diverse array of unrelated species including birds, mammals (terrestrial and aquatic), fish, reptiles, crustaceans and insects (Alerstam, Hedenström & Åkesson, 2003; Dingle & Drake, 2007). Among insects, species of dragonflies, locusts, moths and butterflies are well-known migrators (Chapman, Reynolds & Wilson, 2015), usually involving several generations in the completion of round-trip journeys. One of the most famous cases is

that of the North American populations of *Danaus plexippus* L. (monarch butterfly), which has become a model species for the study of insect migration. This species performs a round-trip migration involving up to five generations between Canada and warmer latitudes in Mexico, where one generation of adult butterflies spends the winter in diapause.

Vanessa cardui L. (the painted lady) is another butterfly performing equally impressive migrations. Although both species seem to share routes in North America, as well as some physiological adaptations and methods of orientation (Nesbit *et al.*, 2009; Chapman *et al.*, 2015), they are not closely related phylogenetically and key differences exist: (1) *D. plexippus* specializes on species of *Asclepias* L. as larval host plant, whereas *V. cardui* is polyphagous and feeds on plants from a variety of families. (2) *D. plexippus* diapauses during the winter, while *V.*

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cardui does not and thereby apparently migrates in successive generations year-round. (3) The distribution range of *V. cardui* is much wider than that of the monarch. It is a virtually cosmopolitan species that can be found everywhere except most of South America and Australia. Thus, *Vanessa cardui* has one of the largest distributional ranges among terrestrial animals that undertake large-scale migratory movements (Shields, 1992). Occasional records exist for extremely cold localities, as for example, near the Arctic polar circle in Svalbard, Norway (Lokki, Malmstrom & Suomalainen, 1978) and close to the Antarctic on the island of Marion, c. 1800 km southeast of Africa's southern tip (Chown & Language, 1994).

Little information is known about the species' global migratory routes, but migration between northwest Africa and Europe has received some attention (Williams, 1930, 1970; Pollard *et al.*, 1998; Stefanescu, Alarcón & Ávila, 2007; Stefanescu *et al.*, 2013). Most evidence is indirect, in the form of presence/absence records, breeding localities, and approximate flight directions. For example, the congruence of favourable trade winds and peaks of arrival in southern Europe allowed inferring potential source areas of the migrants from the Maghreb by backtracking air trajectories (Stefanescu *et al.*, 2007). These data have been assembled into a spatiotemporal model explaining hypothetical migratory routes in this part of the world (Stefanescu *et al.*, 2013). In summary, the migratory cycle in this region is characterised by latitudinal population shifts as the seasons progress: an annual northward advance in spring (March–June, note that northern-hemisphere temperate-climate seasons are consistently used throughout the text) followed by a southward return movement in autumn (September–November). It is thought that at least six generations are involved in this annual movement between the Maghreb and the Sahel (the region between the Sahara Desert and the Afrotropical zone; Fig. 1) and northern Europe (Stefanescu *et al.*, 2013).

A central unsolved question is the destination of south-bound fall European migrants. Given the paucity of data for *V. cardui* in the Maghreb between August and October, Stefanescu *et al.* (2013) suggested that the first generation of southwards migrants from Europe might produce one additional generation in the Mediterranean. In addition, and based on scant observations in the vast Sahel in western Africa, together with a southward *V. cardui* migration detected by an ornithological radar on the coast of Mauritania in 2003 (Swiss Ornithological Inst., unpubl. data), it has also been suggested that some fall migrants from Europe may arrive to the northern edge of the Sahel in Western Africa, likely following the Atlantic coastline (Stefanescu *et al.*,

2013). However, it is unclear if this also applies to central and eastern Africa, how far south the European migrants can reach in a single flight, and whether they cross the Sahara *en masse*. No further evidence potentially linking the annual migratory cycle of *V. cardui* in Europe to the Sahel and further south is available. Importantly, no data on reproduction have been reported for tropical Africa in autumn, except for one observation in northern Nigeria (Boorman & Taylor, 1977).

A second question is the whereabouts of most *V. cardui* specimens between December and February. Stefanescu *et al.* (2013) suggested that the species mostly spends the winter months in the Maghreb, where several generations would occur without undertaking long-distance migration, and restart the migratory behaviour in spring back to Europe. Paradoxically, the species has been recorded at relatively low densities from December to February in northwestern Africa (Stefanescu *et al.*, 2013), as well as in northeastern Africa (Larsen, 1976). Precise sites for massive winter breeding areas have not yet been identified, which is often explained by their presumably variable densities and localities in relation to unpredictable rainfall on these arid North African regions (Nesbit *et al.*, 2009). This hypothesis would entail strong, annual bottlenecks followed by sudden population explosions, often so large that it seems unlikely that the migrations arriving to southern Europe in spring could originate only on the limited populations surviving the winter in the Maghreb. Alternatively, the bulk of individuals may colonise the tropical African latitudes before moving north about February–March. This scenario would help explaining apparent fluctuations in density in the Maghreb–Europe part of the cycle, but no comprehensive studies have surveyed the vast extent of the Sub-Saharan savannah for *V. cardui*.

In summary, the role of Sub-Saharan Africa in the *V. cardui* intercontinental migration between Europe and Africa is uncertain, and frequently regarded as unimportant. Similarly to the long-term explorations that took place in North America for most of the 19th and 20th century and led to the discovery of the phenomenal overwintering sites of *D. plexippus* (Brower, 1995), dedicated fieldwork is still needed in the Old World to locate where most *V. cardui* occur in the winter (December–February). In this paper, we report data suggesting a massive and synchronised early fall colonisation of tropical Africa by this species, with a likely origin in Europe. We revise the current model of *V. cardui* migration to incorporate this region, and hypothesise that subsequent generations could migrate further south into tropical Africa before the return migration in February–March.

