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Distribution and Ecology of Myrmecophilous Crickets in the Province of Granada (Spain)

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Abstract

Myrmecophily, broadly, refers to associations between certain organisms and ants. Among arthropods, one of the most specialized groups to live within ant nests is crickets of the genus *Myrmecophilus* Berthold, 1827. Worldwide distributed, the genus includes numerous species adapted to different hosts whose distribution and ecology have been scarcely studied in many regions. In the Iberian Peninsula, four species have been recorded, mainly from scattered locality records, while programmed samplings across ecosystems are lacking. In this context, this study documents, for the first time, the distribution of crickets of the genus *Myrmecophilus* in the province of Granada, Southeastern Spain, and describes their ecological preferences. Programmed sampling was carried out across different bioclimatic zones and habitat types, and a total of 1,156 ant nests of 19 genera were inspected, resulting in the recording of 78 cricket specimens, all assigned to the species *Myrmecophilus ochraceus* Fischer, 1853. The cricket was restricted to the thermo- and meso-Mediterranean zones and showed a marked preference for open grasslands. A high number of workers below stones and the presence of ant brood increased the likelihood of detecting the orthopteran. Considering all our records in Granada (more than 2000 ant nests inspected and 263 cricket specimens), only three out of 19 ant genera hosted crickets, including four new host ant species for *M. ochraceus*. Our results, together with previous studies, suggest that the only *Myrmecophylus* species inhabiting southern Iberia is *M. ochraceus*, which specializes on *Messor*, *Monomorium*, and *Tetramorium* species as main hosts. The possible implications of a geographical segregation of *Myrmecophilus* species between northern and southern Iberia are discussed.

Introduction

Ant nests can reach large sizes and significantly alter the environment in which they develop (Kovář et al., 2013; De Almeida et al., 2020). Ants are not only ecosystem engineers within their habitats (Kovář et al., 2013), but within their nests they build complex ecosystems that provide a variety of food resources, hygiene, stable temperature and humidity conditions, and protection through the colony's active defense. Ant nests are an ideal habitat for other organisms, known as myrmecophiles, a term derived from the Greek *myrme-* (ant) and *-philos* (lover) (Maggenti et al., 2017).

The biodiversity of myrmecophiles is estimated at around 100,000 species, including beetles, cockroaches, crickets, flies, parasitoid wasps, butterflies and moths, bristletails, springtails, spiders, pseudoscorpions, mites, and woodlice (Pierce et al., 2002; Dekoninck et al., 2007; Geiselhardt et al., 2007; Azevedo et al., 2015; Cassar et al., 2023; revised in Hölldobler & Kwapich, 2022). They exhibit different degrees of integration with ants and life strategies adapted to the nest environment, ranging from obligate relationships to more opportunistic associations. Notably, only 10% of these organisms are obligate myrmecophiles that are entirely dependent on ants for survival (reviewed in Cassar et al., 2023). Among these are certain beetles (*Cholovocera*

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Victor, 1838 and *Thorictus* Germar, 1834), the zygentoman *Neoasterolepisma* Mendes, 1988, springtails (*Cyphoderus* Nicolet, 1842), and orthopterans of the genus *Myrmecophilus* Berthold, 1827, among others (Cassar et al., 2023).

The ecological relationships that these organisms establish with ants can vary widely – from mutualism, as seen between ants and aphids (Offenberg, 2001), to commensalism and predation in springtails (Reznikova, 2001), and to parasitism, as in the case of *Myrmecophilus* crickets that steal food from the colony (Wetterer & Hugel, 2008; Stalling, 2010; Sanno et al., 2021; Hölldobler & Kwapich, 2022).

To live inside ant nests, myrmecophiles have developed a range of adaptations, which may be morphological, chemical, or a combination of both. Macrochelid mites, for example, have evolved specialized structures that allow them to act as ectoparasites or form phoretic relationships with ants, facilitating dispersal or access to new habitats (Azevedo et al., 2015). Other species have developed chemical adaptations, such as mimicking the cuticular hydrocarbons of ants, allowing them to deceive ants and avoid detection. This latter mechanism has been observed in *Myrmecophilus*, which acquires these hydrocarbons through direct contact with worker ants (Akino et al., 1996; Komatsu et al., 2013; Sanno et al., 2021; Hölldobler & Kwapich, 2022).

