

1 RUNNING TITLE: Migration of *Vanessa cardui* into tropical Africa

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3 **DISCOVERY OF MASS MIGRATION AND BREEDING OF THE PAINTED**

4 **LADY BUTTERFLY *VANESSA CARDUI* IN THE SUB-SAHARA: THE**

5 **EUROPE-AFRICA MIGRATION REVISITED**

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ABSTRACT

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

47

48 **KEY WORDS:** biogeography – climate – inter-continental movement – insect –
49 ITCZ – Lepidoptera – Nymphalidae – painted lady – savannah – tropical region.

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52 **INTRODUCTION**

53 Animal migration is an evolutionary response to heterogeneity in both space and time,
54 since it functions as a strategy for exploiting temporary resources associated with non-
55 permanent habitats (Southwood, 1962, 1977; Dingle, 2014). Migratory strategies have
56 evolved independently on a diverse array of unrelated species including birds,
57 mammals (terrestrial and aquatic), fish, reptiles, crustaceans and insects (Alerstam *et*
58 *al.*, 2003; Dingle & Drake, 2007). Among insects, species of dragonflies, locusts,
59 moths and butterflies are well-known migrators (Chapman *et al.*, 2015), usually
60 involving several generations in the completion of round-trip journeys. One of the
61 most famous cases is that of the North American populations of *Danaus plexippus* L.
62 (monarch butterfly), which has become a model for species for the study of insect
63 migration. This species performs a round-trip migration involving up to five
64 generations between Canada and warmer latitudes in Mexico, where one generation of
65 adult butterflies spends the winter in diapause.

66
67 *Vanessa cardui* L. (the painted lady) is another butterfly performing equally
68 impressive migrations. Although both species seem to share routes in north America,
69 as well as some physiological adaptations and methods of orientation (Nesbit *et al.*,
70 2009; Chapman *et al.*, 2015), they are not closely related phylogenetically and key
71 differences exist: 1) *D. plexippus* specializes on species of *Asclepias* L. as larval host
72 plant, whereas *V. cardui* is polyphagous and feeds on plants from a variety of
73 families. 2) *D. plexippus* diapauses during the winter, while *V. cardui* does not and
74 thereby apparently migrates in successive generations year-round. 3) The distribution
75 range of *V. cardui* is much wider than that of the monarch. It is a virtually
76 cosmopolitan species can be found everywhere except most of South America and

77 Australia. Thus, *Vanessa cardui* has one of the largest distributional ranges among
78 terrestrial animals that undertake large-scale migratory movements (Shields, 1992).
79 Occasional records exist for extremely cold localities, as for example, near the Arctic
80 polar circle in Svalbard, Norway (Lokki *et al.*, 1978) and close to the Antarctic on the
81 island of Marion, *ca.* 1800 km southeast of Africa's southern tip (Chown &
82 Language, 1994).
83
84 Little is known about the species' global migratory routes, but migration between
85 northwest Africa and Europe has received some attention (Williams 1930, 1970;
86 Pollard *et al.*, 1998; Stefanescu *et al.*, 2007, 2013). Most evidence is indirect, in the
87 form of presence/absence records, breeding localities, and approximate flight
88 directions. For example, the congruence of favourable trade winds and peaks of
89 arrival in southern Europe allowed inferring potential source areas of the migrants
90 from the Maghreb by backtracking air trajectories (Stefanescu *et al.*, 2007). These
91 data have been assembled into a spatiotemporal model explaining hypothetical
92 migratory routes in this part of the world (Stefanescu *et al.*, 2013). In summary, the
93 migratory cycle in this region is characterised by latitudinal population shifts as the
94 seasons progress: an annual northward advance in spring (March to June, note that
95 northern-hemisphere temperate-climate seasons are consistently used throughout the
96 text) followed by a southward return movement in autumn (September to November).
97 It is thought that at least six generations are involved in this annual movement
98 between the Maghreb and the Sahel (the region between the Sahara Desert and the
99 Afrotropical zone; Fig. 1) and northern Europe (Stefanescu *et al.*, 2013).
100

101 A central unsolved question is the destination of south-bound fall European migrants.
102 Given the paucity of data for *V. cardui* in the Maghreb between August and October,
103 Stefanescu *et al.* (2013) suggested that the first generation of southwards migrants
104 from Europe might produce one additional generation in the Mediterranean. In
105 addition, and based on scant observations in the vast Sahel in western Africa, together
106 with a southward *V. cardui* migration detected by an ornithological radar on the coast
107 of Mauritania in 2003 (Swiss Ornithological Inst., unpubl.), it has also been suggested
108 that some fall migrants from Europe may arrive to the northern edge of the Sahel in
109 Western Africa, likely following the Atlantic coastline (Stefanescu *et al.*,
110 2013). However, it is unclear if this also applies to central and eastern Africa, how far
111 south the European migrants can reach in a single flight, and whether they cross the
112 Sahara *en masse*. No further evidence potentially linking the annual migratory cycle
113 of *V. cardui* in Europe to the Sahel and further south is available. Importantly, no data
114 on reproduction have been reported for tropical Africa in autumn, except for one
115 observation in northern Nigeria (Boorman and Taylor, 1977).

116

117 A second question is the whereabouts of most *V. cardui* specimens between
118 December and February. Stefanescu *et al.* (2013) suggested that the species mostly
119 spends the winter months in the Maghreb, where several generations would occur
120 without undertaking long-distance migration, and restart the migratory behaviour in
121 spring back to Europe. Paradoxically, the species has been recorded at relatively low
122 densities from December to February in northwestern Africa (Stefanescu *et al.*, 2013),
123 as well as in northeastern Africa (Larsen, 1976). Precise sites for massive winter
124 breeding areas have not yet been identified, which is often explained by their
125 presumably variable densities and localities in relation to unpredictable rainfall on

126 these arid North African regions (Nesbit *et al.*, 2009). This hypothesis would entail
127 strong, annual bottlenecks followed by sudden population explosions, often so large
128 that it seems unlikely that the migrations arriving to southern Europe in spring could
129 originate only on the limited populations surviving the winter in the Maghreb.
130 Alternatively, the bulk of individuals may colonise the tropical African latitudes
131 before moving north about February-March. This scenario would help explaining
132 apparent fluctuations in density in the Maghreb-Europe part of the cycle, but no
133 comprehensive studies have surveyed the vast extent of the Sub-Saharan savannah for
134 *V. cardui*.

