Dispersal of the monarch butterfly (*Danaus plexippus*) over southern Spain from its breeding grounds

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Abstract
*Dispersal of the monarch butterfly (*Danaus plexippus*) over southern Spain from its breeding grounds.* From 2000–2016, monarch butterflies were detected at 127 locations away from their usual coastal breeding areas in the south of the Iberian peninsula. These findings were recorded in the summer–autumn period, coinciding with the highest abundance of individuals and the highest proportion of patches occupied in their reproduction areas near the Strait of Gibraltar. These dispersing individuals have no chance of successfully establishing new colonies at these sites because the food plants for egg laying do not grow in the localities where they were detected. However, these dispersive movements could be the source of their successful colonisation on food plants growing in other areas of the Iberian Peninsula and in other Mediterranean countries.

Key words: *Danaus plexippus*, Monarchs, Dispersal, Southern Spain

Resumen
*Dispersión de la mariposa monarca (*Danaus plexippus*) en el sur de España desde las zonas de apareamiento.* Durante el período comprendido entre los años 2000 y 2016, se detectaron mariposas monarca en 127 lugares fuera de las zonas costeras donde se reproducen habitualmente en el sur de la península ibérica. Estos datos se obtuvieron en verano e invierno, coincidiendo con la máxima abundancia de individuos y la mayor proporción de sitios ocupados en sus zonas de reproducción cercanas al estrecho de Gibraltar. Los individuos que se dispersan no tienen ninguna posibilidad de establecer nuevas colonias en estos sitios porque las plantas en las que ponen los huevos no crecen en las localidades en las que fueron detectados. Sin embargo, estos movimientos de dispersión podrían ser la causa de la colonización de plantas alimentarias que crecen en otras zonas de la península ibérica y en otros países del Mediterráneo.

Palabras clave: *Danaus plexippus*, Monarcas, Dispersión, Sur de España

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Introduction

In butterflies, the fundamental functions of imagos are reproduction and dispersion (Gilbert and Singer, 1975). Dispersion refers to the spatial separation between individuals of a population (Begon et al., 1999) and is a basic process in ecology, evolution and conservation biology (Clobert et al., 2001; Bullock et al., 2002).

Numerous empirical studies have studied the differences in the processes of dispersion between species and between sexes, and in different types of landscapes (Fernández et al., 2016). These processes are especially relevant to the understanding of population dynamics in fragmented landscapes (Hanski and Gilpin, 1997; Hanski and Gaggiotti, 2004). An attempt has been made to determine whether dispersion is a consequence of the routine movements carried out by the species in question (for example, in the search for food) or whether, on the contrary, it is the result of specific movements made for that purpose (Van Dyck and Baguette, 2005).

Dispersion in fragmented landscapes can be considered a three–step process that involves the decision to migrate (abandoning a favourable habitat), the crossing through an unfavourable matrix, and migration to another favourable habitat fragment (Clobert et al., 2004). In dispersion studies, the spatial arrangement of these fragments combined with the ability to move between them is critical to understanding the success of the process. In general, in long–distance dispersal through unfavourable habitats (matrices), the trajectories of the butterflies tend to be faster and rectilinear, leading to a decrease in the mortality while crossing the matrices. In contrast, more–sinuous trajectories are characteristic of an exploratory search for resources (nectar, plants for laying eggs, etc.) within the favourable habitat fragment (Fernández et al., 2016). However, the matrix should not be considered an empty habitat that is hostile to the dispersal of butterflies, since the possibility of exploiting it depends on the biology of each species (Zalucki et al., 2015b). As discussed by Dennis (2004), the matrix can provide many sources of nectar and other resources for butterflies. However, in multivoltine species living in environments with strong seasonal fluctuations, the availability of these resources and the quality of this habitat can vary significantly throughout the year (Fernández Haeger et al., 2011b).