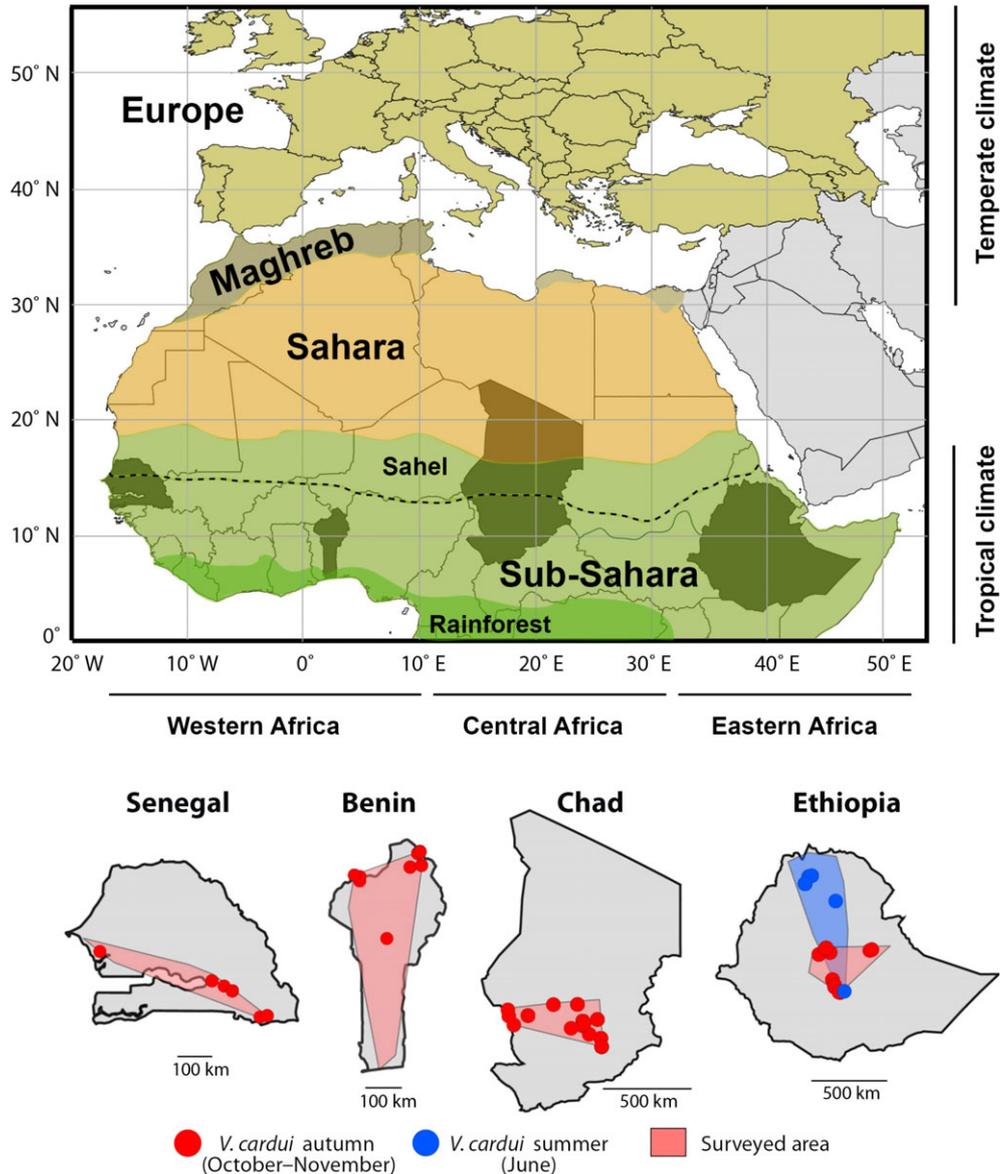


Figure 1. Presence records (dots) for *Vanessa cardui* within the area of sampling for each of the four countries studied. Surveyed areas are represented (blue, summer (June); red, autumn (October–November)).

MATERIAL AND METHODS

RATIONALE FOR EXPLORATION DESIGN

Four field surveys were designed to be consecutive during 2 months in autumn 2014 with the ultimate goal of evaluating potential *V. cardui* arrivals and breeding at sub-Saharan African latitudes. Four countries at strategic longitudes and with significant ecological gradients were selected (Chad, Benin, Senegal and Ethiopia). Collectively, they cover the immediate fringes south of the Sahel and the transition to the tropical savannah (Fig. 1). A prior expedition was conducted in Ethiopia in early June 2014 to investigate the relevance of high elevations as

potential breeding sites for *V. cardui* during the dry season.

The first autumn expedition was conducted in Chad between the 30th of September and the 15th of October 2014. Within this timeframe, 13 days of effective fieldwork and in total 27 localities were surveyed encompassing an area of approximately 97 700 km², between 10.8 and 13.4°N latitude, and 14.5 and 19.9°E longitude (Fig. 1). The route connected suspected breeding sites in central Chad, including the Chari River near N'Djamena, the southern shores of Lake Chad, the Lake Fitri region, the Guera Mountains, and Zakouma National Park.

These topographically varied sites spanned the pronounced transition between the Sahel and the tropical floodplains, which is typical of countries in Central Africa.

Benin was visited next, between the 15th of October and the 1st of November of 2014, allowing for 13 effective fieldwork days. Surveys involved 25 localities delimiting an area of *c.* 83 300 km² between 6.3 and 12.3°N latitude, and 1.5 and 3.3°E longitude (Fig. 1). We selected Benin in order to survey the ecological gradient from tropical forests in the south to grasslands in the north – a marked ecotone occurring over only 600 km. The circuitous route was planned to visit strategic spots including West Niger National Park and Pendjari National Park, both in the north and bordering with Niger and Burkina Faso, respectively.