135

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

147

148 **MATERIALS AND METHODS**

149 **Rationale for exploration design**

150 Four field surveys were designed to be consecutive during two months in autumn
151 2014 with the ultimate goal of evaluating potential *V. cardui* arrivals and breeding at
152 sub-Saharan African latitudes. Four countries at strategic longitudes and with
153 significant ecological gradients were selected (Chad, Benin, Senegal and Ethiopia).
154 Collectively, they cover the immediate fringes south of the Sahel and the transition to
155 the tropical savannah (Fig. 1). A prior expedition was conducted in Ethiopia in early
156 June 2014 to investigate the relevance of high elevations as potential breeding sites
157 for *V. cardui* during the dry season.

158

159 The first autumn expedition was conducted in Chad between the 30th of September
160 and the 15th of October 2014. Within this timeframe, 13 days of effective fieldwork
161 and a total of 27 localities were surveyed encompassing an area of approximately
162 97,700 km², between 10.8° N and 13.4° N latitude, and 14.5° E and 19.9° E longitude
163 (Fig. 1). The route connected suspected breeding sites in central Chad, including the
164 Chari River near N'Djamena, the southern shores of Lake Chad, the Lake Fitri region,
165 the Guera Mountains, and Zakouma National Park. These topographically varied sites
166 spanned the pronounced transition between the Sahel and the tropical floodplains,
167 which is typical of countries in Central Africa.

168

169 Benin was visited next, between the 15th of October and the 1st of November of 2014,
170 allowing for 13 effective fieldwork days. Surveys involved 25 localities delimiting an
171 area of *ca.* 83,300 km² between 6.3° N and 12.3° N latitude, and 1.5° E and 3.3° E
172 longitude (Fig. 1). We selected Benin in order to survey the ecological gradient from
173 tropical forests in the south to grasslands in the north—a marked ecotone occurring
174 over only 600 km. The circuitous route was planned to visit strategic spots including

175 West Niger National Park and Pendjari National Park, both in the north and bordering
176 with Niger and Burkina Faso, respectively.

177

178 A third autumn trip allowed exploring 14 localities during 5 effective field days in
179 Senegal between the 1st and the 8th of November of 2014. Sampling sites were located
180 between 6.3° N and 12.3° N latitude, and 1.5° E and 3.3° E longitude, encompassing
181 an area of *ca.* 29,000 km² (Fig. 1). Senegal's strategic location as a coastal country
182 immediately south of the Sahara made it particularly appealing to study potential
183 westernmost migratory arrivals. A transect from central-west to south-east was
184 designated to span an ecotone ranging from agricultural lands and steppes to dense
185 savannah woodlands (the Guinea savannah).

186

187 The last of the autumn expeditions led us to Ethiopia between the 16th and 29th of
188 November. Accounting for 12 effective fieldwork days, 28 localities were surveyed
189 within a *ca.* 74,700 km² area between 6.5° N and 9.6° N latitude, and 37.5° E and
190 42.5° E longitude (Fig. 1). From the perspective of migratory studies, Ethiopia is
191 interesting for its physical features and geographic location. Its biomes reflect
192 remarkable altitudinal zonation, ranging from deserts to Afro-alpine ericaceous
193 habitats. Our priority was to explore the country's altitudinal gradient, with particular
194 interest in highland croplands as a potential habitat for *V. cardui* after the rainy season
195 (June-September). The prior early summer expedition in Ethiopia was conducted
196 between the 3rd and 23th of June of 2014. About 30 localities during 17 effective days
197 of work were inspected within a *ca.* 157,300 km² area between 6.8° N and 14.4° N
198 latitude, and 36.2° E and 40.0° E longitude (Fig. 1).

199

200 **Data collection in Tropical Africa**

201 The fieldwork design prioritised exploring as much land area and habitat diversity as
202 possible within each country, thus travelling either along E-W and N-S transects. In
203 general, entire days were devoted to prospecting sites along the way. Usually
204 travelling by car, random localities were inspected for *V. cardui*, and inspections
205 could last from one hour to an entire day when involving long hikes or altitudinal
206 surveys. Late afternoons were dedicated to sampling at hilltops where males typically
207 gather to establish territories (Brown and Alcock, 1990).

208

209 Behavioural data for *V. cardui* was recorded at each survey site, including migration,
210 hilltopping, mating, oviposition, and territorial fights. When migratory individuals
211 were detected (*i.e.*, those displaying fast directional flights, often in flocks), we
212 recorded flight direction and frequency of butterflies observed crossing an imaginary
213 10 m line (according to what a single person could supervise). Host plant preferences
214 and the developmental stage of immatures (eggs, larvae, or pupae) was noted,
215 including estimated larval instar. When breeding sites were encountered, abundances
216 were estimated by performing systematic counts of individuals per plant and numbers
217 of plants per area unit. Larvae of *V. cardui* produce silken shelters, which make the
218 larvae easier to locate in the field.

219

220 Adults, early stages, and host plants were collected in the field and all samples were
221 deposited at the Institut de Biologia Evolutiva (CSIC-UPF) in Barcelona, Spain, each
222 with a unique code used to link the specimen to the collection information stored in a
223 database. Butterflies were captured using aerial nets, rapidly killed by pinching the
224 thorax, and stored in glassine envelopes. These were exposed to the sun for few hours

225 to dehydrate them and ensure DNA preservation during fieldwork. Larvae were
226 immediately stored in 100% ethanol tubes after collection. Larval host plants were
227 collected and pressed. For proper long-term storage of field-dried adults, wings were
228 later cut at the base and stored in glassine envelopes, and bodies were transferred to
229 ethanol 100% and stored at -20 °C.

230 **RESULTS**

231 **A flock of migrants in the Sahelian Chad**

232 October is typically the end of the rainy season in Chad and, as a consequence,
233 floodplains south of the Sahel remain inundated and largely inaccessible. Fields,
234 grassland, and forests were green with recent plant growth (Fig. 2A) and plenty of
235 recently emerged insects were noticeable, including other potentially migrant
236 Odonata, Orthoptera, and Lepidoptera. *Vanessa cardui* was among these and many
237 individuals were observed throughout the entire expedition route. A total of 93
238 butterflies were collected, corresponding to 16 of 27 survey localities. Two main
239 behavioural patterns were observed: in the Sahelian region from Lake Chad to Oum
240 Hadjer (a west-east transect) migrating individuals flying south were usually
241 observed, but specimens from the Guera Mountains (Fig. 2B) to the floodplains in the
242 south (Fig. 2C) were sedentary.

