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LOCATION AND WEB SUBSTRATE RECORDS OF *CYRTOPHORA CITRICOLA* (ARANEAE: ARANEIDAE) IN SOUTHERN SPAIN, INCLUDING TENERIFE

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Abstract: Recent new records of *Cyrtophora citricola* (Forskål, 1775) from the Western Hemisphere has stimulated study in its native range for possible comparison with introduced populations. We describe *C. citricola* web substrates, estimate substrate availability, and report its presence or absence in five provinces (Cádiz, Málaga, Granada, Murcia, and Valencia) in its native range, the southern half of the Spanish mainland and Tenerife island, in the Canary Islands. At 204 sites (25-30 per location) surveyed between 29 May and 16 June 2018, we documented *C. citricola* webs on mostly *Agave* spp., *Opuntia* spp., *Austrocylindropuntia* spp., *Yucca* spp., and some *Aloe* spp. We documented spiders at 40% of sites, colonial webs at 63 sites, and nine "super colonies" of more than 70 females, which were usually on very large patches of *Austrocylindropuntia* cacti. 77% of Tenerife and 16% to 40% of mainland sites contain common *C. citricola* substrates. Spider presence was estimated at 80% of the Tenerife sites, higher than all mainland regions except Motril (Granada province). Murcia had the highest egg sac presence estimate, at 90% of sites. No spiders were found at sites near Granada city, although they are present in the province, adding records to the 2010 Iberian spider checklist. Building webs on firm and structurally heterogeneous substrates like *Austrocylindropuntia* may support high *C. citricola* density, contribute to colony persistence, and protect webs from strong winds and harsh weather, reducing associated energy demands in open habitats. The successful use of a variety of anthropogenic and non-native plant substrates likely supports *C. citricola* populations in Spain.
Key words: Araneae, Araneidae, *Cyrtiphora citricola*, *Agave*, *Austrocylindropuntia, Opuntia*, breeding phenology, egg sacs, plant substrate, mainland Spain, Canary Islands.

Datos sobre el emplazamiento y sustrato de las telas de *Cyrtophora citricola* (Araneae: Araneidae) en el sur de España, incluida Tenerife
Resumen: La colonización del hemisferio oeste por la araña *Cyrtophora citricola* (Forskål 1775) ha estimulado su estudio en las zonas en las que se distribuye de forma autóctona, dado que ello permite una posible comparativa con las poblaciones introducidas en otras partes del mundo. Se describen aquí los sustratos de construcción de tela en *C. citricola*, así como cuál es la disponibilidad de sustratos, y se aportan datos de presencia/ausencia de la especie. Todo ello en cinco provincias dentro de su distribución autóctona en la mitad sur de España (Cádiz, Málaga, Granada, Murcia y Valencia), así como en la isla de Tenerife, en las Islas Canarias. Entre el 29 de mayo y el 16 de junio de 2018, se prospectaron 204 localidades (25-30 en cada provincia y Tenerife) y se encontraron telas mayoritariamente en *Agave* spp., *Opuntia* spp., *Austrocylindropuntia* spp., *Yucca* spp. y algunas *Aloe* spp. Se encontraron arañas en el 40% de las localidades, telas coloniales en 63 de ellas y 9 "supercolonias" con más de 70 hembras, que estaban normalmente en grandes manchas del cactus *Austrocylindropuntia*. En cuanto a la presencia de sustratos de tela, en Tenerife se encontraban presentes en el 77% de las localidades, variando de 16 al 40% en la Península. En Tenerife, la presencia de las arañas se confirmó en el 80% de los sitios, siendo esta mayor que en cualquier sitio peninsular excepto Motril (Granada). En las localidades murcianas se encontró que el 90% de ellas tenían sacos de huevos. No se encontraron especímenes cerca de la ciudad de Granada, aunque sí están en la provincia, lo que añade información al listado ibérico. La construcción de telas en sustratos de estructura heterogénea como *Austrocylindropuntia* puede contribuir al mantenimiento de una alta densidad de *C. citricola*, facilitar la persistencia de las colonias y proteger las telas del viento y condiciones climáticas extremas. El uso exitoso de esta variedad de especies exóticas y de origen antropogénico como sustrato, es causa probable del mantenimiento de poblaciones de *C. citricola* de gran tamaño en España.
Palabras clave: Araneae, Araneidae, *Cyrtiphora citricola*, *Agave*, *Austrocylindropuntia, Opuntia*, fenología de la cría, sacos de huevos, sustrato vegetal, España peninsular, Islas Canarias.

Introduction

Cyrtophora citricola (Forskål, 1775) is a species of tropical and subtropical orbweaver often known for its conspicuous webs owing to its colonial nature (Wheeler, 1926; Lubin, 1974; Leborgne *et al.*, 1998). Although adults do not cooperatively forage, engage in parental care, or split colony tasks like social spiders, they instead form persistent aggregations of individual capture webs (Lubin, 1980). Aggregations may be sustained when prey are plentiful and colony members benefit from the ricochet effect (Uetz, 1989) or herd effect from predators such as birds and parasitoid wasps (Lubin, 1980). Colonies can comprise up to "thousands" of individuals (Wheeler, 1926), with adult females capable of laying up to about 10 egg sac cocoons suspended in chains in the center of their tent webs (Kullmann, 1959).

Cyrtophora citricola is a widespread spider species that occurs in the Mediterranean, Middle East, Asia, and Africa (Forskål, 1775; Kullmann, 1958, 1959). Two decades ago, new *C. citricola* records were reported in the Western Hemisphere (Flórez Daza, 1996). Its presence has since been noted in Colombia (Flórez Daza, 1996; Dossman *et al*., 1997; Levi, 1997); the Dominican Republic (Alayon *et al*., 2001; Serra, 2005); Florida, USA (Mannion *et al*., 2002; Edwards, 2006); Cuba (Alayón, 2003); Brazil (Alvares & DeMaria, 2004); Haiti (Starr, 2005); Costa Rica (Viquez, 2007); Jamaica (Crews & Starr, 2015); and other Caribbean islands (Armas, 2010; Sewlal *et al*., 2011). Within some of these locations, *C. citricola* has quickly established and spread (Teruel *et al*., 2014), and has been reported as a pest in Colombian coffee plantations and Florida residential areas (Cardenas-Murillo *et al*., 1997; Serra, 2005; Edwards, 2006). Cardenas-Murillo *et al*. (1997) speculated that *C. citricola*'s dense webbing around terminal twigs of small trees creates microclimatic conditions that interfere with photosynthesis, although evidence of this or other ecological effects of this invasive spider is still needed.

Spider populations, productivity, and interactions are influenced by habitat and substrate characteristics (Riechert & Tracy, 1975; Balfour & Rypstra, 1998; Wolff & Gorb, 2012). Vegetation and other web substrates comprise a microhabitat that provides refuge from predators, environmental cover, and food resources by supporting insect communities (Halaj *et al*., 1998; Rypstra *et al*., 1999). Species-specific plant morphology, structural complexity, and architecture also mediate biotic factors, such as frequencies of prey interception, agonistic conspecific interactions, and cannibalism rates (Pearson, 2009; Langellotto & Denno, 2006). Additionally, substrate availability and selection influence abundance and persistence of individuals and colonies over time.

Growing interest in studying the success of invasive *C. citricola* populations thus motivates understanding the occurrence and substrate associations of *C. citricola* in its native range. Since *C. citricola* is known to build webs on non-native succulents like *Opuntia* spp., *Agave* spp., and *Aloe* spp. in their Mediterranean range (Wheeler, 1926; Chuang, personal observation), we focused this study on their associations with these substrates. In this paper, we describe *C. citricola* web substrates, estimate substrate availability, and indicate presence or absence at sites in six provinces in its southern Spanish range, including Tenerife island from the Canary Islands. We provide site information, localities, and abundances of spiders from seven surveyed regions, and describe the conditions of particularly large colonies observed during our surveys.

Methods

Sampling and data collection

The range of *C. citricola* includes much of the southern and eastern coasts of Spain, so we selected six provinces in that area to base our study on, expanding the resolution of province-level accounts by Cardoso & Morano (2010). To estimate substrate availability, we selected 50 sites from near the capitals of each province (Tenerife, Cádiz, Málaga, Granada, Murcia, and Valencia). Non-urban sites were randomly selected from the landscape view of Google Maps (Google Maps, 2018) and checked in the street view for common *C. citricola* web substrates, e.g., plants (*Opuntia* spp., *Agave* spp., *Austrocylindropuntia* spp., *Yucca* spp., and *Aloe* spp.) as well as guardrails and fences (Teruel *et al*., 2014).

Sites with known web substrates were then selected from the 50 sites in each province for spider and egg sac abundance surveys. In all cases, additional sites were evaluated in Google Maps until 25-30 sites per province had been selected for surveys (Fig. 1). When no spiders were found near the city of Granada, we added 25 sites in nearby Motril (also in the province of Granada). We chose Motril because it shares a similar longitude to Granada but is more coastally located, like the other cities. Random roads in Motril were selected from Google Maps and sites were chosen when we identified suitable web substrates in person.

At each site, we noted whether *C. citricola* spider webs were present, the number of solitary and colonial webs, and the number of females, males, juveniles, and commensal spiders. Solitary webs were defined as webs located at least 1 m apart from conspecifics that lacked any silk connecting them to other webs (Leborgne *et al*., 1998). Temperature, time of day, web substrate, and GPS coordinates were noted. While the search for webs was initiated based on common substrates we identified through Google Maps (e.g., *Opuntia* spp.), we also searched other likely structures where spiders might be found within an approximate 30 m radius from focal substrates (native and non-native plants, metal signs, metal gates, etc.).