According to information gathered from the Orthopteran Species File database (Cigliano et al., 2025), the genus *Myrmecophilus* includes 64 species distributed worldwide (Hölldobler & Kwapich, 2022). Nine of these are found in Europe: *M. acervorum* (Panzer, [1799]), *M. balcanicus* Stalling, 2013, *M. baronii* Baccetti, 1966, *M. fuscus* Stalling, 2013, *M. hirticaudus* Fischer von Waldheim, 1846, *M. myrmecophilus* (Savi, 1819), *M. nonveilleri* Ingrisch & Pavićević, 2008, *M. ochraceus* Fischer, 1853 and *M. orientalis* Stalling, 2010. In a recent study of Mérel et al. (2025), two additional species cited in Europe – *M. gallicus* Stalling, 2017 and *M. aequispina* Chopard, 1923 –, are now considered ecotypes of *M. fuscus* and *M. myrmecophilus*, respectively, and should no longer be treated as valid species.

In Spain, only three species have been reported: *M. ochraceus* Fischer, 1853, *M. fuscus* Stalling, 2013, and *M. acervorum* (Panzer, [1799]) (Espadaler & Olmo-Vidal, 2011; Stalling, 2013a, 2015; Stalling et al., 2015). For the whole Iberian Peninsula, a fourth species, *M. myrmecophilus* (Savi, 1819), has recently been cited as the only record of the genus for Portugal, although based on a single old museum specimen dating back to 1841 whose locality of origin was not clearly registered by collectors, requiring further confirmation by field sampling (Rodríguez-Castilla & Stalling, 2025). Older records from Spain were assigned only to *M. acervorum* and *M. ochraceus*, but in 2013, the species *M. fuscus* was described (Stalling, 2013a), and most previous records of *M. acervorum* were subsequently reassigned to it (revised in Logachev, 2024). However, according to Iorgu et al. (2021) and Stalling et al. (2015), *M. acervorum* is still present in Spain and was found in Barcelona in 2012 by X. Espadaler (coll. T. Stalling).

Myrmecophilus typically lives in ant nests, although it has also been found in termite nests (Stalling, 2010; Temreshev, 2020). These crickets have been observed in a wide variety of habitats, ranging from forests far from the coast to open areas in coastal regions, often associated with anthropogenic environments (Espadaler & Olmo-Vidal, 2011; Stalling & Birrer, 2013; Franc et al., 2015; Stalling et al., 2015; Cassar et al., 2023; Kaczmarczyk-Ziemba et al., 2024; Cassar et al., 2025). A study in Slovakia highlights that the cricket *M. acervorum*, common in the region, prefers altitudes between 105 and 960 meters above sea level and avoids high mountain areas (Franc et al., 2015). Another study on *M. acervorum* reports that this species prefers areas with high humidity and, secondly, temperatures between 22 and 28 °C (Junker, 1997). However, these preferences may vary by region. In fact, *M. acervorum* has also been recorded in northern Europe (Denmark and Sweden), where winter temperatures drop below 0 °C and the climate is generally colder compared to other parts of the continent (Stalling et al., 2017).