A third autumn trip allowed exploring 14 localities during five effective field days in Senegal between the 1st and the 8th of November of 2014. Sampling sites were located between 6.3 and 12.3°N latitude, and 1.5 and 3.3°E longitude, encompassing an area of *c.* 29 000 km² (Fig. 1). Senegal's strategic location as a coastal country immediately south of the Sahara made it particularly appealing to study potential westernmost migratory arrivals. A transect from central-west to south-east was designated to span an ecotone ranging from agricultural lands and steppes to dense savannah woodlands (the Guinea savannah).

The last of the autumn expeditions led us to Ethiopia between the 16th and 29th of November. Accounting for 12 effective fieldwork days, 28 localities were surveyed within a *c.* 74 700 km² area between 6.5 and 9.6°N latitude, and 37.5 and 42.5°E longitude (Fig. 1). From the perspective of migratory studies, Ethiopia is interesting for its physical features and geographic location. Its biomes reflect remarkable altitudinal zonation, ranging from deserts to Afro-alpine ericaceous habitats. Our priority was to explore the country's altitudinal gradient, with particular interest in highland croplands as a potential habitat for *V. cardui* after the rainy season (June–September). The prior early summer expedition in Ethiopia was conducted between the 3rd and 23rd of June of 2014. About 30 localities during 17 effective days of work were inspected within a *c.* 157 300 km² area between 6.8 and 14.4°N latitude, and 36.2 and 40.0°E longitude (Fig. 1).

DATA COLLECTION IN TROPICAL AFRICA

The fieldwork design prioritised exploring as much land area and habitat diversity as possible within each country, thus travelling either along E–W and N–S transects. In general, entire days were devoted

to prospecting sites along the way. Usually travelling by car, random localities were inspected for *V. cardui*, and inspections could last from 1 h to an entire day when involving long hikes or altitudinal surveys. Late afternoons were dedicated to sampling at hilltops where males typically gather to establish territories (Brown & Alcock, 1990).

Behavioural data for *V. cardui* were recorded at each survey site, including migration, hilltopping, mating, oviposition, and territorial fights. When migratory individuals were detected (i.e. those displaying fast directional flights, often in flocks), we recorded flight direction and frequency of butterflies observed crossing an imaginary 10 m line (according to what a single person could supervise). Host plant preferences and the developmental stage of immatures (eggs, larvae, or pupae) was noted, including estimated larval instar. When breeding sites were encountered, abundances were estimated by performing systematic counts of individuals per plant and numbers of plants per area unit. Larvae of *V. cardui* produce silken shelters, which make the larvae easier to locate in the field.

Adults, early stages, and host plants were collected in the field and all samples were deposited at the Institut de Biologia Evolutiva (CSIC-UPF) in Barcelona, Spain, each with a unique code used to link the specimen to the collection information stored in a database. Butterflies were captured using aerial nets, rapidly killed by pinching the thorax, and stored in glassine envelopes. These were exposed to the sun for few hours to dehydrate them and ensure DNA preservation during fieldwork. Larvae were immediately stored in 100% ethanol tubes after collection. Larval host plants were collected and pressed. For proper long-term storage of field-dried adults, wings were later cut at the base and stored in glassine envelopes, and bodies were transferred to ethanol 100% and stored at –20 °C.

RESULTS

A FLOCK OF MIGRANTS IN THE SAHELIAN CHAD

October is typically the end of the rainy season in Chad and, as a consequence, floodplains south of the Sahel remain inundated and largely inaccessible. Fields, grassland, and forests were green with recent plant growth (Fig. 2A) and plenty of recently emerged insects were noticeable, including other potentially migrant Odonata, Orthoptera, and Lepidoptera. *Vanessa cardui* was among these and many individuals were observed throughout the entire expedition route. In total, 93 butterflies were collected, corresponding to 16 of 27 survey localities. Two main behavioural patterns were observed: in