243

244 In most localities within the Sahel, *V. cardui* specimens were observed consistently
245 flying fast towards the south and we frequently scraped dead specimens from the front
246 of our car. Butterflies were always active on hilltops during late afternoons (Fig. 2D).
247 On October 3rd, 2014, a particularly large migratory flock was observed near the
248 village of Karmé (12.55° N, 15.91° E). The locality was in a typical Sahelian plain,
249 with open space and few features or obstacles except for some scattered trees or

250 bushes. We remained in the site from 07:30 h until noon. During the first three hours,
251 an average of 6 butterflies per minute crossed virtual lines of 10 meters. After 11:00
252 h, and thus close to the highest temperature of the day, activity decreased significantly
253 to *ca.* 2 migrants per minute. Considering the uniform vegetation and topography of
254 the region and a consistent pattern for at least 200 adjacent meters that were
255 inspected, these observations lead us to estimate that several thousand butterflies
256 migrated south to this locality.

257

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

266

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

275

276 **A remarkable butterfly emergence in Benin**

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

282

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

290

291 A second site was encountered in the village of Karimama, near the Niger River and
292 the border with Niger (12.07° N, 3.18° E). A massive emergence of adults took place
293 in an abandoned field within town. The dominant plants in the field were grasses and
294 *Senna obtusifolia* (Fabaceae, Caesalpinioideae), with few trees (*Azadirachta indica* A.
295 Juss.). Oviposition was observed on a different, smaller, and unidentified Fabaceae
296 (see Fig. 2G). A relatively abundant Malvaceae (*Waltheria indica* L.) was apparently
297 avoided by *V. cardui* larvae, but was used as host plant by other Nymphalidae.
298 However, adults frequently visited the plant and imbibed sticky droplets on the leaves
299 and flower buds. Individuals were warming up early in the morning, staying either on

300 plants or on the ground. Although activity increased as the day advanced, the
301 butterflies persistently stayed flying or resting within the field limits. Considering an
302 approximate area of 7000 m² for that field and an average 3 recently emerged
303 butterflies per m², we estimated about 21,000 adult butterflies (see Fig. 2I). Moreover,
304 no fewer than 2 pupae per m² on average were counted, but this figure may be
305 underestimated because they were more difficult to detect than adults. We examined
306 the site over two consecutive days and saw no decrement in butterfly number or hints
307 of migratory movements. On the contrary, the total number of adults increased the
308 morning of the second day, when many more adults emerged, though some pupae still
309 remained intact. Predation by spiders and mantises was observed (Fig. 2J), agamid
310 lizards frequently attempted to attack adults, and domestic hen patrolled the field,
311 presumably searching for pupae. Only two larvae were found in the entire field.
312 Noteworthy, evidence of parasitism was not detected here or elsewhere in our trips.
313 *Vanessa cardui* was absent from neighbouring fields with similar characteristics.
314 Taken together, the evidences suggest that most of the observed individuals were the
315 offspring of a single, synchronised migratory swarm, temporally independent of the
316 population at the Alibori River 53 km away, which had only larvae and eggs at that
317 moment.

318

319 Multiple other colonies of *V. cardui* were observed near the Niger River. In the open
320 flood plains abutting the river (12.09° N, 3.18° E), adults were distributed all along
321 the shores, with up to 50 worn males displaying territorial behaviour in particular
322 spots. Another visited locality (12.03° N, 3.12° E) allowed us to estimate *ca.* 1000
323 butterflies, generally with high wing wear, occurring in an area of approximately
324 50,000 m² (after counting two butterflies, on average, in 10 x10 m plots). This habitat

325 was drier than other sites and was dominated by flowering *Guiera senegalensis* J. F.
326 Gmel. (Combrataceae) on which the butterflies were nectaring. Like in Karimama, the
327 same small legume plant was consistently selected by *V. cardui* females for
328 oviposition, while other nymphalid larvae were found on *Waltheria indica*.
329 Polymorphism in adult size and larval colour were often observed in the Niger River
330 region, and even an unmelanised adult form was found (Fig. 2K).

331

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

339

340 **Immature stages and worn adults during the dry season in Senegal**

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

347

348 Although the dry season was rapidly advancing and the rains for 2014 had been lower
349 than average, *V. cardui* was found along the route. A total of 33 adults were collected,

350 and many more seen, at 6 of the 14 surveyed localities, although mostly in the region
351 of Tambacounda. The Guinea savannah and the mountains of the Bassari Country in
352 the south-east supported denser populations than the other areas. On the contrary,
353 densities were the lowest in grasslands and coastal habitats, where the dry season was
354 notoriously more advanced. Generally, the captured specimens were notably worn,
355 suggesting that they were old and might have undergone a long migratory journey.
356 Males were found fighting for territories on hilltops, even when these were not
357 cleared of trees or dense vegetation. Oviposition was observed and early stage larvae
358 and eggs were found in Kédougou province on two different plants: a legume
359 (Fabaceae) (presumably the same found in Benin) (Fig. 2G) and a species of
360 Asteraceae (Fig. 2O)—both usually present in disturbed areas (Fig. 2P).

361

362 **The Ethiopian Highlands**

363 The abundance of *V. cardui* in the second half of November in Ethiopia was
364 extraordinary. High densities of adults and immatures were recorded, and 65 adult
365 specimens were collected in 13 localities, as were larvae in 7 of the 28 localities
366 inspected. Larvae were recorded in large concentrations, mainly on *Carduus* spp. and
367 *Cirsium* spp. thistles (Asteraceae). Late instars and empty silken shelters were the
368 most common, although early instars were also present, which suggests that several
369 waves of migrants could have arrived at the same localities. Many breeding sites were
370 found across the highlands, always above 2300 m and typically in ruderal areas (field
371 margins, derelict land, road banks, etc.) (Fig. 2Q). Urban areas had high densities of
372 immatures as well, often in streets, abandoned lots, or landfill sites in Addis Ababa.
373 Most of the adults that we collected appeared to have emerged recently and frequently
374 excreted meconium. This observation was consistent with the abundance of empty

375 silken shelters observed in the breeding sites. Thus, apparently most of the new
376 generations had already emerged, which agrees with annual rainfall peaks occurring
377 from July to September. Indeed, the visited localities below 2000 m, where the dry
378 season was advanced, did not have healthy host plants and neither adults nor larvae
379 were recorded.