Statistical analyses

We used the 'rstan' package in R to create Bayesian models in the Stan programming language (Stan Development Team, 2018). These were used to estimate the proportion of sites with suitable web substrates, spider presence, and egg sac presence in each of the six provinces surveyed. We assumed that our data came from a Bernoulli distribution, and fitted the models with flat priors with a uniform probability distribution between 0 and 1. We calculated a distribution of posterior estimates from 10,000 Markov chain Monte Carlo iterations using two independent chains. We tested the hypotheses that regions had equal proportions by determining whether overlaps in the calculated 95% Highest Density Intervals occurred.

Results

We conducted web surveys between 29 May and 16 June 2018 between the hours of 08:00 and 20:00. Temperatures varied between 13.8° and 30.0° C in the field. Surveys were done in mixed coastal grassland, scrub, and forested habitats, near residential areas and small-scale agriculture. Habitats were generally dominated by grasses, sparse shrubs and trees, and medium to large plants (ca. 1 to 3 m diameter) known to host *C. citricola* populations (e.g., *Agave* spp., *Austrocylindropuntia* spp., *Opuntia* spp.) (Fig. 2). Deviations from these trends are noted in Appendix A.

Location and substrate records

In Appendix A, the locations, substrates, and numbers of *C. citricola* webs, egg sac chains, and spiders are provided, including solitary and colonial webs, males, females, juveniles, and commensals. Of the 204 sites surveyed, available plant substrates included *Opuntia* spp. (66 sites), *Agave americana* (62 sites), *Agave americana* 'Marginata' (25 sites), *Yucca* spp. (24 sites), *Austrocylindropuntia* spp. (22 sites), *Agave attenuata* (10 sites), other *Agave* spp. (15 sites), *Aloe* spp. (4 sites), *Cupressus* spp. (2 sites), and *Thuja* spp. (2 sites) (Appendix B, Fig. 3). Guard rails (17 sites), fences (12 sites), signs (3 sites), and a bridge railing (1 site) were also surveyed. Although there is some question about *Agave* spp. identifications, we maintained species-level and varietal information in instances where identifications were more certain.

We documented webs at 42% of sites, and of those sites, only 1 to 2 webs were documented at 56% of sites. Similarly, spiders were documented at 40% of sites, but of those sites, only 1 to 2 spiders were documented at 26% of sites; the mean (± SD) number of total spiders at the 61 sites with greater than 2 spiders was 47 ± 89 spiders. With the exception of Tenerife and Valencia, most sites seemed to be occupied by mature females, many of which looked gravid. The percent of each plant substrate, represented at more than 20 sites, with webs and spiders varied from 68% of *Austrocylindropuntia* spp. to 25% on *Aloe* spp., respectively. While 3 out of 3 signs had webs and spiders, only 4 out of 17 guard rails did, and none were documented on 12 fences and 1 bridge railing that were surveyed.

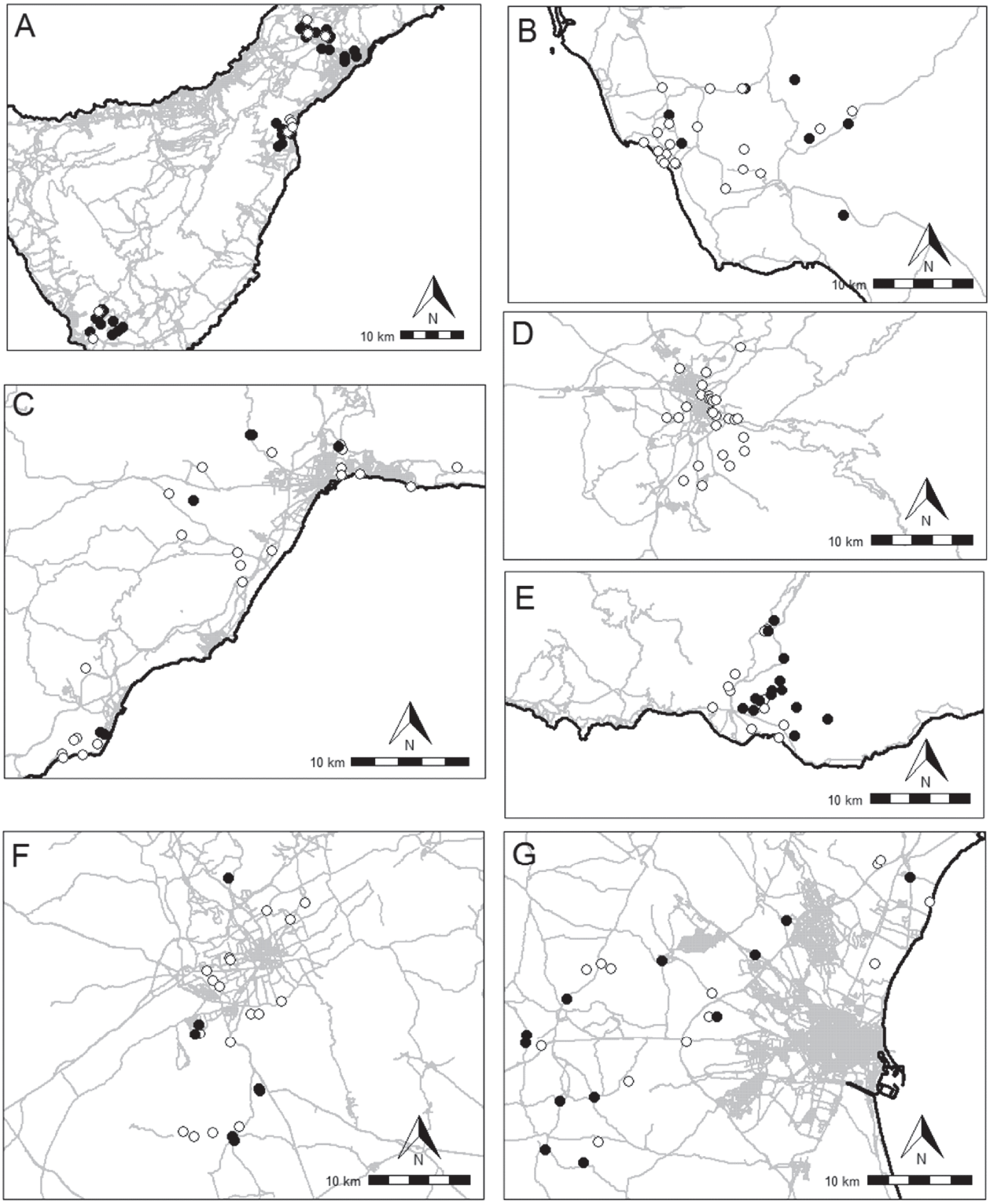


Fig. 1. Sites surveyed for *C. citricola* spider and egg sac presence in **A**) Tenerife, Canary Islands centered at Santa Cruz de Tenerife, Candelaria, and Arona; **B**) Cádiz Province; **C**) Málaga Province; **D**) Granada and **E**) Motril in Granada Province; **F**) Murcia Province; and **G**) Valencia Province. Filled and unfilled circles indicate sites with spider presence and absence, respectively. The grey lines represent major roads in the province.

The scale insect, *Dactylopius opuntiae* (Cockerell) (Hemiptera: Dactyliiopidae), released to control invasive *Opuntia* spp. (Shaw *et al*., 2018), was frequently observed in the field with dying *Opuntia* spp. Comparisons with earlier observations made at some of the same sites on the mainland suggest that *Opuntia* spp. have been declining or have died since 2016 (Chuang, personal observation).

Bayesian estimates of web substrate availability, spider presence, and egg sac presence

Of the areas we surveyed, only Tenerife differs substantially from all of the other regions in substrate availability (Fig. 4A, Table I). An estimated 77% of Tenerife sites contain substrates where *C. citricola* is commonly found, especially *Opuntia* spp. and *Agave* spp. An estimated 16% to 40% of