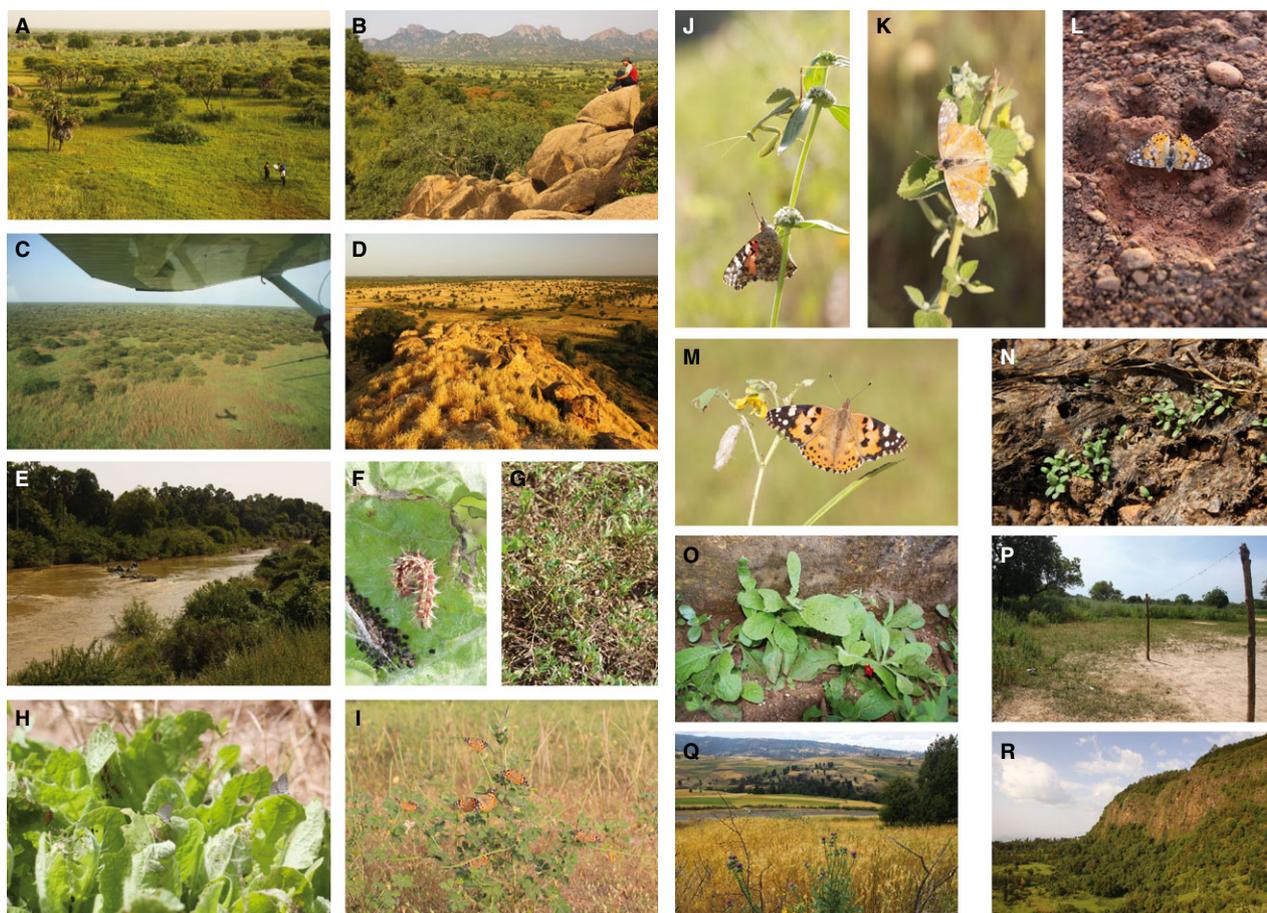


Figure 2. Primary habitats, host plants, and noteworthy sights for *Vanessa cardui* in tropical Africa in autumn (October–November) 2014. A, A fertile Sahelian plain near Lake Chad. B, Woodlands at the Guera Mountains, Chad. C, Floodplains in Zakouma National Park, southern Chad. D, A hilltop in a typical Sahelian landscape in Chad. E, *V. cardui* breeding sites were found next to the Alibori River in West Niger National Park, northern Benin. F, Fifth instar larva, northern Benin. G, Larval host plant (likely within the Lamiidae) in West Niger National Park, Benin. H, A Faboideae (Fabaceae) larval host plant widely used by *V. cardui* in Benin and Senegal. I, At least ten *V. cardui* butterflies alight on a *Senna obtusifolia* (Fabaceae, Caesalpinioideae) plant after a massive emergence in northern Benin. J, A fresh *V. cardui* specimen warming at dawn next to an empty pupal case in Karimama, Northern Benin. K, Mantises were predated on *V. cardui* in Karimama, northern Benin. L, An unusual unmelanised adult near the river Niger, northern Benin. M, Oviposition was observed on tiny plants growing on desiccating muddy patches in Pendjari National Park, Benin. N, A *V. cardui* butterfly possibly originating in Europe alights on a lion footprint in Pendjari National Park, Benin. O, Herbs (likely Asteridae) used by *V. cardui* larvae in the Bassari Country, Senegal. P, Anthropogenically modified habitats in Senegal were used as breeding sites. Q, Agricultural lands in the Ethiopian highlands in autumn offer ample resources for *V. cardui* reproduction. R, Regions above 3000 m in Ethiopia apparently presented optimal conditions for *V. cardui* in summer, but the species was never abundant here.

the Sahelian region from Lake Chad to Oum Hadjer (a west–east transect) migrating individuals flying south were usually observed, but specimens from the Guera Mountains (Fig. 2B) to the floodplains in the south (Fig. 2C) were sedentary.

In most localities within the Sahel, *V. cardui* specimens were observed consistently flying fast towards the south and we frequently scraped dead specimens from the front of our car. Butterflies were always

active on hilltops during late afternoons (Fig. 2D). On October 3rd, 2014, a particularly large migratory flock was observed near the village of Karmé (12.55°N, 15.91°E). The locality was in a typical Sahelian plain, with open space and few features or obstacles except for some scattered trees or bushes. We remained in the site from 07:30 h until noon. During the first 3 h, an average of six butterflies per minute crossed virtual lines of 10 m. After 11:00 h,

and thus close to the highest temperature of the day, activity decreased significantly to *c.* 2 migrants per minute. Considering the uniform vegetation and topography of the region and a consistent pattern for at least 200 m adjacent that were inspected, these observations lead us to estimate that several thousand butterflies migrated south to this locality.

South of the Sahel, in the Guera Mountains, presence of water was more frequent and the vegetation was lush, resulting in a markedly improved habitat for potential migrants arriving from the north. Large aggregations of adults (in the order of hundreds) were found regularly in valleys with streams and fields – usually nectaring and performing only short, slow flights. In the floodplains of Zakouma National Park and neighbouring areas, no signs of migratory behaviour or consistent flying directions were observed. For the first time mating was observed, which, although no larvae were located, suggested that a new generation was imminent.