380

381 Patterns of abundance in autumn contrasted with data from June 2014. Although
382 regions above 3000 m apparently had optimal conditions similar to those in the fall
383 (Fig. 2R), only few *V. cardui* were present. A total of only 24 specimens were
384 collected at only 5 of 30 sites visited in June, mostly in the Simien Mountains, except
385 for one in Bale and one at the central highlands. These adults were always found
386 above 2700 m (average 3060 m and up to 3490 m) and no traces of immatures were
387 found.

388

389 **DISCUSSION**

390 **Across the Sahara? Origin of the sub-Saharan populations**

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

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

425 Europe to Central Africa would involve as little as 4 days. Based on these estimates,
426 reproduction and completion of the life cycle after migration is arguably possible
427 given the lifespan of *V. cardui* adults (*ca.* 4 weeks), notably long compared to most
428 butterflies.

429

430 The possibility that the large populations documented in Tropical Africa are
431 disconnected from the European pool and are the product populations that survive the
432 dry season in situ and demographically explode after the onset of the rainy season is
433 unlikely because the inexistence of reports for substantial populations in this region
434 from May to August, as well as because it does not agree with our observation of a
435 southward migration in central Chad. Undeniably, the Ethiopian highlands would be
436 the best candidate for such hypothetical dry-season refuges, but our surveys during
437 June detected hardly any specimens of *V. cardui*. We thus consider likely that the
438 populations detected in autumn in tropical Africa have an origin in Europe.

439

440 **The role of tropical Africa**

441 In the African northern hemisphere, the advance of migratory insects polewards in
442 February-May and towards the equator in August-November is a general phenomenon
443 that is strongly related to seasonality and prevailing winds (Pedgley *et al.*, 1995).

444 Until now, it was unknown whether *V. cardui* was also involved in such a migratory
445 system beyond the Maghreb. Our data confirms that the occurrence of migration and
446 breeding for this species in tropical Africa is a widespread phenomenon covering the
447 east, centre and west, and extending south to at least 6° N latitude. Unlike typical
448 African species, the African migration system seems to be connected to the European
449 system in the case of *V. cardui*. We propose that its latitudinal migratory range

450 encompasses the temperate region (with seasonality determined by temperature) and
451 the tropical region (with seasonality determined by rainfall). A link between Europe
452 and tropical Africa was already envisaged by Owen decades ago (1971), although
453 direct evidence confirming this hypothesis is lacking.

454

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

468

469 Generally, migrant species follow the advance or the retreat of the ITCZ, and a
470 reversal of the migration course during the fall has been demonstrated for many
471 insects (Pedgley *et al.*, 1995). The regions where most *V. cardui* spend the winter
472 (December-February) are still an enigma and arguably the missing gap linking fall
473 southwards and spring northwards movements. The most accepted scenario at present
474 posits that winter breeding regions are scattered across north Africa, mostly in the

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

500 African Republic and DR Congo, and elevated regions and savannah in Uganda and
501 Kenya in the east.

502

503 The ocean at the Gulf of Guinea and limited habitat in western tropical Africa may
504 force a proportion of the fall offspring to migrate north along the coast to the
505 Maghreb, as suggested by Stefanescu *et al.* (2013). This route is unlikely to be used
506 by most migrants, though, because the species is usually not as abundant during the
507 winter in northern Africa as it is in the fall in the Sub-Saharan savannah. Certainly,
508 several winter refugia may exist from the Canary Islands to the Middle East, but
509 densities in those localities are apparently low and fluctuate with weather variability
510 (Stefanescu *et al.*, 2013). Whether the populations present in the Maghreb during late
511 autumn and winter correspond to the laggard waves of migrants from Europe, actual
512 re-colonisations from the Sahel, or a mixture of both, deserve detailed investigation.
513 Nevertheless, our data suggest an additional hypothesis: that an additional generation
514 (or generations) are produced in the tropics during December-February, which later
515 join the remnant winter populations in northern Africa in early spring. As a
516 consequence, migrations across the Sahara would happen twice every year,
517 southwards in early fall and northwards in early spring.

518

519 It is important to note that the annual number of generations of *V. cardui* is probably
520 underestimated. It is often postulated that 6 or 7 generations complete the cycle, but
521 two factors call this into question. First, high temperatures speed up larval
522 development considerably (*ca.* 15 days at 20 °C for 10 h + 30 °C for 14 h daily, based
523 on our field observations and laboratory tests), while low temperatures increase
524 development time (up to 4 weeks at 12 °C for 14h + 20 °C for 10h daily, according to

525 our laboratory tests). Second, the fairly long lifetime of adults (*ca.* 4 weeks) entails a
526 long period of fertility and females can probably lay eggs for about 3 weeks. As a
527 consequence, the offspring of a single female could take part in multiple migratory
528 waves and it is hard to precisely define the number of generations that actually
529 complete the cycle, which could be 10 or more.

530

531 In summary, the temporal and abundance patterns described in this work, when
532 viewed in the context of the global weather patterns in Africa and taking into account
533 the evolutionary significance of population sizes, motivates us to modify the
534 prevailing spatiotemporal model for the annual migration of *V. cardui* (Fig. 3) to
535 include tropical Africa. The model proposed broadly coincides with the Palaeartic-
536 African bird migration system, where approximately 343 species and *ca.* 3000 million
537 birds annually migrate between tropical Africa and Europe (Moreau, 1972; Newton,
538 2008; Hahn *et al.*, 2009). This suggests potential evolutionary convergence between
539 birds and insects in adopting synchronic migratory routes to exploit the same
540 temporary resources and climatic conditions in tropical Africa, or possibly for the
541 insectivore birds to feed on the migrating insects. Other Palaeartic insects might also
542 include tropical Africa in their migratory routes, but there is virtually no data on
543 temporal presence/absence south of the Sahara for most of these taxa. The multi-
544 generational migration strategy typical of the insects contrasts with the round-trip
545 movements of individual birds. This shows how organisms' different physiological
546 limitations may generate diversity and complexity in migratory traits and strategies,
547 but still be overcome and lead to the convergence of broad spatiotemporal patterns
548 determined by common environmental factors (Alerstam *et al.*, 2011). It is precisely
549 this view that allows for unifying organismal movement research into an ecological

550 and evolutionary framework (Alerstam *et al.*, 2003; Dingle, 2006; Roff & Fairbairn,
551 2007; Nathan *et al.*, 2008).