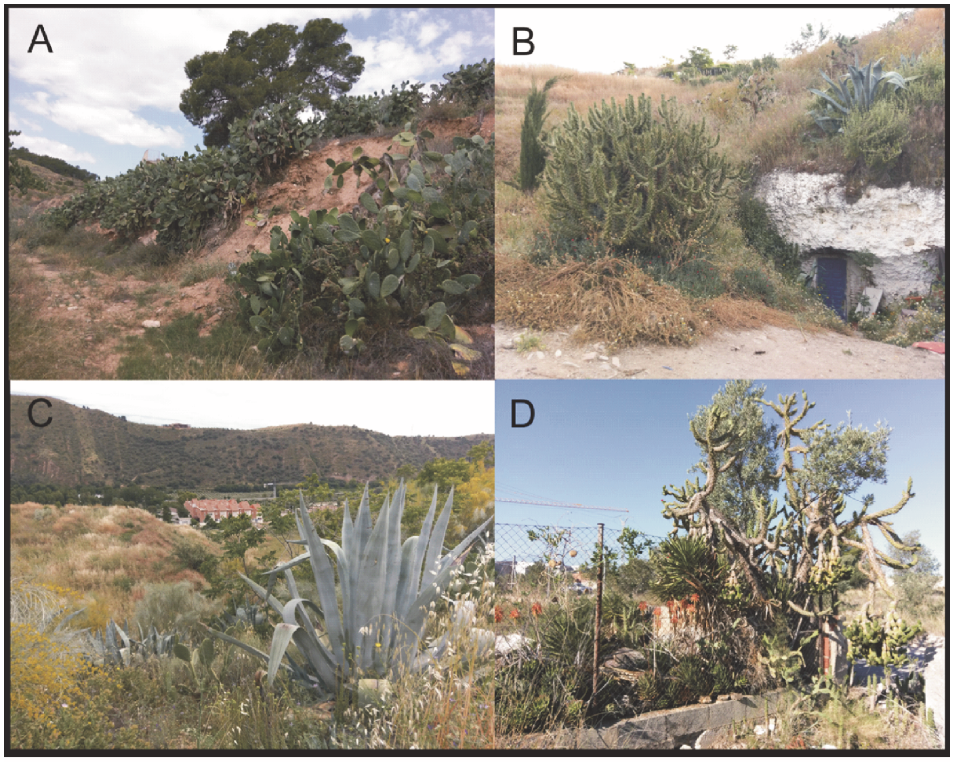


Fig. 2. Representative *Cyrtophora citricola* habitats in southern Spain with: **A**) *Opuntia* sp., **B**) *Cupressus* sp., *Austrocylindropuntia* sp., *Opuntia* sp., and *Agave* sp., **C**) *Agave* sp., and **D**) *Aloe* sp., *Yucca* sp., *Austrocylindropuntia* sp., and *Opuntia* sp.

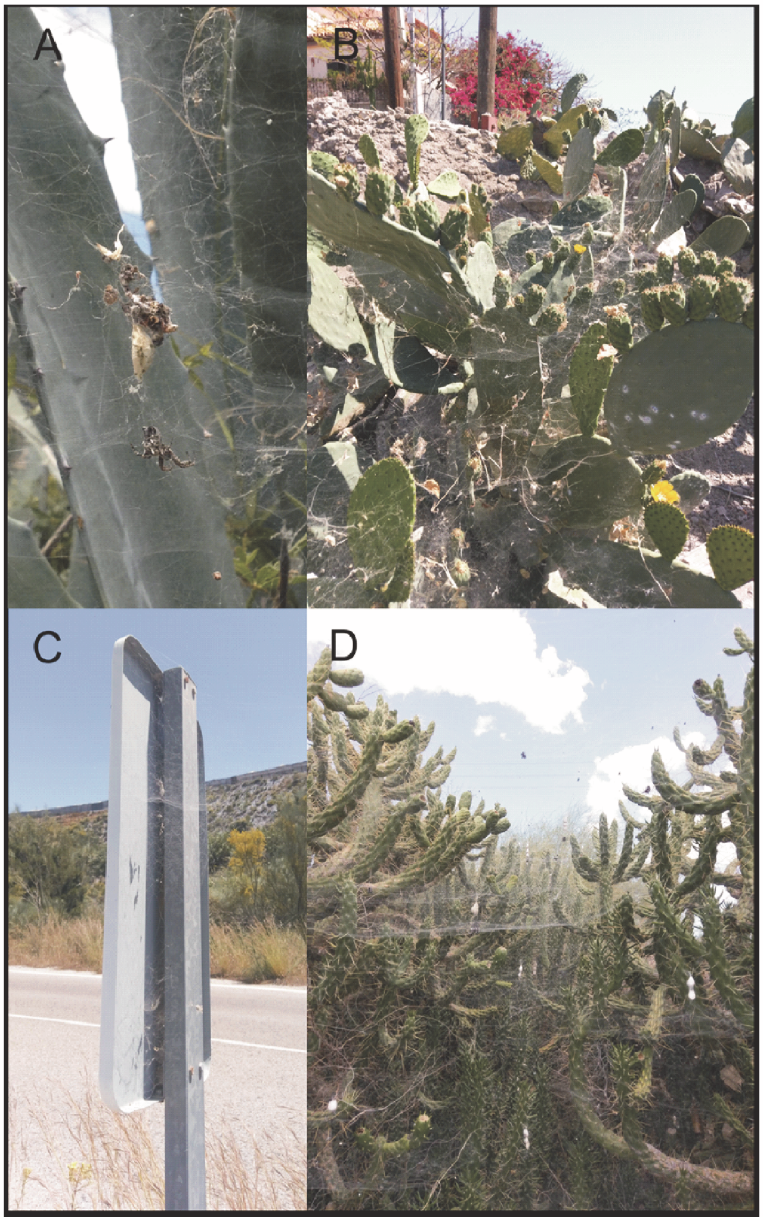
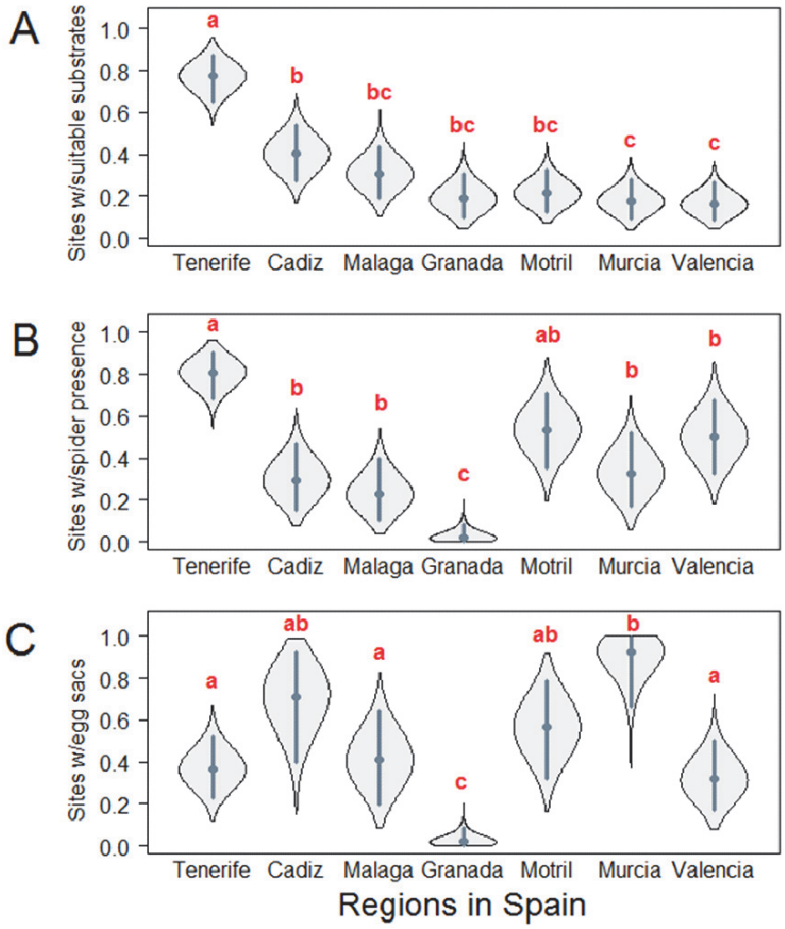


Fig. 3. *Cyrtophora citricola* web substrates in southern Spain: **A**) *Agave americana*, **B**) *Opuntia* sp., **C**) a metal sign, and **D**) *Austrocylindropuntia subulata*, in which various egg sacs are visible.

► **Fig 4.** Density plots of the posterior estimates of the proportion of sites: **A**) with suitable web substrates, **B**) with *C. citricola* present, and **C**) with egg sacs present for each of the seven areas surveyed. The 95% Highest Density Interval is indicated with the interior line segment, along with the median value for each region denoted with a circle.



mainland sites contain common web substrates, with greater substrate availability in Cádiz compared to Murcia and Valencia.

Our models estimate spider presence at 80% of Tenerife sites, which is higher than all mainland regions but Motril (Fig. 4B, Table I). Presence in Cádiz, Málaga, Motril, Murcia, and Valencia is similar, ranging from 23% to 54% of sites. No spiders were found at any of the sites near the city of Granada, accounting for a significantly lower estimate of 2%.

Despite having the highest web substrate availability and spider presence estimates, Tenerife was not determined to have comparably high egg sac presence estimates (Fig. 4C, Table I). Instead, there was no significant difference in estimates among many of the locations, with the exception of Murcia, which had the highest estimate of 90% of sites with egg sacs present. Once again, sites near the city of Granada had the lowest estimate, because no spiders were observed in any of the 40 sites surveyed.

Table I. Parameter estimates from binomially distribution Bayesian models of the proportion of sites with suitable habitats, sites with *C. citricola* present, and sites with egg sacs present.

Proportion of Sites w/Suitable Habitat							
	Tenerife	Cádiz	Málaga	Granada	Motril	Murcia	Valencia
Theta mean	0.77	0.40	0.31	0.19	0.22	0.18	0.16
SD	0.06	0.07	0.06	0.05	0.05	0.05	0.05
95% HDI	0.65-0.87	0.28-0.54	0.19-0.44	0.10-0.31	0.13-0.32	0.09-0.28	0.08-0.27
Proportion of Sites w/*C. citricola* Present							
	Tenerife	Cádiz	Málaga	Granada	Motril	Murcia	Valencia
Theta mean	0.80	0.30	0.23	0.02	0.54	0.33	0.50
SD	0.06	0.08	0.08	0.02	0.09	0.09	0.09
95% HDI	0.68-0.91	0.15-0.47	0.10-0.39	0-0.08	0.35-0.71	0.17-0.52	0.32-0.68
Proportion of Sites w/Spiders and Egg Sacs Present							
	Tenerife	Cádiz	Málaga	Granada	Motril	Murcia	Valencia
Theta mean	0.37	0.70	0.41	0.02	0.56	0.90	0.32
SD	0.08	0.14	0.12	0.02	0.12	0.09	0.09
95% HDI	0.23-0.52	0.40-0.93	0.20-0.64	0-0.08	0.32-0.79	0.66-1.00	0.17-0.50

Super colonies

Colonial webs were documented at 63 sites: 29 at Tenerife, 12 at Valencia, 7 each at Motril and Murcia, 6 at Cádiz, and 4 at Málaga (Appendix A). "Super colonies" of *C. citricola* containing about 70 females or more were encountered in all areas surveyed except for near the cities of Motril and Granada in the province of Granada. In total, nine of the 204 sites hosted sprawling super colonies that commonly covered the entirety of their plant substrates (Appendix A). In all but one case, these colonies were found on large patches of *Austrocylindropuntia* spp. that often measured at least 10 m x 7 m in area.