On October 12th, 2014, an intriguing observation at the base of Mount Guera suggested the possibility of nocturnal migration, in the locality of Mukulu, near Bitkine (11.87°N, 18.20°E). At night, approximately at 22:00 h, a *V. cardui* imago suddenly landed on a table at our campsite, although only a red lamp was on to avoid attracting insects. A storm forming a few km south of this locality brought rains and strong winds an hour later. This observation may be linked to nocturnal migratory movements following trade winds (Chapman *et al.*, 2015) or a behavioural response to air pressure changes that precede storms (Burt & Pedgley, 1997).

A REMARKABLE BUTTERFLY EMERGENCE IN BENIN

We found *V. cardui* at 9 of 25 localities explored in Benin. All were dense aggregations in the extreme north (above 11.2°N) of the country – mainly in West Niger National Park, Pendjari National Park, and surrounding areas. A single individual was found below this latitude, at 9.7°N. In total, 90 adults were collected, plus several vials with larvae from three different localities.

The two breeding sites in West Niger National Park were found in different environments. The first flanked the shores of the Alibori River (11.66°N, 2.91°E), a forested tropical habitat (Fig. 2E). It encompassed an area of 400 m², and we estimated *c.* 1000 caterpillars (average of 25 larvae per plant group and a total count of 40 plant groups) (Fig. 2F). Eggs were also found, but no pupae. The host plant species probably belongs to the Lamiidae (Fig. 2H). Oviposition behaviour was also observed by typically quite worn females.

A second site was encountered in the village of Karimama, near the Niger River and the border with

Niger (12.07°N, 3.18°E). A massive emergence of adults took place in an abandoned field within town. The dominant plants in the field were grasses and *Senna obtusifolia* (Fabaceae, Caesalpinioideae), with few trees (*Azadirachta indica* A. Juss.). Oviposition was observed on a different, smaller, and unidentified Fabaceae (see Fig. 2G). A relatively abundant Malvaceae (*Waltheria indica* L.) was apparently avoided by *V. cardui* larvae, but was used as host plant by other Nymphalidae. However, adults frequently visited the plant and imbibed sticky droplets on the leaves and flower buds. Individuals were warming up early in the morning, staying either on plants or on the ground. Although activity increased as the day advanced, the butterflies persistently stayed flying or resting within the field limits. Considering an approximate area of 7000 m² for that field and an average three recently emerged butterflies per m², we estimated about 21 000 adult butterflies (see Fig. 2I). Moreover, no fewer than two pupae per m² on average were counted, but this figure may be underestimated because they were more difficult to detect than adults. We examined the site over 2 consecutive days and saw no decrement in butterfly number or hints of migratory movements. On the contrary, the total number of adults increased the morning of the second day, when many more adults emerged, though some pupae still remained intact. Predation by spiders and mantises was observed (Fig. 2J), agamid lizards frequently attempted to attack adults, and domestic hen patrolled the field, presumably searching for pupae. Only two larvae were found in the entire field. Noteworthy, evidence of parasitism was not detected here or elsewhere in our trips. *Vanessa cardui* was absent from neighbouring fields with similar characteristics. Taken together, the evidences suggest that most of the observed individuals were the offspring of a single, synchronised migratory swarm, temporally independent of the population at the Alibori River 53 km away, which had only larvae and eggs at that moment.

Multiple other colonies of *V. cardui* were observed near the Niger River. In the open flood plains abutting the river (12.09°N, 3.18°E), adults were distributed all along the shores, with up to 50 worn males displaying territorial behaviour in particular spots. Another visited locality (12.03°N, 3.12°E) allowed us to estimate *c.* 1000 butterflies, generally with high wing wear, occurring in an area of approximately 50 000 m² (after counting two butterflies, on average, in 10 × 10 m plots). This habitat was drier than other sites and was dominated by flowering *Guiera senegalensis* J. F. Gmel. (Combretaceae) on which the butterflies were nectaring. Like in Karimama, the same small legume plant was consistently selected by *V. cardui* females for oviposition, while

other nymphalid larvae were found on *Waltheria indica*. Polymorphism in adult size and larval colour were often observed in the Niger River region, and even an unmelanised adult form was found (Fig. 2K).

Occurrences in the north were recorded up to Pendjari National Park, in the northwestern corner of Benin. There, immatures at breeding localities were less dense than in the Niger region and were feeding mostly on young asterid plants. The adults found in the area were all worn and usually solitary. Females were seen ovipositing on tiny plants sprouting in desiccating muddy patches (Fig. 2N), among the footprints of wild mammals (Figure 2L). The grassland that was partly flooded during the rainy season was drying rapidly, thus offering fresh plant resources only for a limited time.

IMMATURE STAGES AND WORN ADULTS DURING THE DRY SEASON IN SENEGAL

It has been reported that *V. cardui* is apparently absent during the winter months (from December to March) in Senegal (Stefanescu *et al.*, 2013). This pattern coincides with the peak of the dry season, when vegetation is dry, often burnt, and food resources are therefore scarce. Typically, Senegal's rainy season runs from July to October, and our visit at the beginning of November was timed to coincide with the end of the optimal period for resources exploitation by potential migrants.

Although the dry season was rapidly advancing and the rains for 2014 had been lower than average, *V. cardui* was found along the route. In total, 33 adults were collected, and many more seen, at six of the 14 surveyed localities, although mostly in the region of Tambacounda. The Guinea savannah and the mountains of the Bassari Country in the south-east supported denser populations than the other areas. In contrast, densities were the lowest in grasslands and coastal habitats, where the dry season was notoriously more advanced. Generally, the captured specimens were notably worn, suggesting that they were old and might have undergone a long migratory journey. Males were found fighting for territories on hilltops, even when these were not cleared of trees or dense vegetation. Oviposition was observed and early stage larvae and eggs were found in Kédougou province on two different plants: a legume (Fabaceae) (presumably the same found in Benin) (Fig. 2G) and a species of Asteraceae (Fig. 2O) – both usually present in disturbed areas (Fig. 2P).