The monarch butterfly (*Danaus plexippus*) is probably one of the best–studied insects in the world (Oberhauser et al., 2015, and references therein). It is of American origin that was first described in the mid–nineteenth century in New Zealand (1840), and a little later Australia (1870), where it seems to have arrived by migrating from island to island across the Pacific (Zalucki and Clarke, 2004).

Around this time it was also recorded in various Atlantic archipelagos —Madeira (1860), the Azores (1864), the British Isles (1876) and the Canary Islands (1880)— and in the Iberian Peninsula (Portugal and Gibraltar), in 1886. In 1988 it was first recorded in North Africa (Fernández Haeger et al., 2015). Although the first monarch butterfly in the Campo de Gibraltar (Spain) was recorded in 1886, it did not appear again in the scientific literature (Gonella, 2001) until 1963. In the mid–1980s monarchs again attracted the attention of entomologists, although these occasional sightings in the south of Spain have been interpreted as migrating or wandering individuals from Atlantic archipelagos. The existence of stable populations in the vicinity of the Strait of Gibraltar has been documented at least since 1994; in this location, they reproduce on species of the Asclepiadaceae (Fernández Haeger and Jordano Barbudo, 2009 and references therein).

In this vicinity of the Strait of Gibraltar, the monarchs are centred around their fundamental food plants, *Asclepias curassavica*, *Gomphocarpus fruticosus* and *G. physocarpus.* These plants have a fragmented distribution as they form stands in frost–free coastal areas in the southern Iberian Peninsula and North Africa (Fernández Haeger et al., 2015) (fig. 1). The presence of stands of their food plants is favoured by moist soils (edges of streams, ponds, springs, wet meadows, etc.) throughout the year, and by intense livestock pressure. The butterflies appear in flight throughout the year in a succession of generations. They do not have a migratory behaviour equivalent to that of the monarchs of North America, but movements of marked individuals between vegetation fragments separated by more than 2 km have been recorded (Fernández Haeger et al., 2011b). In this way the butterflies persist in this area, maintaining the dynamics of a patchy population structured on the basis of the fragmented populations of its food plants. Asclepiadaceae flower from March to December and produce large amounts of nectar (Wyatt and Broyles, 1994). Since they are in full bloom during the summer, when most herbaceous plant species of the Mediterranean have dried out, they are doubly attractive to butterflies at this time of year because they provide both nectar for the adults and abundant food for the caterpillars (Fernández Haeger et al., 2011a; 2011b).

In recent years, and especially in 2016, numerous imagos have been recorded in flight or feeding on nectar far from the areas where the food plants of their caterpillars grow. These individuals can be considered vagrants and could contribute to the expansion of the range of the species in the Iberian Peninsula. The objective of this work was to produce a map of all the sightings of monarch butterflies recorded outside their known breeding areas from 2000 to 2016 in southern Spain, and also to interpret these dispersive movements in relation to the possibilities of success for their expansion in the south of the Iberian Peninsula.

Material and methods

The observations of monarch butterflies considered here have various origins. First, 10 citations are from bibliographic references published by different authors over the study period (Gonella, 2001; Gil–T., 2006; Huertas–Dionisio, 2007; Laffitte et al., 2010; Moreno–Benítez, 2015). Three further citations come from the