552

553 The migration between Europe and Africa is only a part of the worldwide migratory
554 system of *V. cardui*. Our knowledge on the global patterns by this species is still very
555 limited, but it is evident that migration is a key aspect in the biology of the species.
556 Surprisingly, the migratory behaviour may be an evolutionarily labile trait in the
557 genus *Vanessa*. When reconstructing a phylogenetic tree for this genus, Wahlberg *et*
558 *al.* (2007) noticed an intriguing pattern in the degree of vagility in the group, where
559 frequently the sister species of the most mobile and widespread species were those
560 restricted geographically or even island endemics. This pattern suggests that shifts
561 between migratory and sedentary behaviour may be involved in speciation in the
562 group. Therefore, migratory behaviour may evolve rapidly once pre-adaptations –in
563 the form of physiological capacity for active and powerful flight, long lifespan, etc.–
564 are in place, as is the case for the genus *Vanessa*. It seems that some populations of *V.*
565 *cardui* where environmental conditions allow breeding year-round are sedentary, as
566 for example the populations in Hawaii, although short-range altitudinal migration may
567 take place (Shields, 1992). Such a sedentary behaviour has been also described for a
568 number of monarch butterfly populations (Altizer & Davis, 2010). Our observations
569 in Africa point out the presence of *V. cardui* both in natural (savannah, river margins
570 and highlands) and deteriorated (fields, farms, gardens, road margins and construction
571 sites) habitats. The efficient use of artificial environments by this species suggests that
572 current and future anthropogenic effects, as well as climatic changes, may affect its
573 migration patterns in unexpected ways. For example, novel routes could become
574 possible, or populations could adapt to a sedentary behaviour in artificially irrigated

575 fields in arid areas of Africa or in the increasingly warm Mediterranean region.
576 Nevertheless, not only availability of resources and climatic conditions may be
577 governing the evolution of migratory behaviour and its patterns. Species interactions
578 should also be taken into account, including sexual interference with closely related
579 species (which could explain the absence of the species in S. America and Australia),
580 parasitoids (Stefanescu *et al.*, 2012) and pathogens (Altizer *et al.*, 2015).

581

582 The hypotheses suggested by our field observations could be tested using stable
583 isotope and molecular phylogeographic analyses, methods that can assess the
584 geographical localisation where larval development took place and population
585 connectivity, respectively. Samples were collected to test these hypotheses, and future
586 studies will hopefully shed light on the migratory routes of this fascinating species.

587

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603

604

605 **LITERATURE CITED**

606

607 **Alerstam T, Hedenström, Åkesson, S. 2003.** Long-distance migration: evolution and
608 determinants. *Oikos* **103**: 247-260.

609

610 **Alerstam T, Chapman JW, Bäckman J, Smith AD, Karlsson H, Nilsson C,**
611 **Reynolds DR, Klaassen RHG, Hill JK. 2011.** Convergent patterns of long-distance
612 nocturnal migration in noctuid moths and passerine birds. *Proceedings of the Royal*
613 *Society B: Biological Sciences* **278**: 3074-3080.

614

615 **Altizer S, Davis AK. 2010.** Populations of monarch butterflies with different
616 migratory behaviors show divergence in wing morphology. *Evolution* **64**: 1018-1028.

617

618 **Altizer S, Hobson KA, Davis AK, De Roode JC, Wassenaar LI. 2015.** Do healthy
619 monarchs migrate farther? Tracking natal origins of parasitized vs. uninfected
620 monarch butterflies overwintering in Mexico. *PLoS ONE* **10**: e0141371.

621

622 **Boorman J, Taylor WP. 1977.** The breeding of the painted lady butterfly, *Vanessa*
623 *cardui*, in Nigeria. *Nigerian Field* **42**: 84-87.

624

625 **Brower LP. 1995.** Understanding and misunderstanding the migration of the monarch
626 butterfly (Nymphalidae) in North America: 1857-1995. *Journal of the Lepidopterists'*
627 *Society* **49**: 304-385.

628

629 **Brown WD, Alcock J. 1990.** Hilltopping by the red admiral butterfly: mate searching
630 alongside congeners. *Journal of Research on the Lepidoptera* **29**: 1-10.

631

632 **Burt PJA, Pedgley DE. 1997.** Nocturnal insect migration: effects of local winds.
633 *Advances in Ecological Research* **27**: 61-92.

634

635 **Cardé RT. 2008a.** Insect migration: Do migrant moths know where they are heading?
636 *Current Biology* **18**: 472-474.

637

638 **Cardé RT. 2008b.** Animal migration: Seasonal reversals of migrant moths. *Current*
639 *Biology* **18**: 1007-1009.

640

641 **Chapman JW, Drake VA, Reynolds DR. 2011.** Recent insights from radar studies
642 of insect flight. *Annual Review of Entomology* **56**: 337-356.

643

644 **Chapman JW, Reynolds DR, Wilson K. 2015.** Long-range seasonal migration in
645 insects: Mechanisms, evolutionary drivers and ecological consequences. *Ecology*
646 *Letters* **18**: 287-302.

647

648 **Chown SL, Language K. 1994.** Recently established Diptera and Lepidoptera on
649 sub-Antartic Marion Island. *African Entomology* **2**: 57-60.

650

651 **Dingle H. 2006.** Animal migration: Is there a common migratory syndrome? *Journal*
652 *of Ornithology* **147**: 212-220.

653

654 **Dingle H. 2014.** *Migration: The Biology of Life on the Move*. 2nd edn. Oxford:
655 Oxford University Press.

656

657 **Dingle H, Drake VA. 2007.** What is migration? *BioScience* **57**: 113-121.

658

659 **Hahn S, Bauer S, Liechti F. 2009.** The natural link between Europe and Africa—2.1
660 billion birds on migration. *Oikos* **118**: 624-626.

661

662 **Larsen TB. 1976.** The importance of migration to the butterfly faunas of Lebanon,
663 East Jordan, and Egypt (Lepidoptera, Rhopalocera). *Notulae Entomologicae* **56**: 73-
664 83.

665

666 **Lokki J, Malmstrom KK, Suomalainen E. 1978.** Migration of *Vanessa cardui* new
667 record and *Plutella xylostella* (Lepidoptera) to Spitsbergen in the summer 1978.
668 *Notulae Entomologicae* **58**: 121-123.

669

670 **McNeil JN. 1987.** The true armyworm, *Pseudaletia unipuncta*: A victim of the Pied
671 Piper or a seasonal migrant? *Insect Science and its Application* **8**: 591-597.

672

673 **Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse, PE.**
674 **2008.** A movement ecology paradigm for unifying organismal movement research.

675 *Proceedings of the National Academy of Sciences of the United States of America*
676 **105**: 19052-19059.