THE ETHIOPIAN HIGHLANDS

The abundance of *V. cardui* in the second half of November in Ethiopia was extraordinary. High

densities of adults and immatures were recorded, and 65 adult specimens were collected in 13 localities, as were larvae in seven of the 28 localities inspected. Larvae were recorded in large concentrations, mainly on *Carduus* spp. and *Cirsium* spp. thistles (Asteraceae). Late instars and empty silken shelters were the most common, although early instars were also present, which suggests that several waves of migrants could have arrived at the same localities. Many breeding sites were found across the highlands, always above 2300 m and typically in ruderal areas (field margins, derelict land, road banks, etc.) (Fig. 2Q). Urban areas had high densities of immatures as well, often in streets, abandoned lots, or landfill sites in Addis Ababa. Most of the adults that we collected appeared to have emerged recently and frequently excreted meconium. This observation was consistent with the abundance of empty silken shelters observed in the breeding sites. Thus, apparently most of the new generations had already emerged, which agrees with annual rainfall peaks occurring from July to September. Indeed, the visited localities below 2000 m, where the dry season was advanced, did not have healthy host plants and neither adults nor larvae were recorded.

Patterns of abundance in autumn contrasted with data from June 2014. Although regions above 3000 m apparently had optimal conditions similar to those in the fall (Fig. 2R), only few *V. cardui* were present. In total only 24 specimens were collected at only five of 30 sites visited in June, mostly in the Simien Mountains, except for one in Bale and one at the central highlands. These adults were always found above 2700 m (average 3060 m and up to 3490 m) and no traces of immatures were found.

DISCUSSION

ACROSS THE SAHARA? ORIGIN OF THE SUB-SAHELIAN POPULATIONS

Vanessa cardui was abundant in all four surveyed countries and we found direct or indirect evidence of mass reproduction during the autumn, coinciding with the disappearance of the species in Europe. South-bound migrants arrived en masse in Chad in late September and early October. Directional, migratory movement abated as they reached the verdant savannah at the end of the rainy season. Given that deserts extend north to the Mediterranean coast at the central longitudes of Africa, these migrants most likely originated in the central/eastern longitudes of Europe. The reports for northern Benin included potential migrants (worn, adult specimens) and huge new emergences about the 20th of October, the end of the rainy season. At the beginning of

November, Senegal was becoming increasingly dry, but worn adults and breeding areas were still present at the climatically most favourable areas in the south. Lastly, in eastern Africa (Ethiopia) countless recently emerged adults and late immatures were found. Taken together, the results of our fieldwork provide evidence suggesting that most European populations may undertake long-range migratory flights to tropical Africa, thus crossing the combined hazards of the Mediterranean Sea and the completely hostile Sahara Desert. If this hypothesis is confirmed with direct evidence, *V. cardui* would undergo an outstanding intercontinental migration, as individuals would traverse distances > 4000 km during their lifespan – one of the longest migratory flights for any insect. Is it feasible for a butterfly travelling over such a distance? *Vanessa cardui* is a species with a physiology and ecology highly adapted to the migratory behaviour and particularly to endure long flights (e.g. Williams, 1970; Nesbit *et al.*, 2009). Interestingly, while most butterflies perform migration within the flight boundary layer, two other strategies allowing enhanced flying capacities have evolved in particular species: (1) Ascent on thermal updraughts or by means of ‘slope lift’, then gliding across country has been documented in the nymphalids *D. plexippus* and *Nymphalis antiopa* L., as well as in the dragonfly *Pantala flavescens* Fabricius, under appropriate weather conditions. (2) Approximately downwind heading and relatively continuous powered flight using high-altitude winds, which is apparently characteristic of *V. cardui* and allows much faster displacement than the other two flight modes (Chapman *et al.*, 2015). Moreover, nocturnal migration does seem to be possible for *V. cardui* under certain circumstances (Ryrholm & Källander, 1986; Chapman *et al.*, 2015). In terms of speed, Stefanescu *et al.* (2007) estimated that *V. cardui*, when aided by favourable winds, could move at 45 km h^{-1} . At this constant speed, a 4000 km journey from Central Europe to Central Africa would involve as little as 4 days. Based on these estimates, reproduction and completion of the life cycle after migration is arguably possible given the lifespan of *V. cardui* adults (c. 4 weeks), notably long compared with most butterflies.

The possibility that the large populations documented in tropical Africa are disconnected from the European pool and are the product populations that survive the dry season *in situ* and demographically explode after the onset of the rainy season is unlikely because the inexistence of reports for substantial populations in this region from May to August, as well as because it does not agree with our observation of a southward migration in central Chad. Undeniably, the Ethiopian highlands would be the

best candidate for such hypothetical dry-season refuges, but our surveys during June detected hardly any specimens of *V. cardui*. We thus consider likely that the populations detected in autumn in tropical Africa have an origin in Europe.

THE ROLE OF TROPICAL AFRICA

In the African northern hemisphere, the advance of migratory insects polewards in February–May and towards the equator in August–November is a general phenomenon that is strongly related to seasonality and prevailing winds (Pedgley, Reynolds & Tatchell, 1995). Until now, it was unknown whether *V. cardui* was also involved in such a migratory system beyond the Maghreb. Our data confirms that the occurrence of migration and breeding for this species in tropical Africa is a widespread phenomenon covering the east, centre and west, and extending south to at least 6°N latitude. Unlike typical African species, the African migration system seems to be connected to the European system in the case of *V. cardui*. We propose that its latitudinal migratory range encompasses the temperate region (with seasonality determined by temperature) and the tropical region (with seasonality determined by rainfall). A link between Europe and tropical Africa was already envisaged by Owen (1971) decades ago, although direct evidence confirming this hypothesis is lacking.