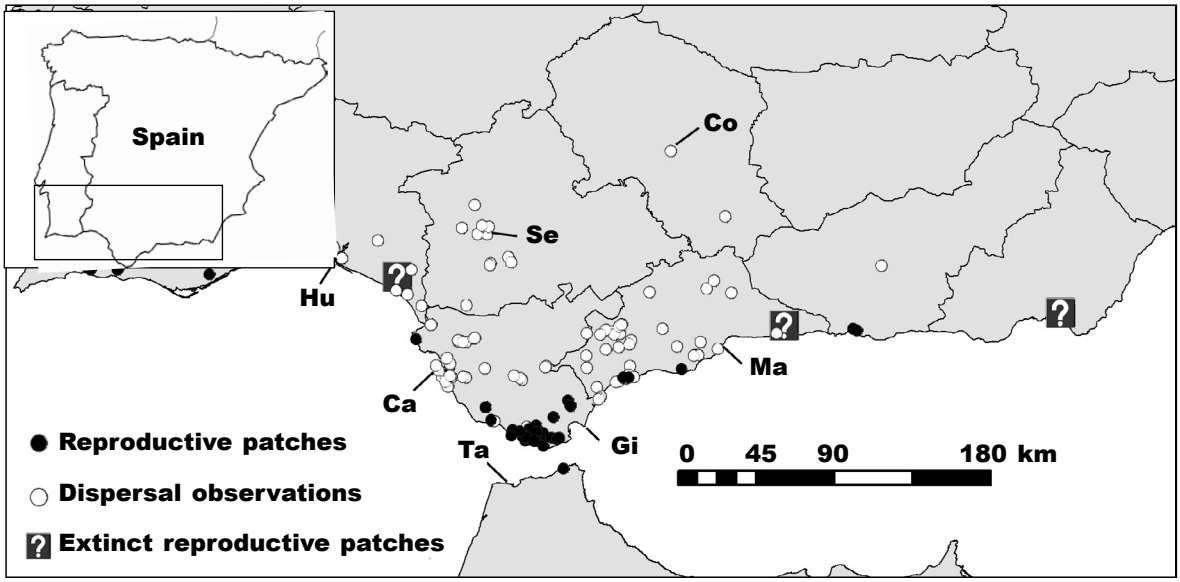

Fig. 1. Spatial distribution in the south of the Iberian Peninsula and in the north of Africa of the localities where the Monarch butterfly reproduces and the location of dispersal individuals during 2000–2016: Hu, Huelva; Se, Sevilla; Co, Cordoba; Ca, Cadiz; Gi, Gibraltar; Ta, Tangier; Ma, Malaga.

Fig. 1. Distribución espacial en el sur de la península ibérica y en el norte de África de las localidades en las que la mariposa monarca se reproduce y localización de los individuos que se dispersaron durante 2000–2016: Hu, Huelva; Se, Sevilla; Co, Córdoba; Ca, Cádiz; Gi, Gibraltar; Ta, Tánger; Ma. Málaga.

registers in the collection of the Andalusian Society of Entomology of the Museum of Natural Sciences of Guadalcázar (Cordoba), and 31 sightings were provided by individuals on the Facebook social network groups *Mariposas diurnas de Andalucía* and *Sociedad Andaluza de Entomología*. Another 53 sightings were provided by naturalists in the area and 30 more were provided by ourselves. Some of these latter observations were obtained during the periodic censuses that are carried out within the project BMS Spain, in the province of Cadiz. Since identification of the monarch butterfly is unmistakable within the butterfly fauna of southern Spain, all observer records were treated as valid.

Results

Figure 1 shows the geographical locations of the areas where reproduction of the species has been verified, along with the sightings corresponding to vagrant individuals collected during the study period (2000–2016, n = 127). The areas of reproduction include the Portuguese Algarve, a small coastal area between the towns of Chipiona and Rota (recently discovered), the coastal zone near the Strait of Gibraltar, some enclaves of the Costa del Sol, and North Africa. Other enclaves where the butterfly has reproduced in the past (Doñana, Torrox or Almeria) are also represented on the map, although these have now disappeared due to human intervention (Tarrier, 1994; Fernández Haeger et al., 2009).

As shown in the map, most of the observations of dispersive butterflies are near the coast, although some inland localities are especially notable, such as Güejar–Sierra (Granada), Ronda (Málaga), Cabra (Córdoba), and Córdoba. The observation at highest altitude was at Güejar Sierra (964 m a.s.l.) and that furthest from the coast was in the city of Córdoba. It is of note that the food plants (*A. curassavica*, *G. fruticosus* and *G. physocarpus*) of the caterpillars were not noted in any of these localities, so all these individuals can be considered vagrants in search of new areas where they can successfully establish themselves.

Some sightings refer to consecutive days in the same locality. Although they have been considered as different individuals, we do not rule out the possibility that they are the same individuals attracted to the nectar of plants in bloom.