The largest super colony was found on several 10 m long patches of *Austrocylindropuntia subulata*. These plants were growing next to a metal fence outside a residence by the side of a rural road (Vejer de la Frontera, Cádiz Province, 36.352390 N, -5.947369 W). The patches were interspersed with *Eucalyptus* sp. trees and other vegetation, although the silk from individual capture webs united webs from different patches into a single colony. The network of webs was dense enough that some webs were fully suspended in the air above the plant substrate below, and at heights of about 5 m to 7 m. Because these webs were merely anchored by other webs

instead of a sturdier foundation, they seemed particularly vulnerable to mild wind gusts and were frequently observed being buffeted in different directions. Given the size of the *A. subulata* substrate and the amount of dry plant debris deposited on the colony from neighboring *Eucalyptus* sp. trees, it was impossible to determine an accurate count of the colony size. However, approximately 500 mature female webs were counted from all of the patches in this colony.

Discussion

We documented *C. citricola* webs on mostly *Agave* spp., *Opuntia* spp., *Austrocylindropuntia* spp., *Yucca* spp., and some *Aloe* spp. in the southern regions of Spain. These common substrates represent large, perennial plants that have a sturdy foundation for web anchor points, and all but *Yucca* are succulent. Their fleshy stems and leaves do not bend as readily in the wind as other vegetation in these habitats, such as grasses, forbs, and bushes. The relatively flat surfaces of *Opuntia* cladodes and large *Agave* and *Aloe* leaves may act as a wind barrier, preventing damage from strong wind gusts likely prevalent in open habitats preferred by *Cyrtophora* (Lubin, 1973). Wind also has a higher noise amplitude than anthropogenic and background acoustic sounds, and diminishes prey detection abilities in orbweavers (Wu & Elias, 2014). Strong perturbations in webs built on flimsy substrates likely interfere with an individual's ability to detect finer, airborne and substrate-borne stimuli from potential prey or possibly even predators. *Cyrtophora* spiders make dense, long-lasting webs that are infrequently repaired (Lubin 1973) because the activity and silk expenditure involved with web construction is energetically expensive (Anderson, 1970; Prestwich, 1977). *Cyrtophora citricola*'s preference for building webs on firm substrates (Brenes, 2012) like these plants thus may allow it to overcome strong winds and harsh weather, and reduce associated energy demands in open habitats.

The general structure of the plants observed may also favor spacing requirements of *Cyrtophora* webs, especially colonies (Rao & Poyyamoli, 2001). Female *C. citricola* can build webs up to about 45 cm in diameter (Pasquet & Leborgne, 1997), and these spiders prefer direct sunlight over shady habitats. *Yucca*, *Agave*, and *Aloe* leaves are arranged in a rosette pattern, with sharp, spiny leaves funneling out from a partially-enclosed space in the middle. The largest female webs in each colony are often found in the largest space at the center of these plants, with smaller individuals occupying spaces between more closely situated outward-spiraling leaves.

Opuntia ficus-indica, one of the common *Opuntia* plants we observed with *C. citricola*, is a widespread species in Spain that grows to 20 to 30 m wide and up to 5 m tall (Benson & Walkington, 1965). Outwardly branching, elliptical cladodes and long spines provide ample web attachment sites for orbweavers. *Opuntia* easily reproduce clonally when broken cladodes take root, creating multiple interlocking individuals in large patches (Padrón *et al*., 2011), which can support larger aggregations of spider webs. Like *Opuntia*, *Austrocylindropuntia subulata* is a clonal cactus that grows to 5 m in height, with multi-branching vegetative segments (Cáceres & Roque, 2017). Varying heights of each cylindrical segment as well as dense spines means this cactus provides a multitude of anchoring points for large webs and colonies. Spiders often require specific architectural features and arrangements to create webs (Riechert & Gillespie, 1986), and the high accessibility of potential attachment points on these cacti likely help support larger densities of individuals. The density of spines and sheer size of *A. subulata* may defend *C. citricola* colonies against larger vertebrate threats such as birds as well as human interference. Colonies nestled at the center of large patches of this cactus are thus difficult to access. The perennial nature of these succulents may further provide a stable habitat across multiple years, facilitating colony persistence.

Interestingly, most of these plants are native to the New World, and not to Spain (Vilà *et al*., 2003; Padrón *et al*., 2011). *Opuntia ficus-indica* may trace its domestication to central Mexico (Griffith, 2004), but it has an extensive history of propagation as food and fodder throughout the Mediterranean (Griffith, 2004). Christopher Columbus is thought to have brought it and related species to Europe in 1493 (Russell & Felker, 1987), where their ethnobotanical popularity led to widespread cultivation in arid and semiarid habitats across the Old World (Anderson, 2001). *Cyrtophora citricola* has long been associated with *Opuntia* substrates; earlier names of *Epeira opuntiae* Dufour 1820, *Epeira cacti-opuntiae* Lucas, 1838, and *Cyrtophora opuntiae* Simon, 1874 were eventually synonymized, but hint at this historic association nonetheless (Wheeler, 1926). The other plants follow similar invasion histories of escaping from cultivated or garden contexts and becoming common across the Mediterranean landscape (Quézel *et al*., 1990; Silva *et al*., 2015; Aymerich & Gustamante, 2015). For instance, multiple *Agave* species were introduced to southeastern Spain as ornamentals in the 1940s (Martín-Galindo, 1988), and have since spread in grasslands and rocky, sloped habitats (Nobel, 1988).

The widespread nature of *Opuntia*, *Austrocylindropuntia*, *Agave*, *Yucca*, and *Aloe* likely supplement the range of suitable habitats for *C. citricola* in their native range. Among these plants, *Opuntia* and *Austrocylindropuntia* are cacti, and with 21 recorded species, Spain has the most invasive cacti species in Europe (Essl & Kobler, 2009). They readily colonize dry grasslands, Mediterranean scrub, and rock vegetation found in southern Spain and the Canary Islands (Essl & Kobler, 2009), where they are limited to growing on acid siliceous bedrock in the dry, open habitats that are favored by *Cyrtophora* (Lubin, 1973). On Tenerife, the density of *Opuntia dillenii* has been estimated at around 1200 individuals/hectare in the more invaded areas, which is higher than on the mainland (Padrón *et al*., 2011). In our study, we also found that Tenerife had more sites with suitable web substrates, such as *Opuntia* spp. which corresponded with more sites with *C. citricola* present. This pattern was less clear in mainland regions, where Murcia and Valencia had the lowest proportion of sites with suitable web substrates, but comparable sites with spider presence to the other regions. Differences in climate (e.g., temperature and precipitation, Table II) might influence plant and arthropod productivity, and might explain greater web substrate availability and colonial webs at Tenerife compared with the other areas surveyed, although climate on the island also varies across the three main sampling areas.

Web substrate availability is similar in Granada, where *Agave* are common atop hillsides overlooking the city (Sacromonte and Albaicín districts) as well as in areas with less human disturbance. Despite this, it was the only surveyed area with no evidence of *C. citricola*, whether living specimens, old webs, or signs of egg sacs. These findings are par-

tially supported by the 2010 Iberian Spider Checklist (Cardoso & Morano, 2010), where *C. citricola* was not listed in Granada Province, although we found them in over half of the sites near the coastal city of Motril within this province. *Cyrtophora citricola* is more commonly found along the southern and eastern coasts of Spain, but has also been observed much further inland than the city of Granada, e.g., in Jaén and Córdoba (Cardoso & Morano, 2010). We note that survey sites near the city of Granada had comparatively low annual temperatures (Table II), and climatic factors may explain why *C. citricola* was not found here.

The presence of egg sacs provides information about the breeding phenology of these spiders. Because many sites contained solely adult females in late May and early June, we believe associated egg sacs represent the first reproductive efforts of the season from overwintering spiders. Relatively low egg sac presence estimates were calculated at Málaga, Valencia, and Tenerife, the latter despite high web substrate availability and spider presence estimates. On the other hand, Murcia had a significantly higher egg sac presence estimate of 90% of sites. The lower egg sac presence in the most northerly location in Valencia, along with smaller instar spiders observed at those sites, suggests delayed development and breeding seasonality that is likely related to lower temperatures (Li & Jackson, 1996). For *Cyrtophora cicatrosa* spiders, development in increasing temperatures up to about 32° C results in a faster time to maturation and fewer days to the first creation of an egg sac (Palanichamy, 1985). Murcia had a higher proportion of sites with egg sacs, along with a higher mean annual high temperature. Temperature alone might not explain breeding phenology, though. Riechert & Tracy (1975) suggest that egg production is related to prey consumed, which is influenced by spider activity and available prey, both of which are related to web-site characteristics, e.g., wind speed, solar radiation, humidity, air temperature, thermal radiation, substrate, and surrounding vegetation.