677

678 **Nesbit RL, Hill JK, Woiwod IP, Sivell D, Bensusan KJ, Chapman JW. 2009.**
679 Seasonally-adaptive migratory headings mediated by a sun compass in the painted
680 lady butterfly (*Vanessa cardui*). *Animal Behaviour* **78**: 1119-1125.

681

682 **Newton I. 2008.** *The migration ecology of birds*. London: Academic Press.

683

684 **Owen DF. 1971.** *Tropical Butterflies*. Oxford: Clarendon Press.

685

686 **Pedgley DE, Reynolds DR, Tatchell GM. 1995.** Long-range insect migration in
687 relation to climate and weather: Africa and Europe. In: Drake, V.A. & A.G.
688 Gatehouse, eds. *Insect migration: tracking resources through space and time*.
689 Cambridge: Cambridge University Press, 3-29.

690

691 **Pollard E, van Swaay CAM, Stefanescu C, Lundsten KE, Maes D. 1998.**
692 Migration of the painted lady butterfly *Cynthia cardui* in Europe: evidence from
693 monitoring. *Diversity and Distributions* **4**: 243-253.

694

695 **Rabb RL, Stinner RE. 1978.** The role of insect dispersal and migration in population
696 processes. *NASA Conference Publication* **2070**: 3-16.

697

698 **Roff DA, Fairbairn DJ. 2007.** The evolution and genetics of migration in insects.
699 *BioScience* **57**: 155-64.

700

701 **Ryrholm N, Källander C. 1986.** Nocturnal migration in nymphalid butterflies.

702 *Entomologisk Tidskrift* **107**: 107-109.

703

704 **Shields O. 1992.** World distribution of the *Vanessa cardui* group (Nymphalidae).

705 *Journal of the Lepidopterists' Society* **46**: 235-238.

706

707 **Southwood TRE. 1962.** Migration of terrestrial arthropods in relation to habitat.

708 *Biological Reviews* **37**: 171-214.

709

710 **Southwood TRE. 1977.** Habitat, the templet for ecological strategies? *Journal of*

711 *Animal Ecology* **46**: 337-365.

712

713 **Stefanescu C, Alarcón M, Àvila A. 2007.** Migration of the painted lady butterfly,

714 *Vanessa cardui*, to north-eastern Spain is aided by African wind currents. *Journal of*

715 *Animal Ecology* **76**: 888-898.

716

717 **Stefanescu C, Alarcón M, Izquierdo R, Páramo F, Àvila A. 2011.** Moroccan

718 source areas of the painted lady butterfly *Vanessa cardui* (Nymphalidae:

719 Nymphalinae) migrating into Europe in spring. *Journal of the Lepidopterists' Society*

720 **65**: 15-26.

721

722 **Stefanescu C, Askew RR, Corbera J, Shaw MR. 2012.** Parasitism and migration in

723 southern Palaearctic populations of the painted lady butterfly, *Vanessa cardui*

724 (Lepidoptera: Nymphalidae). *European Journal of Entomology* **109**: 85-94.

725

726 **Stefanescu C, Páramo F, Åkesson S, Alarcón M, Ávila A, Brereton T, Carnicer J,**

727 **Cassar LF, Fox R, Heliölä J, Hill JK, Hirneisen N, Kjellén N, Kühn E, Kuussaari**

728 **M, Leskinen M, Liechti F, Musche M, Regan EC, Reynolds DR, Roy DB,**

729 **Ryrholm N, Schmaljohann H, Settele J, Thomas CD, van Swaay C, Chapman**

730 **JW. 2013.** Multi-generational long-distance migration of insects: studying the painted

731 lady butterfly in the Western Palaearctic. *Ecography* **36**: 474-486.

732

733 **Stinner RE, Barfield CS, Stimac JL, Dohse L. 1983.** Dispersal and movement of

734 insect pests. *Annual Review of Entomology* **28**: 319-335.

735

736 **Williams CB. 1930.** *The Migration of Butterflies*. Edinburgh: Oliver & Boyd.

737

738 **Williams CB. 1970.** The migrations of the painted lady butterfly, *Vanessa cardui*

739 (Nymphalidae), with special reference to North America. *Journal of the*

740 *Lepidopterists' Society* **24**: 157-175.

741

742

743 **FIGURES**

744

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

748

749 **Figure 2.** Primary habitats, host plants, and noteworthy sights for *Vanessa cardui* in
750 tropical Africa in autumn (October-November) 2014. A) A fertile Sahelian plain near
751 Lake Chad. B) Woodlands at the Guera Mountains, Chad. C) Floodplains in Zakouma
752 National Park, southern Chad. D) A hilltop in a typical Sahelian landscape in Chad.
753 E) *V. cardui* breeding sites were found next to the Alibori river in West Niger
754 National Park, northern Benin. F) Fifth instar larva, northern Benin. G) Larval host
755 plant (likely within the Lamiidae) in West Niger National Park, Benin. H) A
756 Faboideae (Fabaceae) larval host plant widely used by *V. cardui* in Benin and
757 Senegal. I) At least ten *V. cardui* butterflies alight on a *Senna obtusifolia* (Fabaceae,
758 Caesalpinioideae) plant after a massive emergence in northern Benin. J) A fresh *V.*
759 *cardui* specimen warming at dawn next to an empty pupal case in Karimama,
760 Northern Benin. K) Mantises were predated on *V. cardui* in Karimama, northern
761 Benin. L) An unusual unmelanised adult near the river Niger, northern Benin. M)
762 Oviposition was observed on tiny plants growing on desiccating muddy patches in
763 Pendjari National Park, Benin. N) A *V. cardui* butterfly possibly originating in Europe
764 alights on a lion footprint in Pendjari National Park, Benin. O) Herbs (likely
765 Asteridae) used by *V. cardui* larvae in the Bassari Country, Senegal. P)
766 Anthropogenically-modified habitats in Senegal were used as breeding sites. Q)
767 Agricultural lands in the Ethiopian highlands in autumn offer ample resources for *V.*