In most cases it was not possible to determine the sex of the individuals since they were observed in flight at a certain distance. However, sex was determined in 17 cases, corresponding to 12 males and five females.

The large majority of sightings were obtained in the summer and early autumn (July–October, fig. 2). It seems, therefore, that these butterflies tend to fly outside their breeding grounds in the second half of the year (summer–autumn). From January to May, only one specimen was observed, this being in March.

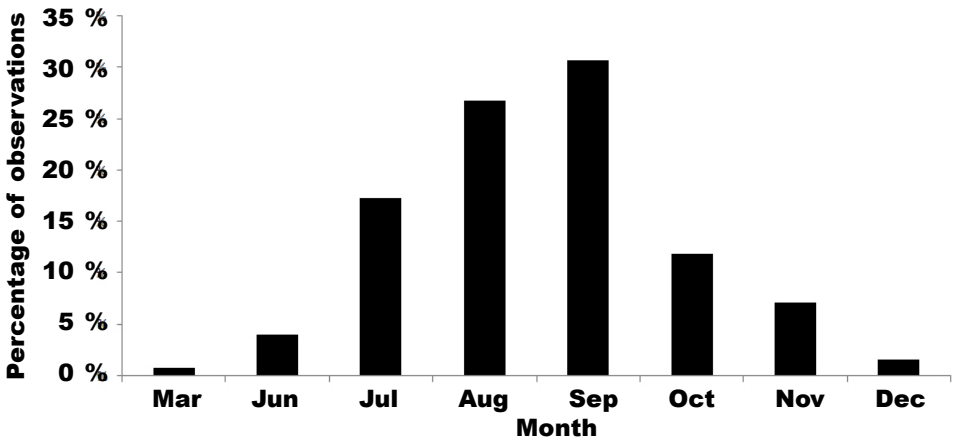

Fig. 2. Monthly distribution of the number of sightings of individuals recorded outside the breeding habitat, from 2000 to 2016 (*n* = 127).

*Fig. 2. Distribución mensual del número de avistamientos de individuos registrados fuera del hábitat de reproducción, entre los años 2000 y 2016 (*n = *127).*

Discussion

In the south of the Iberian Peninsula, the monarch butterfly behaves as a non–migratory, multivoltine species, showing no winter diapause and forming local populations associated with stands of *A. curassavica*, *G. fruticosus* and *G. physocarpus* (Fernández Haeger et al., 2011b). Although, we have occasionally detected some eggs on *Cynanchum acutum* (Asclepiadaceae), this plant species has a very restricted distribution in our geographical area and lacks the biomass to maintain a local population of monarchs. In addition, it does not maintain aerial biomass during the winter (John et al., 2015).

Over the year, both the occupancy of patches and the abundance of individuals vary markedly, with minimum values occurring in winter and maximum values in late summer and early autumn (Fernández Haeger et al., 2015). Hence, during the winter, the butterflies are concentrated in a few highly favourable patches. Over the course of the year they are able to colonise other patches, and both the occupation of patches and the maximal abundance of individuals occur in late summer and early autumn. In other species of butterflies, the abundance of local populations is related to the size of the fragment, abundance of food plants for larvae, and abundance of nectar sources (Krauss et al., 2004; Lenda and Skórka, 2010). These first two factors are also key to the establishment of new populations (Kuussaari et al., 2015). In the case of *D. plexippus* in southern Spain, the largest local populations are generally associated with stands where *A. curassavica* is abundant, as opposed to those with only *G. fruticosus* (Fernández Haeger et al., 2015).

In the most favourable fragments, the local populations reach high densities, so that after the development of successive generations of caterpillars, the food plants are practically defoliated by late summer/early autumn (fig. 3). As a result, the quality of the stand drops sharply, forcing the imagos to abandon it in search of more favourable stands where they can find nectar and lay their eggs.