Cyrtophora citricola is known to create large, high-density colonies. In this study, we catalogued nine super colonies of *C. citricola*. Group-living in spiders is often contingent on abundant prey resources (Uetz & Hieber, 1997), where high prey availability supports denser aggregations of individuals and reduces cannibalism (Rypstra, 1983). Success of *C. citricola* "super colonies" may be influenced by richer prey associated with human habitation; in Israel, Rao & Lubin (2010) only observed colonies of greater than 100 individuals near a garbage dump and at a pump station. At least one of the sites where we observed a super colony (37.917260 N, -1.205022 W) was similarly located on a hill used as a dumpsite, and *C. citricola* is known to use manmade substrates like guard rails and fences (Edwards, 2006).

Most of the super colonies observed in southern Spain occurred on *Austrocylindropuntia* spp. cactus patches. The habitat heterogeneity provided by this large and structurally complex plant likely supports larger spider densities found on *Austrocylindropuntia* spp. compared to patches of *Agave* and smaller plants. Its uneven columnar structure and spiny surface supports high surface area for maximizing web density and this structural heterogeneity may offer individuals more places to hide from would-be cannibalism events (Huffacker, 1958; Rypstra *et al*., 1983). Individual spacing requirements and substrate limitation also determine spider abundance (Colebourn, 1974; Rypstra, 1983). Increasing complexity of vegetation structure in grasslands leads to higher recruitment of orbweavers (Gomez *et al*., 2016), and suggests that web substrates limit spider densities. Notably, the rapid 700 km spread of an invasive Cuban *C. citricola* population has been linked to dense colonies occurring nearly continuously along kilometers of telephone wires and fences (Teruel *et al*., 2014). The successful use of a variety of anthropogenic and plant substrates likely influence the spread and densities of *C. citricola*.

Table II. Annual average temperatures (°C) and precipitation (mm) in *C. citricola* survey locations. Source: Agencia Estatal de Meterologia http://www.aemet.es/en/lineas_de_interes/datos_y_estadistica

	Temperature		Precipitation
	Avg. Min	Avg. Max	
Tenerife (Santa Cruz de Tenerife)	13.0	20.5	517
Tenerife (Candelaria)	18.4	24.6	225
Tenerife (Arona)	17.9	24.8	133
Cádiz	15.4	21.6	524
Málaga	13.7	23.3	534
Granada	9.0	22.3	353
Motril	13.1	23.5	350
Murcia	12.3	24.9	297
Valencia	22.3	13.8	475

Understanding and predicting *C. citricola*'s interactions and impacts in its introduced range requires additional study in its native and introduced ranges. Possible dependence on evolutionarily nonsympatric plants that serve as web substrates, particularly *Opuntia*, complicates predictions because these systems are currently in flux. We observed evidence of the spread of *D. opuntiae* across the surveyed regions; although it has been intentionally introduced to many areas of the world as a biocontrol agent, it was unintentionally spread in Spain, where it kills *Opuntia* (Shaw *et al*., 2018). Interestingly, now the biocontrol agent *D. opuntiae* is the target of biocontrol where *Opuntia* is valued. Any declines in *Opuntia* populations in Spain owing to *D. opuntiae* may be temporary if burgeoning control of *D. opuntiae* also spreads to Spain, e.g., regionally using the coccinellid beetle *Cryptolaemus montrouzieri* Mulsant or D-limonene in Morocco (Bouharroud *et al*., 2018), using the coccinellid *Chilocorus cacti* L. from Mexico (Hernández-González & Cruz-Rodríguez, 2018), or *Fusarium* from Brazil (Carneiro-Leão *et al*., 2018). Accordingly, predicting outcomes of *C. citricola's* interactions when it colonizes particular substrates also involves understanding potential impacts to those substrates. Additionally, interactions between *C. citricola* and its adventive plant substrates, and biocontrol agents that might influence those substrates, provides an interesting case study about possible impacts to native species following intentional and unintentional human-aided dispersal of multiple non-native species.

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(*) References available at www.sea-entomologia.org

Appendix A
Locations, substrates, and numbers of *C. citricola* webs, egg sac chains, and spiders in six Spain regions