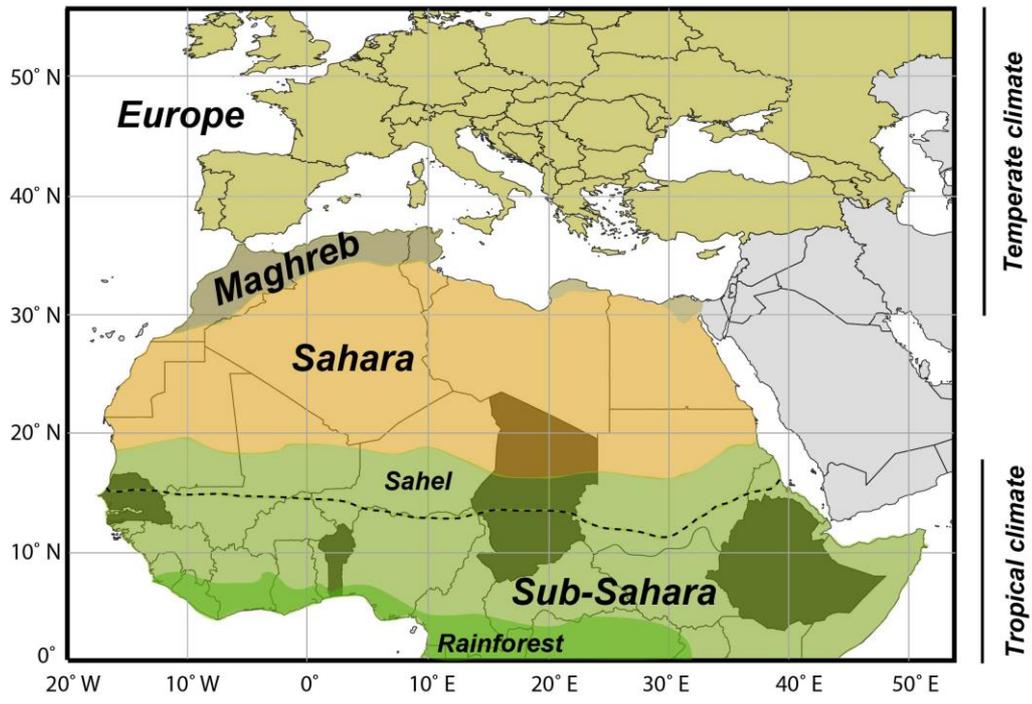
768 *cardui* reproduction. R) Regions above 3000 m in Ethiopia apparently presented
769 optimal conditions for *V. cardui* in summer, but the species was never abundant here.

770

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

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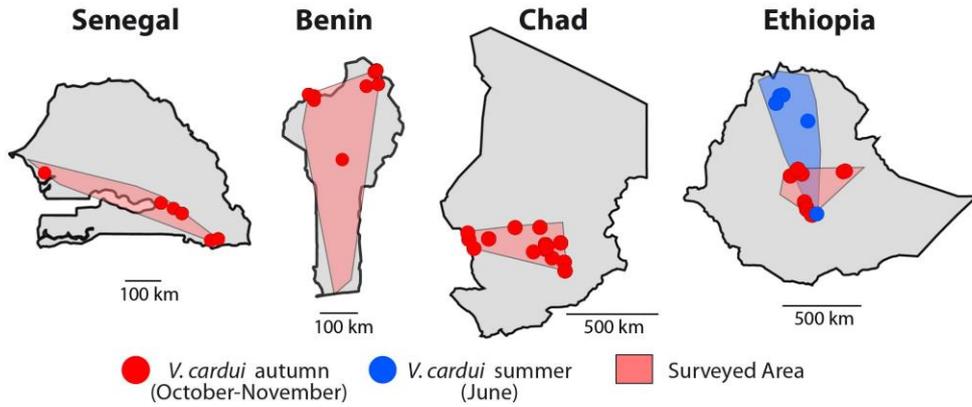
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Western Africa

Central Africa

Eastern Africa

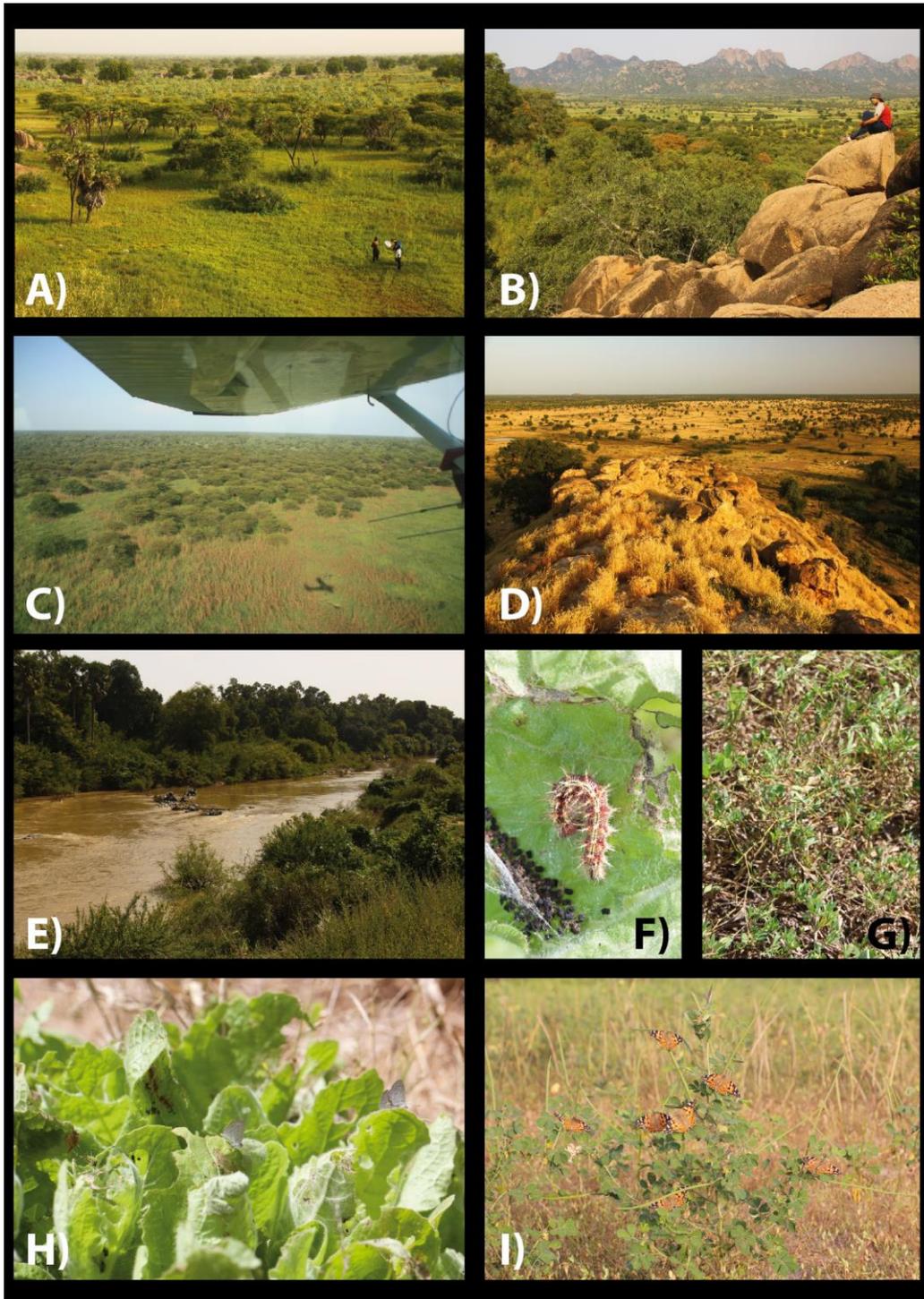


● *V. cardui* autumn (October-November) ● *V. cardui* summer (June) ■ Surveyed Area