The sexual behaviour of the monarchs means that, in many cases, the females try to avoid fragments that have a high density of males so as to avoid harassment and to devote more time to egg–laying (Frey et al., 1998), as occurs in other species (Shapiro, 1970). We observed that the sex ratio (males/females) in a set of 478 individuals captured randomly throughout the year (2016) in two fragments in the Tarifa area was 2.04. This ratio rose to 3.6 in October 2016 in one of the sampled fragments (unpublished data), suggesting that females try to find new places for egg–laying, especially during autumn.

Therefore, during late summer and autumn in the south of the Peninsula, recurrent conditions that promote the dispersal of the *Danaus* are repeated. Accordingly, we recorded diverse observations of dispersive individuals in different localities and at varying distances with respect to the coastal areas of reproduction. The observations of dispersive individuals occurred mainly between June and December, coinciding to a great extent with the time when population numbers in breeding areas are higher (Fernández Haeger et al., 2015).

Leaving the stand during the summer and crossing the matrix of unfavourable habitats is complicated for butterflies because most herbaceous plants have dried up and nectar sources are scarce (personal observation; Zalucki and Lammers, 2010). Although no specific observations for monarchs are available, it is possible that butterflies move along river courses to reach other favourable fragments, as described in Viejo et al. (1992) for other species of butterflies.

Fig. 3. Caterpillars in the last stage of development devouring apical parts of *A. curassavica* and *G. fruticosus* (A and B). Both photos were taken in October 2011. As a result of such herbivore pressure, stands of hundreds of plants can be completely defoliated (C). The final outcome is a sudden loss of stand quality, as seen in the third image, and the dispersal of the butterflies.

Fig. 3. Orugas en el último estadio de desarrollo alimentándose de las partes apicales de A. curassavica *y* G. fruticosus *(A y B). Ambas fotografías fueron tomadas en octubre de 2011. Como consecuencia de esta presión herbívora, los tallos de cientos de plantas pueden defoliarse por completo (C). El resultado final es la pérdida repentina de calidad del tallo, tal como se aprecia en la tercera imagen, y la dispersión de las mariposas.*

Such movement along the riparian forests offers greater possibilities to find nectar source plants, a more favourable microclimate and occasionally refuge from the wind.

The present study also reveals the appearance of the species during 2016 in southern areas of the Iberian Peninsula where the species was thought to be absent or rare. This expansion has been especially striking in two specific areas: the Bahía de Cádiz and inland areas of the province of Málaga. The monitoring of the butterflies carried out by one of the authors in different plots of the same area shows that: (1) from 2011 to 2015, only two specimens were detected in an intensely–sampled plot in Jerez; (2) the species was not previously detected in the BMS censuses carried out intensively in six plots of the same area throughout the year; and (3), in 2016, the species was detected for the first time (a total of six individuals) in three BMS transects, in San Fernando, El Marquesado and Jerez. The species was recorded in 2016 in various mountainous areas in the interior of Málaga and even in the province of Córdoba. It appears, therefore, that the dispersal of the monarchs from their coastal breeding areas was especially important in 2016, coinciding with an exceptional abundance in these areas (unpublished data).

The dispersive movements reported in this work suggest that the monarch butterflies could extend their permanent distribution area to other zones in the south of the Iberian Peninsula. At a global scale, the potential–distribution model developed by Zalucki et al. (2015a) predicts the existence of favourable coastal zones for the monarch in North Africa, southern Europe, and the Middle East —which it could certainly reach due to its great capacity for flight. This capacity has enabled it to cross the Pacific and the Atlantic successfully. However, the colonisation of these zones depends critically on the presence of *A. curassavica* and/or *G. fruticosus.*

When butterflies crossing the Atlantic reach the coastal areas of the south of the Iberian Peninsula they find stands of their food plants (Fernández Haeger et al., 2009, 2015). This is not the case for those arriving at the European coasts at more northern latitudes (such as northern parts of the Iberian Peninsula, France, Ireland, United Kingdom) where the food plants do not exist and monarchs are unable to reproduce (Asher et al., 2001).