The Intertropical Convergence Zone (ITCZ) is a critical phenomenon for understanding seasonal changes of climate in Africa. This geographic belt represents the contact zone where the trade winds of the Northern and the Southern Hemispheres come together. The resulting convective activity affects seasonal precipitation patterns across the continent. The location of the ITCZ varies throughout the year north or south of the equator by a total amplitude of as much as 40° of latitude. It reaches its northernmost limit during the northern-hemisphere summer just south of the Sahara at about 15–20°N, dumping rain on the region. These rains stimulate rapid plant growth in the savannah and Sahelian grasslands and, as a consequence, insect populations thrive in the following months (September–November), as was the case for *V. cardui*. A seasonal reversal occurs during September, when the ITCZ starts moving southwards, pushed by the advance of the Harmattan winds, finally reaching the equator in West Africa and 20°S in East Africa in December.

Generally, migrant species follow the advance or the retreat of the ITCZ, and a reversal of the migration course during the fall has been demonstrated for many insects (Pedgley *et al.*, 1995). The regions where most *V. cardui* spend the winter (December–February) are still an enigma and arguably the

missing gap linking fall southwards and spring northwards movements. The most accepted scenario at present posits that winter breeding regions are scattered across north Africa, mostly in the Maghreb, an area believed to represent the source populations of the often massive spring outbreaks (Stefanescu *et al.*, 2007, 2011, 2013). Such a scenario would involve a remarkable dead-end for the populations south of the Sahara here reported. The biological significance of migratory dead-ends in insects has been discussed at length (Rabb & Stinner, 1978; Stinner *et al.*, 1983; McNeil, 1987; Cardé, 2008a, b; Chapman, Drake & Reynolds, 2011; Chapman *et al.*, 2015). For example, southwards return migrations of many long-range migrant species at the end of the European summer are hard to document, a phenomenon that led to the proposal of the so-called 'Pied Piper Effect': the hypothesis that windborne insects reach northern temperate areas and perish before returning to the winter breeding regions in the south (Stinner *et al.*, 1983). Because large-scale return migrations are now well documented thanks to technological advances (e.g. entomological radars) (Chapman *et al.*, 2011), this hypothesis lacks support and such sink routes are hard to explain from an evolutionary perspective. If we reject a dead-end for the *V. cardui* populations we documented, then where do their offspring spend the winter (December–February), given that most studied areas were becoming extremely dry? We hypothesise that the next generation of *V. cardui* migrates further south following the retreat of the ITCZ and, as a consequence, the end of the rains, which seems to represent a time window with suitable winds and with environmental conditions especially adequate for both vegetation and insects. The ITCZ strip is a region with virtually no wind and it may represent an important barrier for insects usually aided by high-elevation trade winds in their migratory movements. If we consider the ITCZ as the southern boundary for the Europe–Africa *V. cardui* migration, and since rain forests are unsuitable for this butterfly, then the December–February generation(s) may reach the elevated regions of the Gulf of Guinea Highlands (Cameroon and Nigeria) in the west, the savannah in Central African Republic and DR Congo, and elevated regions and savannah in Uganda and Kenya in the east.

The ocean at the Gulf of Guinea and limited habitat in western tropical Africa may force a proportion of the fall offspring to migrate north along the coast to the Maghreb, as suggested by Stefanescu *et al.* (2013). This route is unlikely to be used by most migrants, though, because the species is usually not as abundant during the winter in northern Africa as it is in the fall in the Sub-Saharan savannah.

Certainly, several winter refugia may exist from the Canary Islands to the Middle East, but densities in those localities are apparently low and fluctuate with weather variability (Stefanescu *et al.*, 2013). Whether the populations present in the Maghreb during late autumn and winter correspond to the laggard waves of migrants from Europe, actual recolonisations from the Sahel, or a mixture of both, deserve detailed investigation. Nevertheless, our data suggest an additional hypothesis: that an additional generation (or generations) are produced in the tropics during December–February, which later join the remnant winter populations in northern Africa in early spring. As a consequence, migrations across the Sahara would happen twice every year, southwards in early fall and northwards in early spring.

It is important to note that the annual number of generations of *V. cardui* is probably underestimated. It is often postulated that six or seven generations complete the cycle, but two factors call this into question. First, high temperatures speed up larval development considerably (c. 15 days at 20 °C for 10 h + 30 °C for 14 h daily, based on our field observations and laboratory tests), while low temperatures increase development time (up to 4 weeks at 12 °C for 14 h + 20 °C for 10 h daily, according to our laboratory tests). Second, the fairly long lifetime of adults (c. 4 weeks) entails a long period of fertility and females can probably lay eggs for about 3 weeks. As a consequence, the offspring of a single female could take part in multiple migratory waves and it is hard to precisely define the number of generations that actually complete the cycle, which could be 10 or more.

In summary, the temporal and abundance patterns described in this work, when viewed in the context of the global weather patterns in Africa and taking into account the evolutionary significance of population sizes, motivates us to modify the prevailing spatiotemporal model for the annual migration of *V. cardui* to include tropical Africa (Fig. 3). The model proposed broadly coincides with the Palaearctic–African bird migration system, where approximately 343 species and c. 3000 million birds annually migrate between tropical Africa and Europe (Moreau, 1972; Newton, 2008; Hahn, Bauer & Liechti, 2009). This situation suggests potential evolutionary convergence between birds and insects in adopting synchronic migratory routes to exploit the same temporary resources and climatic conditions in tropical Africa, or possibly for the insectivore birds to feed on the migrating insects. Other Palaearctic insects might also include tropical Africa in their migratory routes, but there is virtually no data on temporal presence/absence south of the Sahara for most of these taxa.