Province or City	Latitude	Longitude	Web Substrate	Webs	Solitary Webs	Colonial Webs	Egg Sac Chains	Total Spiders	Females	Males	Juveniles	Commensals	Date	Time	Temperature (°C)
Tenerife	28.491905	-16.348977	25 *Agave* sp., 2 *Opuntia* sp.	7	6	1	0	11	6	4	1	(*)	5/29/2018	14:15	21.1
Tenerife	28.503500	-16.358600	1 *Agave* sp., 1 *Opuntia* sp.	5	1	4	2	30	21	4	5	14	5/29/2018	15:20	18.9
Tenerife	28.510720	-16.351003	2 *Agave attenuata*, 2 *Opuntia* sp.	3	1	2	3	10	9	0	1	20	5/29/2018	16:17	21.1
Tenerife	28.516990	-16.347835	15 *Agave* sp., 2 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	5/29/2018	16:39	21.1
Tenerife	28.497330	-16.344852	3 *Agave americana*, 12 *Yucca* sp.	0	0	0	0	0	0	0	0	0	5/29/2018	17:50	18.9
Tenerife	28.500060	-16.343867	1 *Agave* sp.	1	1	0	0	1	1	0	0	6	5/29/2018	18:34	17.8
Tenerife	28.498090	-16.333105	8 *Yucca* sp., 1 Arecaceae	1	0	1	0	0	4	0	0	1	5/29/2018	18:50	15.6
Tenerife	28.503100	-16.316400	3 *Aloe* sp., 1 *Yucca* sp.	1	1	0	0	1	1	0	0	0	5/29/2018	19:25	15.0
Tenerife	28.496990	-16.314340	4 *Agave americana*, *Yucca* sp.	1	0	1	0	4	4	0	0	7	5/30/2018	10:50	18.9
Tenerife	28.493390	-16.316770	4 *Yucca* sp.	0	0	0	0	0	0	0	0	0	5/30/2018	11:08	18.9
Tenerife	28.493490	-16.308900	1 Agave americana, 3 *Opuntia* sp.	2	0	2	3	143	91	32	20	69	5/30/2018	11:30	22.2
Tenerife	28.489600	-16.311436	5 *Opuntia* sp.	2	0	2	0	9	5	4	0	1	5/30/2018	11:50	22.2
Tenerife	28.475460	-16.322901	1 *Agave americana*	4	0	4	0	24	17	7	0	11	5/30/2018	13:58	23.9
Tenerife	28.473710	-16.310227	3 *Opuntia* sp., 3 *Yucca* sp.	2	1	0	0	2	2	0	0	0	5/30/2018	14:20	22.8
Tenerife	28.463230	-16.286279	2 *Opuntia* sp.	3	2	1	0	6	2	3	1	0	5/30/2018	14:58	22.8
Tenerife	28.456870	-16.285647	40 *Agave* sp., 1 *Opuntia* sp.	12	7	5	0	37	27	1	9	1	5/30/2018	15:23	22.8
Tenerife	28.463720	-16.267242	8 *Agave attenuata*	4	3	1	0	5	4	1	0	1	5/30/2018	16:38	22.8
Tenerife	28.471690	-16.269877	3 *Opuntia* sp.	1	0	1	0	5	5	0	0	0	5/30/2018	16:59	22.8
Tenerife	28.360610	-16.375654	13 *Opuntia* sp.	4	1	3	0	14	10	3	1	2	5/30/2018	18:40	22.2
Tenerife	28.338700	-16.387800	2 *Opuntia* sp.	6	3	3	0	35	27	8	0	10	5/30/2018	18:03	21.1
Tenerife	28.335421	-16.394022	1 *Austrocylindropuntia* sp.	2	0	2	1	27	8	2	17	0	5/30/2018	19:55	20.6
Tenerife	28.352661	-16.371955	1 *Austrocylindropuntia* sp.	3	0	3	33	250	250	(*)	(*)	(*)	5/31/2018	8:00	21.1
Tenerife	28.373170	-16.375678	2 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	5/31/2018	8:08	17.2
Tenerife	28.369200	-16.372749	4 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	5/31/2018	8:21	18.9
Tenerife	28.355560	-16.378746	4 *Opuntia* sp.	1	1	0	2	0	0	0	0	0	5/31/2018	8:33	17.8
Tenerife	28.355490	-16.378331	5 *Agave americana*, 5 *Opuntia* sp.	4	1	3	1	26	15	2	9	(*)	5/31/2018	9:04	17.8
Tenerife	28.362980	-16.370778	1 *Agave americana,* 1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	5/31/2018	9:39	18.9
Tenerife	28.367960	-16.397849	7 *Opuntia* sp.	5	3	2	0	15	11	1	3	(*)	5/31/2018	10:11	18.3
Tenerife	28.359840	-16.388664	1 *Opuntia* sp.	4	4	0	0	4	4	0	0	0	5/31/2018	10:30	18.3
Tenerife	28.350950	-16.387631	30 *Opuntia* sp.	28	2	26	2	397	260	104	33	55	5/31/2018	10:52	18.9
Tenerife	28.064460	-16.664981	2 *Agave* sp.	3	2	1	0	4	2	2	0	3	5/31/2018	12:48	22.8
Tenerife	28.069570	-16.655462	1 *Agave* sp., 15 *Opuntia* sp.	11	6	5	3	52	29	14	9	0	5/31/2018	13:20	22.8
Tenerife	28.075510	-16.648579	1 *Agave* sp., 1 *Opuntia* sp.	14	2	12	8	83	49	16	18	16	5/31/2018	13:58	22.8
Tenerife	28.084380	-16.663634	1 *Agave americana* 'Marginata*'*	1	0	1	0	2	1	1	0	0	5/31/2018	15:13	23.3
Tenerife	28.080510	-16.684397	1 *Opuntia* sp., 2 *Austrocylindropuntia* sp.	5	2	3	0	24	14	4	6	4	5/31/2018	16:40	23.9
Tenerife	28.088110	-16.692094	guard rails	3	2	1	1	4	2	1	1	1	5/31/2018	17:41	23.9
Tenerife	28.098300	-16.686972	3 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	5/31/2018	17:49	23.9
Tenerife	28.069010	-16.701709	1 *Agave* sp., 1 *Agave attenuata,* 1 *Opuntia* sp.	3	2	1	0	6	3	2	1	0	5/31/2018	15:32	21.1
Tenerife	28.058760	-16.696572	guard rails	0	0	0	0	0	0	0	0	0	5/31/2018	17:08	23.3
Tenerife	28.093810	-16.685440	1 *Agave attenuata*	12	3	9	0	51	40	8	3	9	6/1/2018	9:29	17.2
Tenerife	28.100220	-16.682680	2 *Opuntia* sp.	1	0	1	1	3	3	0	0	0	6/1/2018	8:02	14.4
Tenerife	28.100000	-16.682600	2 *Opuntia* sp.	10	2	8	1	64	46	15	3	5	6/1/2018	8:47	15.0
Tenerife	28.099510	-16.679436	3 *Opuntia* sp.	2	2	0	0	2	2	0	0	0	6/1/2018	9:37	17.2
Tenerife	28.101230	-16.680783	10 *Opuntia* sp.	2	2	0	0	2	2	0	0	0	6/1/2018	10:15	16.7
Cádiz	36.346020	-6.096739	guard rails	0	0	0	0	0	0	0	0	0	6/3/2018	9:23	17.2
Cádiz	36.321090	-6.088753	1 *Agave americana* 'Marginata'*,* 1 *Cupressus* sp., 1 *Thuja* sp.*,* guard rails	1	1	0	0	1	1	0	0	1	6/3/2018	9:42	17.2
Cádiz	36.313210	-6.088596	fences by agricultural plots	0	0	0	0	0	0	0	0	0	6/3/2018	9:58	17.2
Cádiz	36.304770	-6.102005	guard rails	0	0	0	0	0	0	0	0	0	6/3/2018	10:11	17.2
Cádiz	36.295951	-6.117616	3 *Agave americana*	0	0	0	0	0	0	0	0	0	6/3/2018	10:30	17.8
Cádiz	36.285434	-6.091525	21 *Agave americana* 'Marginata'	0	0	0	0	0	0	0	0	0	6/3/2018	10:58	19.4
Cádiz	36.287930	-6.100706	42 *Agave americana* 'Marginata'	0	0	0	0	0	0	0	0	0	6/3/2018	11:33	19.4
Cádiz	36.280140	-6.097822	15 *Agave americana*	0	0	0	0	0	0	0	0	0	6/3/2018	11:48	19.4
Cádiz	36.277180	-6.093733	4 *Agave americana* (cut down)	0	0	0	0	0	0	0	0	0	6/3/2018	11:59	19.4
Cádiz	36.276620	-6.081191	3 *Agave americana* 'Marginata'	0	0	0	0	0	0	0	0	0	6/3/2018	12:37	20.0
Cádiz	36.277210	-6.082134	7 *Agave americana*, 1 *Yucca* sp.	0	0	0	0	0	0	0	0	0	6/3/2018	12:59	20.0
Cádiz	36.294510	-6.087898	1 *Opuntia* sp. (dying)	0	0	0	0	0	0	0	0	0	6/3/2018	13:34	20.6
Cádiz	36.295450	-6.074652	1 *Agave americana* 'Marginata', 1 *Yucca* sp.	6	1	5	17	53	43	8	2	17	6/3/2018	9:06	13.3
Cádiz	36.253500	-6.025371	3 *Agave americana* 'Marginata'	0	0	0	0	0	0	0	0	0	6/3/2018	15:28	20.6
Cádiz	36.271270	-6.005273	13 *Agave americana* 'Marginata'	0	0	0	0	0	0	0	0	0	6/3/2018	15:51	20.6
Cádiz	36.289710	-6.003927	guard rails	0	0	0	0	0	0	0	0	0	6/3/2018	16:05	20.6
Cádiz	36.267340	-5.985577	1 *Austrocylindropuntia* sp.	0	0	0	0	0	0	0	0	0	6/3/2018	14:26	20.6
Cádiz	36.229860	-5.891799	11 *Agave americana* 'Marginata'	4	0	4	3	23	21	2	0	10	6/3/2018	16:58	21.1
Cádiz	36.345124	-6.006381	1 *Agave americana* 'Marginata', 1 *Agave attenuata*, guard rails	0	0	0	0	0	0	0	0	0	6/4/2018	8:40	14.4
Cádiz	36.344460	-6.042068	guard rails	0	0	0	0	0	0	0	0	0	6/4/2018	12:02	16.1
Cádiz	36.345033	-6.006353	1 *Opuntia* sp. (dying)	1	0	1	0	4	2	2	0	0	6/4/2018	12:11	16.1
Cádiz	36.344678	-6.003166	8 *Agave americana* 'Marginata'	2	0	2	3	26	22	4	0	0	6/4/2018	12:31	16.1
Cádiz	36.352390	-5.947369	1 *Austrocylindropuntia* sp.	2	1	1	27	(*)	500	(*)	20	(*)	6/4/2018	13:37	18.9
Cádiz	36.299880	-5.930864	1 *Ilex* sp., 3 other shrubs	1	1	0	1	1	1	0	0	0	6/4/2018	15:02	20.0
Cádiz	36.308060	-5.917845	8 *Thuja* sp.	0	0	0	0	0	0	0	0	0	6/4/2018	15:20	20.0
Cádiz	36.313200	-5.886846	14 *Agave* sp.	6	5	1	16	49	48	1	0	18	6/4/2018	15:44	20.0
Cádiz	36.324010	-5.882142	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/4/2018	17:00	18.9
Cádiz	36.310280	-6.057125	guard rails	0	0	0	0	0	0	0	0	0	6/4/2018	17:58	18.9
Málaga	36.507400	-4.674500	20 small to medium *Agave americana*	0	0	0	0	0	0	0	0	0	6/5/2018	10:51	18.3
Málaga	36.504160	-4.673609	1 *Austrocylindropuntia* sp.	0	0	0	0	0	0	0	0	0	6/5/2018	11:40	19.4
Málaga	36.506470	-4.655574	8 *Agave americana* 'Marginata', 4 *Agave americana*	0	0	0	0	0	0	0	0	0	6/5/2018	11:58	21.1
Málaga	36.514830	-4.641468	6 *Agave americana* 'Marginata'	0	0	0	0	0	0	0	0	0	6/5/2018	12:18	22.2
Málaga	36.519480	-4.660470	guard rails	0	0	0	0	0	0	0	0	0	6/5/2018	12:45	22.2
Málaga	36.517550	-4.663656	3 *Yucca* sp., 6 *Agave attenuata*	0	0	0	0	0	0	0	0	0	6/5/2018	13:09	23.9
Málaga	36.524013	-4.638802	20 *Agave* sp.	3	2	1	2	6	6	0	0	3	6/5/2018	13:47	23.9