In the south of the Iberian Peninsula, *A. curassavica*, *G. fruticosus* and *G. physocarpus* are naturalised species. The first of these was introduced from Central America by the Spanish and the other two were brought from southern Africa by the Portuguese (Fernández Haeger et al., 2015). Their presence in the Doñana National Park and the work carried out to eradicate them probably determined their inclusion in the list of invasive species in Andalusia (Dana et al., 2005), although they are not currently listed in the *Catálogo Español de Especies Exóticas Invasoras–Flora*, of the Ministerio de Agricultura, Pesca, Alimentación y Medio Ambiente (http://www.mapama.gob.es/es/biodiversidad/temas/conservacion–de–especies/especies–exoticas–invasoras/ce_eei_flora.aspx), where other species of the Asclepiadaceae (*Araujia sericifera* and *Calotropis procera*), considered invasive in the Canary Islands, do appear.

Although of native origin and despite the effective long–range airborne dispersal of their seeds, the plants that the monarch caterpillars feed on do not have the characteristics of invasive plants. This is because they are pioneer species that only thrive in disturbed sites, and because they compete poorly with various native species (rushes, brambles, reeds, oleanders, etc.) that displace them easily in secondary succession processes. They are also very sensitive to frost, especially *A. curassavica*, and need a lot of moisture in the soil. Therefore, their distribution is limited to enclaves that maintain high soil moisture throughout the year, they are subject to frequent disturbance (e.g. extensive cattle ranching, clearing, flooding), and they are located in low–lying, frost–free coastal areas with high annual sunshine hours (Valdés et al., 1987; Blanca et al., 2011; Fernández Haeger et al., 2010).

The observations of monarch butterflies outside their breeding areas documented in this work correspond to dispersive individuals with very little or no chance of success in these enclaves due to the absence or scarcity of their food plants. Since the climatic conditions are adequate in many other areas of the Mediterranean zone (Zalucki et al., 2015a), the previous spreading of these plants —in a natural or artificial way— is the key factor that would facilitate the expansion of monarch butterfly territories.

Finally, during the last few years, exotic butterflies —in many cases including monarchs— have been released in ceremonial events (weddings, baptisms, funerals). This seems to be the reason for the presence of monarchs on islands as far away as Ibiza and Cyprus (John et al., 2015). During the summer of 2015, several specimens of *Hypolimnas misippus* and *D. plexippus* appeared in gardens near the River Guadalquivir in Córdoba. The origin of both species was a ceremonial release in memorial of deceased children and they disappeared a few days later. These monarch records have not been considered in this work, but an isolated specimen detected in 2016 has been included due to the high abundance of monarchs in southern Spain during that year and no evidence of more ceremonial releases.

Although escaped butterflies from insect houses cannot be discounted, the presence of monarchs in the south of the Iberian Peninsula (Málaga and Cádiz) predates the existence of these facilities (Torres Mendez, 1979; Verdugo Páez, 1981; Tapia Domínguez, 1982). For southern Portugal, the first colonies were described in 2003 (Palma and Bivar de Sousa, 2003), although they must have been established long before this date.

The insect house located in Benalmádena (Málaga) began its activity in 2011 but monarchs were detected in this area more than 30 years earlier (Torres Mendez, 1979). In its vicinity, in the park of La Paloma of Benalmádena, there is a flourishing colony of monarchs that persists due to an artificial flower bed of *A. curassavica*. Some years, there is a phenomenon equivalent to that described by ourselves in the south of Cádiz: the density of caterpillars is such that they

consume the total biomass of *A. curassavica* available and there is a high mortality of caterpillars due to starvation. At such times, most imagos are forced to leave this enclave to find other, more–favourable sites.

Finally, since *G. fruticosus* is widespread in coastal areas of other countries across the Mediterranean basin to Anatolia, including some of the main islands (e.g. Balearics, Corsica, Sardinia, Crete), the dispersal movements of monarch butterflies from their breeding areas in the south of the Iberian Peninsula, documented in this work, could be the origin of their successful establishment in other countries of the Mediterranean basin.

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