783

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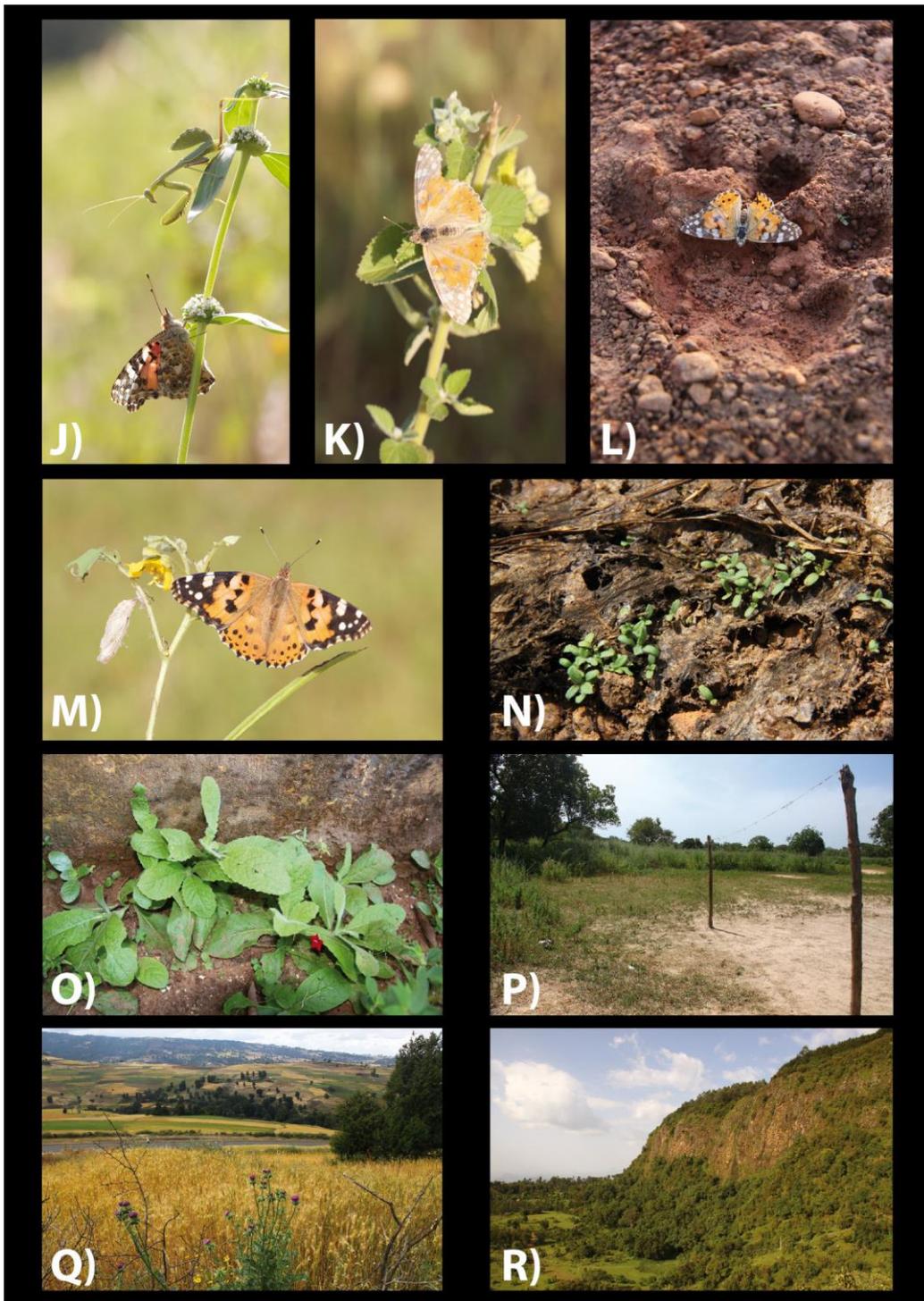
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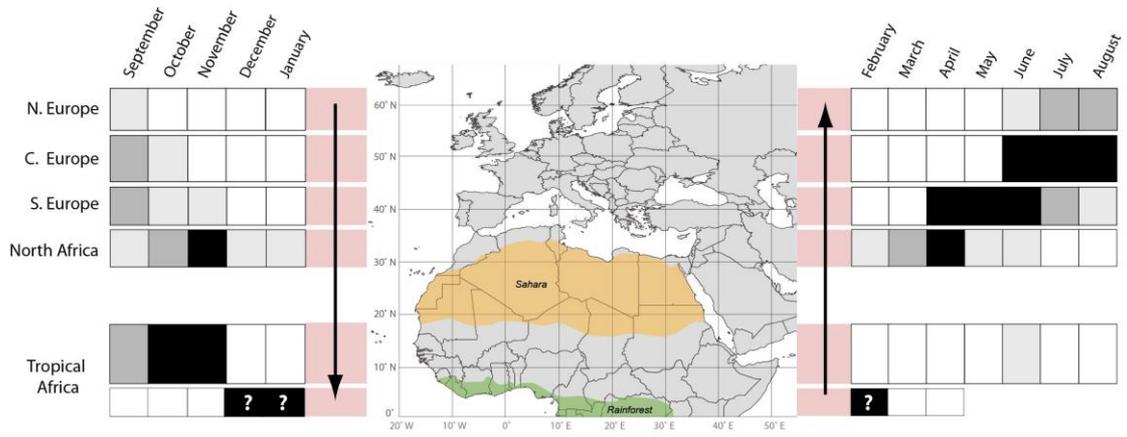


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