Province or City	Latitude	Longitude	Web Substrate	Webs	Solitary Webs	Colonial Webs	Egg Sac Chains	Total Spiders	Females	Males	Juveniles	Commensals	Date	Time	Temperature (°C)
Málaga	36.522430	-4.635029	4 *Yucca* sp., 1 *Agave americana* 'Marginata', 1 *Austrocylindropuntia* sp., 2 *Agave americana*	3	2	1	2	3	3	0	0	0	6/5/2018	14:30	25.0
Málaga	36.573240	-4.652747	*1 Agave americana 'Marginata'*	0	0	0	0	0	0	0	0	0	6/5/2018	15:22	24.4
Málaga	36.702400	-4.549343	17 *Agave americana* 'Marginata'	1	1	0	1	1	1	0	0	0	6/5/2018	10:09	20.0
Málaga	36.639700	-4.502622	1 *Agave attenuata*, 4 *Yucca* sp.	0	0	0	0	0	0	0	0	0	6/5/2018	17:36	26.1
Málaga	36.651950	-4.504797	1 *Agave americana*	0	0	0	0	0	0	0	0	0	6/5/2018	17:55	25.6
Málaga	36.662020	-4.507552	5 *Yucca* sp., guard rails	0	0	0	0	0	0	0	0	0	6/5/2018	18:11	25.0
Málaga	36.663730	-4.474553	12 *Yucca* sp.	0	0	0	0	0	0	0	0	0	6/5/2018	18:33	25.0
Málaga	36.675670	-4.561006	fences	0	0	0	0	0	0	0	0	0	6/6/2018	8:41	20.0
Málaga	36.707590	-4.572419	fences (next to citrus orchard)	0	0	0	0	0	0	0	0	0	6/6/2018	9:05	19.4
Málaga	36.728130	-4.541182	1 *Opuntia* sp. (dying)	0	0	0	0	0	0	0	0	0	6/6/2018	9:29	20.0
Málaga	36.753182	-4.495311	11 *Agave americana* 'Marginata'	3	0	3	11	77	30	1	46	0	6/6/2018	10:09	17.8
Málaga	36.753332	-4.493273	1 *Austrocylindropuntia* sp.	2	1	1	29	140	140	(*)	(*)	(*)	6/6/2018	13:20	22.2
Málaga	36.739420	-4.474136	11 *Agave americana*, 1 *Agave americana* 'Marginata'	0	0	0	0	0	0	0	0	0	6/6/2018	13:08	22.8
Málaga	36.745500	-4.409034	21 *Agave americana*, 1 *Austrocylindropuntia* sp.	0	0	0	0	0	0	0	0	0	6/6/2018	13:41	22.2
Málaga	36.743980	-4.410362	14 *Agave americana*	1	1	0	1	1	1	0	0	0	6/6/2018	13:59	22.8
Málaga	36.741920	-4.407379	7 *Agave americana*	0	0	0	0	0	0	0	0	0	6/6/2018	13:50	22.8
Málaga	36.727530	-4.407689	13 *Agave americana* 'Marginata'	0	0	0	0	0	0	0	0	0	6/6/2018	15:03	22.8
Málaga	36.722200	-4.407628	7 *Agave americana*	0	0	0	0	0	0	0	0	0	6/6/2018	15:17	24.4
Málaga	36.713352	-4.341135	12 *Agave americana*	0	0	0	0	0	0	0	0	0	6/6/2018	15:57	26.1
Málaga	36.722790	-4.390552	11 *Agave americana*	0	0	0	0	0	0	0	0	0	6/6/2018	15:25	24.4
Málaga	36.728173	-4.297677	14 *Agave americana*	0	0	0	0	0	0	0	0	0	6/6/2018	16:25	26.1
Granada	37.110240	-3.619046	fences	0	0	0	0	0	0	0	0	0	6/8/2018	9:40	17.8
Granada	37.105290	-3.597728	fences	0	0	0	0	0	0	0	0	0	6/8/2018	10:04	17.8
Granada	37.123430	-3.602093	fences	0	0	0	0	0	0	0	0	0	6/8/2018	10:25	18.3
Granada	37.122830	-3.567371	2 *Agave americana*, 3 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/8/2018	10:53	20.6
Granada	37.132540	-3.575151	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/8/2018	11:09	20.6
Granada	37.136340	-3.550494	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/8/2018	11:36	20.6
Granada	37.148200	-3.552159	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/8/2018	12:04	20.6
Granada	37.158790	-3.582543	1 *Agave americana 'Marginata'*	0	0	0	0	0	0	0	0	0	6/8/2018	16:26	26.7
Granada	37.164840	-3.568260	10 *Agave americana*, 3 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/8/2018	16:45	26.7
Granada	37.164650	-3.561261	8 *Agave americana*, 2 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/8/2018	17:19	26.7
Granada	37.165560	-3.558169	14 *Agave americana*, 2 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/8/2018	17:34	26.7
Granada	37.186162	-3.598631	11 *Agave americana*	0	0	0	0	0	0	0	0	0	6/9/2018	8:21	14.4
Granada	37.185130	-3.590251	5 *Agave americana*	0	0	0	0	0	0	0	0	0	6/9/2018	8:45	17.2
Granada	37.183090	-3.590872	25 *Agave americana*	0	0	0	0	0	0	0	0	0	6/9/2018	9:08	12.8
Granada	37.183075	-3.588673	1 *Austrocylindropuntia* sp., 3 *Opuntia* sp. (dying)	0	0	0	0	0	0	0	0	0	6/9/2018	9:26	12.8
Granada	37.181170	-3.585752	8 *Agave americana*	0	0	0	0	0	0	0	0	0	6/9/2018	10:45	15.6
Granada	37.181821	-3.582668	7 *Agave americana*, 2 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/9/2018	10:37	15.6
Granada	37.195250	-3.597573	2 *Agave americana*	0	0	0	0	0	0	0	0	0	6/9/2018	11:40	21.1
Granada	37.206080	-3.593280	fences	0	0	0	0	0	0	0	0	0	6/9/2018	12:07	21.1
Granada	37.209730	-3.623227	1 *Agave americana*	0	0	0	0	0	0	0	0	0	6/9/2018	12:52	18.9
Granada	37.175700	-3.615859	guard rails	0	0	0	0	0	0	0	0	0	6/9/2018	13:54	18.9
Granada	37.166129	-3.624574	6 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/9/2018	14:05	18.9
Granada	37.166420	-3.637704	guard rails	0	0	0	0	0	0	0	0	0	6/9/2018	14:13	18.9
Granada	37.229460	-3.555691	1 *Agave* sp., 1 *Aloe* sp.	0	0	0	0	0	0	0	0	0	6/9/2018	14:56	20.6
Granada	37.171330	-3.587068	24 *Agave americana*, 14 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/9/2018	15:49	21.1
Granada	37.168250	-3.583088	16 *Agave americana*, 8 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/9/2018	16:00	21.1
Granada	37.170300	-3.585991	17 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/9/2018	16:26	21.1
Motril	36.763120	-3.566679	2 *Opuntia* sp., fences	0	0	0	0	0	0	0	0	0	6/10/2018	10:26	15.6
Motril	36.767542	-3.568720	fences	0	0	0	0	0	0	0	0	0	6/10/2018	10:41	15.6
Motril	36.778711	-3.560707	5 *Opuntia* sp., guard rails	0	0	0	0	0	0	0	0	0	6/10/2018	11:15	15.6
Motril	36.755769	-3.537261	7 *Agave americana*	0	0	0	0	0	0	0	0	0	6/10/2018	11:37	16.7
Motril	36.755754	-3.537248	1 *Agave attenuata*, 2 *Yucca* sp.	1	1	0	0	1	0	0	1	0	6/10/2018	12:07	22.2
Motril	36.754059	-3.532944	1 *Euphorbia* sp.	1	0	1	0	3	1	0	2	0	6/10/2018	12:19	22.2
Motril	36.755461	-3.527836	6 *Agave americana*	0	0	0	0	0	0	0	0	0	6/10/2018	12:55	23.9
Motril	36.759513	-3.519734	3 *Opuntia* sp., 3 *Austrocylindropuntia* sp.	2	0	2	4	11	9	2	0	0	6/10/2018	13:40	23.9
Motril	36.763614	-3.508384	36 *Agave americana*	2	1	1	0	17	3	2	12	0	6/10/2018	15:02	24.4
Motril	36.748268	-3.491119	3 *Agave americana*, 2 *Opuntia* sp., 1 *Austrocylindropuntia* sp.	1	1	0	1	1	1	0	0	0	6/10/2018	16:00	21.7
Motril	36.731944	-3.505167	fences	0	0	0	0	0	0	0	0	0	6/10/2018	16:33	24.4
Motril	36.728209	-3.541896	3 *Aloe* sp., 1 *Yucca* sp.	0	0	0	0	0	0	0	0	0	6/10/2018	16:50	18.9
Motril	36.747814	-3.586227	27 *Agave attenuata*, 8 *Yucca* sp.	0	0	0	0	0	0	0	0	0	6/10/2018	17:08	18.9
Motril	36.817532	-3.523330	6 *Yucca* sp.	1	1	0	0	1	1	0	0	0	6/11/2018	11:02	20.0
Motril	36.819376	-3.524431	2 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/11/2018	11:24	20.0
Motril	36.817621	-3.527471	2 *Opuntia* sp. (dying)	0	0	0	0	0	0	0	0	0	6/11/2018	11:37	20.0
Motril	36.827308	-3.516404	55 *Agave americana*	6	3	3	12	31	16	0	15	0	6/11/2018	11:52	20.0
Motril	36.793290	-3.505404	2 *Agave americana*, 2 signs	2	1	1	2	20	5	0	15	0	6/11/2018	13:09	22.2
Motril	36.772935	-3.510272	guard rails, 2 signs	1	1	0	0	1	1	0	0	0	6/11/2018	13:31	20.0
Motril	36.764188	-3.518781	guard rails, sign, 8 *Agave americana*	1	1	0	0	1	1	0	0	0	6/11/2018	13:46	20.0
Motril	36.747337	-3.527944	13 *Agave attenuata*, 11 *Aloe* sp., 3 *Yucca* sp.	0	0	0	0	0	0	0	0	0	6/11/2018	14:13	21.7
Motril	36.745007	-3.539276	3 *Agave americana*	1	1	0	1	1	1	0	0	0	6/11/2018	14:35	21.7
Motril	36.746718	-3.552001	1 *Austrocylindropuntia* sp.	1	0	1	3	30	3	2	25	0	6/11/2018	15:03	21.7
Motril	36.720498	-3.511516	4 *Agave* sp., 3 *Yucca* sp., bridge railing	0	0	0	0	0	0	0	0	0	6/11/2018	16:04	22.2
Motril	36.722157	-3.493401	4 *Agave americana*, 3 *Opuntia* sp.	1	1	0	1	0	0	0	0	0	6/11/2018	16:31	26.1
Motril	36.737565	-3.456293	22 *Agave americana*	1	0	1	1	2	2	0	0	0	6/11/2018	16:58	26.1
Murcia	37.826960	-1.205695	fences	0	0	0	0	0	0	0	0	0	6/12/2018	11:41	21.1
Murcia	37.831720	-1.218125	1 *Agave americana*	0	0	0	0	0	0	0	0	0	6/12/2018	11:58	21.1
Murcia	37.830980	-1.185529	1 *Agave americana*	0	0	0	0	0	0	0	0	0	6/12/2018	12:23	21.1
Murcia	37.827770	-1.162705	1 *Austrocylindropuntia* sp.	2	1	1	4	7	7	0	0	0	6/12/2018	12:39	26.7
Murcia	37.823620	-1.160626	1 *Austrocylindropuntia* sp.	5	2	3	(*)	85	69	16	0	0	6/12/2018	13:57	27.8
Murcia	37.835650	-1.154672	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/12/2018	16:55	29.4
Murcia	37.867120	-1.131624	1 *Agave americana*	1	0	1	9	11	11	0	0	0	6/12/2018	17:16	31.1
Murcia	37.869460	-1.133570	1 *Agave americana*	6	6	0	4	6	6	0	0	0	6/12/2018	17:55	31.1