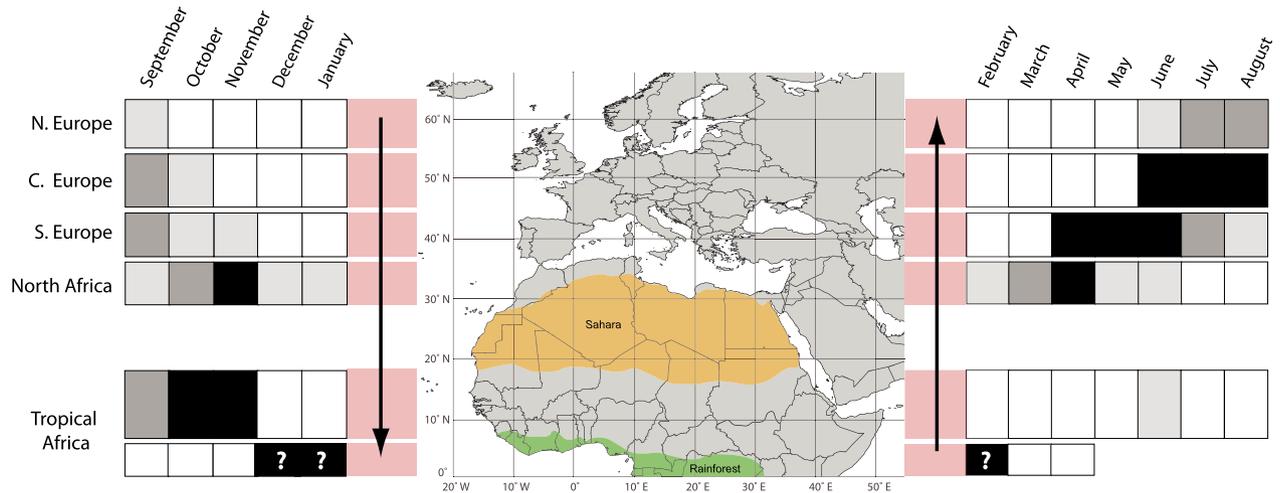


Figure 3. Spatiotemporal hypothesis for the Europe–North Africa migration of *Vanessa cardui*, which has been expanded to include tropical and east Africa. Rows represent approximate latitudes, columns denote months of the year, and the darkness of boxes indicates relative abundance (for both adults and immatures). Increasing abundance is indicated with increasingly darker colours. The situation during December–February in tropical Africa remains unclear, and question marks illustrate our hypothesis but denote uncertainty whether the species spends the winter in tropical African savannah and highlands close to the equator. Arrows indicate southwards or northwards migration. The Sahara Desert (orange) and the rainforest (green) are habitats that seem to be unsuitable for *V. cardui*.

The multi-generational migration strategy typical of the insects contrasts with the round-trip movements of individual birds. This shows how organisms' different physiological limitations may generate diversity and complexity in migratory traits and strategies, but still be overcome and lead to the convergence of broad spatiotemporal patterns determined by common environmental factors (Alerstam *et al.*, 2011). It is precisely this view that allows for unifying organismal movement research into an ecological and evolutionary framework (Alerstam *et al.*, 2003; Dingle, 2006; Roff & Fairbairn, 2007; Nathan *et al.*, 2008).

The migration between Europe and Africa is only a part of the worldwide migratory system of *V. cardui*. Our knowledge on the global patterns by this species is still very limited, but it is evident that migration is a key aspect in the biology of the species. Surprisingly, the migratory behaviour may be an evolutionarily labile trait in the genus *Vanessa*. When reconstructing a phylogenetic tree for this genus, Wahlberg *et al.* (2007) noticed an intriguing pattern in the degree of vagility in the group, where frequently the sister species of the most mobile and widespread species were those restricted geographically or even island endemics. This pattern suggests that shifts between migratory and sedentary behaviour may be involved in speciation in the group. Therefore, migratory behaviour may evolve rapidly once pre-adaptations –in the form of physiological capacity for active and powerful flight, long lifespan, etc.– are in place, as is the case for the genus

Vanessa. It seems that some populations of *V. cardui* where environmental conditions allow breeding year-round are sedentary, as for example the populations in Hawaii, although short-range altitudinal migration may take place (Shields, 1992). Such a sedentary behaviour has been also described for a number of monarch butterfly populations (Altizer & Davis, 2010). Our observations in Africa point out the presence of *V. cardui* both in natural (savannah, river margins and highlands) and deteriorated (fields, farms, gardens, road margins and construction sites) habitats. The efficient use of artificial environments by this species suggests that current and future anthropogenic effects, as well as climatic changes, may affect its migration patterns in unexpected ways. For example, novel routes could become possible, or populations could adapt to a sedentary behaviour in artificially irrigated fields in arid areas of Africa or in the increasingly warm Mediterranean region. Nevertheless, not only availability of resources and climatic conditions may be governing the evolution of migratory behaviour and its patterns. Species interactions should also be taken into account, including sexual interference with closely related species (which could explain the absence of the species in S. America and Australia), parasitoids (Stefanescu *et al.*, 2012) and pathogens (Altizer *et al.*, 2015).

The hypotheses suggested by our field observations could be tested using stable isotope and molecular phylogeographic analyses, methods that can assess

the geographical localisation where larval development took place and population connectivity, respectively. Samples were collected to test these hypotheses, and future studies will hopefully shed light on the migratory routes of this fascinating species.

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