Province or City	Latitude	Longitude	Web Substrate	Webs	Solitary Webs	Colonial Webs	Egg Sac Chains	Total Spiders	Females	Males	Juveniles	Commensals	Date	Time	Temperature (°C)
Murcia	37.868830	-1.132958	1 *Agave americana*	1	0	1	4	4	4	0	0	0	6/12/2018	18:32	29.4
Murcia	37.910140	-1.165033	1 *Agave americana*	0	0	0	0	0	0	0	0	0	6/12/2018	19:12	30.6
Murcia	37.935380	-1.141953	1 *Agave americana*	0	0	0	0	0	0	0	0	0	6/12/2018	19:37	27.8
Murcia	37.935230	-1.133280	1 *Agave americana*	0	0	0	0	0	0	0	0	0	6/12/2018	19:57	27.8
Murcia	37.946570	-1.107280	1 *Austrocylindropuntia* sp.	0	0	0	0	0	0	0	0	0	6/12/2018	20:27	22.8
Murcia	37.965170	-1.184643	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/13/2018	8:30	17.8
Murcia	37.959830	-1.177370	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/13/2018	8:47	21.7
Murcia	37.973650	-1.191692	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/13/2018	9:09	22.8
Murcia	37.984700	-1.166470	guard rails	0	0	0	0	0	0	0	0	0	6/13/2018	10:01	21.7
Murcia	37.983199	-1.164592	16 *Yucca* sp.	0	0	0	0	0	0	0	0	0	6/13/2018	12:10	21.7
Murcia	38.055429	-1.166955	1 scrub (dead), 3 *Yucca* sp.	4	2	2	2	12	12	0	0	0	6/13/2018	11:06	25.0
Murcia	38.026520	-1.124041	1 *Agave* sp., 1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/13/2018	11:45	27.8
Murcia	38.018880	-1.097766	1 *Agave americana*	0	0	0	0	0	0	0	0	0	6/13/2018	12:13	21.7
Murcia	38.033440	-1.081465	1 *Agave americana*	0	0	0	0	0	0	0	0	0	6/13/2018	12:55	25.0
Murcia	37.917810	-1.198926	1 *Cupressus* sp.	0	0	0	0	0	0	0	0	0	6/13/2018	13:38	23.3
Murcia	37.917260	-1.205022	1 *Austrocylindropuntia* sp.	1	0	1	5	80	80	(*)	(*)	(*)	6/13/2018	16:04	25.0
Murcia	37.925800	-1.200915	1 *Austrocylindropuntia* sp.	1	0	1	24	100	100	(*)	(*)	(*)	6/13/2018	16:00	25.0
Valencia	39.385700	-0.644715	fences	0	0	0	0	0	0	0	0	0	6/14/2018	9:50	18.9
Valencia	39.378559	-0.704493	1 *Agave americana* 'Marginata', 1 *Opuntia* sp.	1	0	1	1	24	15	8	0	1	6/14/2018	10:29	18.9
Valencia	39.367770	-0.660949	1 *Opuntia* sp.	1	0	1	0	20	8	7	0	5	6/14/2018	11:06	21.1
Valencia	39.419890	-0.687201	1 *Agave americana*	1	0	1	0	3	2	1	0	0	6/14/2018	11:37	21.1
Valencia	39.437110	-0.610747	1 *Austrocylindropuntia* sp.	0	0	0	0	0	0	0	0	0	6/14/2018	12:10	22.8
Valencia	39.470780	-0.545955	1 *Agave americana*	0	0	0	0	0	0	0	0	0	6/14/2018	12:43	25.0
Valencia	39.492960	-0.520833	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/14/2018	13:09	26.1
Valencia	39.492940	-0.511755	1 *Austrocylindropuntia* sp.	2	2	0	1	2	2	0	0	0	6/14/2018	13:28	26.1
Valencia	39.513710	-0.516819	1 *Agave americana* 'Marginata'	0	0	0	0	0	0	0	0	0	6/14/2018	14:02	27.8
Valencia	39.541430	-0.573151	1 *Opuntia* sp.	1	1	0	0	1	1	0	0	0	6/14/2018	14:27	25.6
Valencia	39.535156	-0.630554	1 *Austrocylindropuntia* sp.	0	0	0	0	0	0	0	0	0	6/14/2018	15:00	27.2
Valencia	39.538685	-0.641459	6 *Agave americana*	0	0	0	0	0	0	0	0	0	6/14/2018	15:19	27.2
Valencia	39.533710	-0.658294	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/14/2018	15:38	27.2
Valencia	39.508556	-0.679438	4 *Agave americana* 'Marginata'	10	7	3	1	22	15	4	1	2	6/14/2018	16:26	27.2
Valencia	39.468080	-0.708202	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/14/2018	16:57	26.7
Valencia	39.476740	-0.724921	1 *Agave americana*	3	3	0	0	3	3	0	0	0	6/14/2018	17:32	27.2
Valencia	39.470550	-0.726195	1 *Agave americana* 'Marginata'	2	1	1	1	5	5	0	0	0	6/14/2018	17:53	26.7
Valencia	39.576480	-0.433121	1 *Agave americana*	1	0	1	1	2	2	0	0	0	6/15/2018	8:30	18.3
Valencia	39.546830	-0.468353	1 *Yucca* sp.	6	1	5	0	38	23	1	4	10	6/15/2018	9:24	17.8
Valencia	39.423378	-0.648919	1 *Austrocylindropuntia* sp.	2	0	2	33	160	110	(*)	50	(*)	6/15/2018	10:07	20.6
Valencia	39.538700	-0.334025	1 *Agave* sp.	0	0	0	0	0	0	0	0	0	6/15/2018	12:10	26.1
Valencia	39.592120	-0.272511	1 *Yucca* sp.	0	0	0	0	0	0	0	0	0	6/15/2018	13:08	28.3
Valencia	39.613950	-0.294451	1 *Agave americana* 'Marginata', 1 *Yucca* sp.	5	2	3	2	22	19	1	2	0	6/15/2018	13:39	26.7
Valencia	39.625230	-0.331621	1 *Opuntia* sp.	0	0	0	0	0	0	0	0	0	6/15/2018	14:01	27.2
Valencia	39.628596	-0.327369	3 *Agave americana*	0	0	0	0	0	0	0	0	0	6/15/2018	14:11	27.2
Valencia	39.829393	-0.047338	11 *Agave americana*	5	3	2	11	46	23	2	0	21	6/15/2018	14:56	27.2

(*): Accurate counts were prevented by very large and/or inaccessible colonies owing to impenetrable spines

Appendix B.
Common substrates with frequency of associated *C. citricola* webs and spiders

		with Webs		with 1 to 2 Webs		with > 2 Webs	
	# Sites	#	%	#	%	#	%
Substrate	204	85	42	48	56	37	44
Agave sp.*	15	10	67	1	7	9	60
Agave americana	62	21	34	14	23	7	11
Agave americana 'Marginata'	25	12	48	6	24	6	24
Agave attenuata	10	5	50	1	10	4	40
Aloe sp.	4	1	25	1	25	0	0
Austrocylindropuntia sp.	22	15	68	10	45	5	23
Cupressus sp.	2	1	50	1	50	0	0
Opuntia sp.	66	31	47	15	23	16	24
Thuja sp.	2	1	50	1	50	0	0
Yucca sp.	24	11	46	6	25	5	21
signs	3	3	100	3	100	0	0
guard rails	17	4	24	3	18	1	6
bridge railing	1	0	0	0	0	0	0
fences	12	0	0	0	0	0	0
Substrate	204	82	40	21	26	61	74
Agave sp.*	15	10	67	1	7	9	60
Agave americana	62	20	32	6	10	14	23
Agave americana 'Marginata'	25	12	48	3	12	9	36
Agave attenuata	10	5	50	1	10	4	40
Aloe sp.	4	1	25	1	25	0	0
Austrocylindropuntia sp.	22	15	68	3	14	12	55
Cupressus sp.	2	1	50	1	50	0	0
Opuntia sp.	66	29	44	5	8	24	36
Thuja sp.	2	1	50	1	50	0	0
Yucca sp.	24	10	42	4	17	6	25
signs	3	3	100	2	67	1	33
guard rails	17	4	24	3	18	1	6
bridge railing	1	0	0	0	0	0	0
fences	12	0	0	0	0	0	0

* *Agave* sp. other than *A. americana*, *A. americana* 'Marginata', or *A. attenuata*