In the Iberian Peninsula, the distribution of these crickets remains largely unknown, although several recent studies suggest there may be a segregation of these species between the northern half (*M. fuscus* and *M. acervorum*) and the southern half of the peninsula (*M. ochraceus*) (Espadaler & Olmo-Vidal, 2011; Stalling, 2013a; Stalling et al., 2015; Logachev, 2024). Even though up to date only *M. ochraceus* has been recorded in southern Spain, inhabiting nests of *Messor*, *Tetramorium* and *Monomorium* (reviewed in Logachev, 2024), no detailed studies or systematic samplings of myrmecophilous crickets have yet been conducted in any region of the Iberian Peninsula. In this context, the province of Granada represents an especially suitable area for such research, as the region hosts a wide variety of ecosystems from the seaside to high mountains, including dry and humid areas and, accordingly, a great diversity of ants (Ortiz & Tinaut, 1988; Jiménez & Tinaut, 1992; Tinaut et al., 1994; Tinaut et al., 2007). Other European species of the genus *Myrmecophilus* use a variety of ant species as hosts that also occur in Granada. For example, *M. acervorum* is usually associated with *Crematogaster*, *Formica*, *Lasius*, *Myrmica*, and *Tetramorium*; *M. baronii* with *Camponotus* and *Messor*; while species such as *M. myrmecophilus* and *M. orientalis* use *Pheidole* as hosts (Stalling, 2013b, 2017; Stalling et al., 2020; Iorgu et al., 2021; Cassar et al., 2023; Sandoval Cortés et al., 2024; Logachev, 2024). Additionally, the non-native species *M. quadrispinus* can be found parasitizing invasive ants of the genera *Pheidole*, *Nylanderia*, *Paratrechina*, and *Solenopsis*, which are widely distributed in coastal areas of the Mediterranean region (Hsu et al., 2020; Cassar et al., 2023). Therefore, it is likely that other *Myrmecophilus* species may find favorable conditions for establishment in Granada.

In this context, this work aims to study the presence and geographic distribution of Myrmecophilus species in the province of Granada through a programmed field sampling plan, identify host ant species, and characterize the factors explaining the crickets' presence. If the distribution of species of the genus in Spain is determined by ecological factors (hypothesis 1), we would expect to find several different species along the gradient of habitats and the variety of hosts present in Granada (prediction 1), each restricted to particular ecologies (prediction 2). For this purpose, sampling was carried out in three types of vegetation formations: grassland-shrubland, broadleaf forest, and coniferous forest; across three bioclimatic zones: thermo-, meso-, and supra-Mediterranean. Additionally, we will test whether the presence of crickets in nests is linked to the availability of ant brood below stones (hypothesis 2), as a proxy to evaluate the best conditions to search for these myrmecophiles.

Materials and Methods

Study Area

The study was conducted between 2024 and 2025 in the province of Granada, focusing on localities with representative habitats. These included three grassland-shrubland areas (including thyme scrub, needlegrass steppes, and esparto grasslands), three coniferous forests, and three broadleaf forests within each of the three bioclimatic zones (when available; see below) where the presence of these crickets is considered most likely: thermo-Mediterranean, meso-Mediterranean, and supra-Mediterranean (Fig 1). Fieldwork was conducted from February to June, coinciding with peak ant activity, when brood is transported to the surface beneath stones that function as heat reservoirs (Dean & Turner, 1991). Additionally, to account for temperature variations across the region, sampling began in coastal areas in February and gradually moved toward higher altitudes, concluding in the mountains.

Each bioclimatic zone is characterized by distinct climate and vegetation types (Pardo et al., 2016; Loidi, 2017; Arcos et al., 2023). Although these zones cannot be strictly defined by altitude alone, approximate elevation ranges were used based on the values proposed by Valle (1985) and Del Río Sánchez et al. (2019):

Thermo-Mediterranean bioclimatic zone. This zone is characterized by an average annual temperature of 17 °C to 19 °C and is typically found at elevations between 0 and 600 meters above sea level, near the coast. The climate has hot summers and mild winters, with frost being rare.

Meso-Mediterranean bioclimatic zone. With an average annual temperature between 13 °C and 17 °C, this zone is generally located at elevations between 600 and 1300 meters above sea level. Situated further inland, it experiences hot summers and colder winters, with frost occurring more frequently.

Supra-Mediterranean bioclimatic zone. This zone has an average annual temperature of 8 °C to 13 °C and occurs at higher elevations, typically between 1300 and 2050 meters above sea level.

Sampling was carried out in each bioclimatic zone with three replicates per habitat, focusing on three habitat types: grassland-shrubland, coniferous forests, and broadleaf

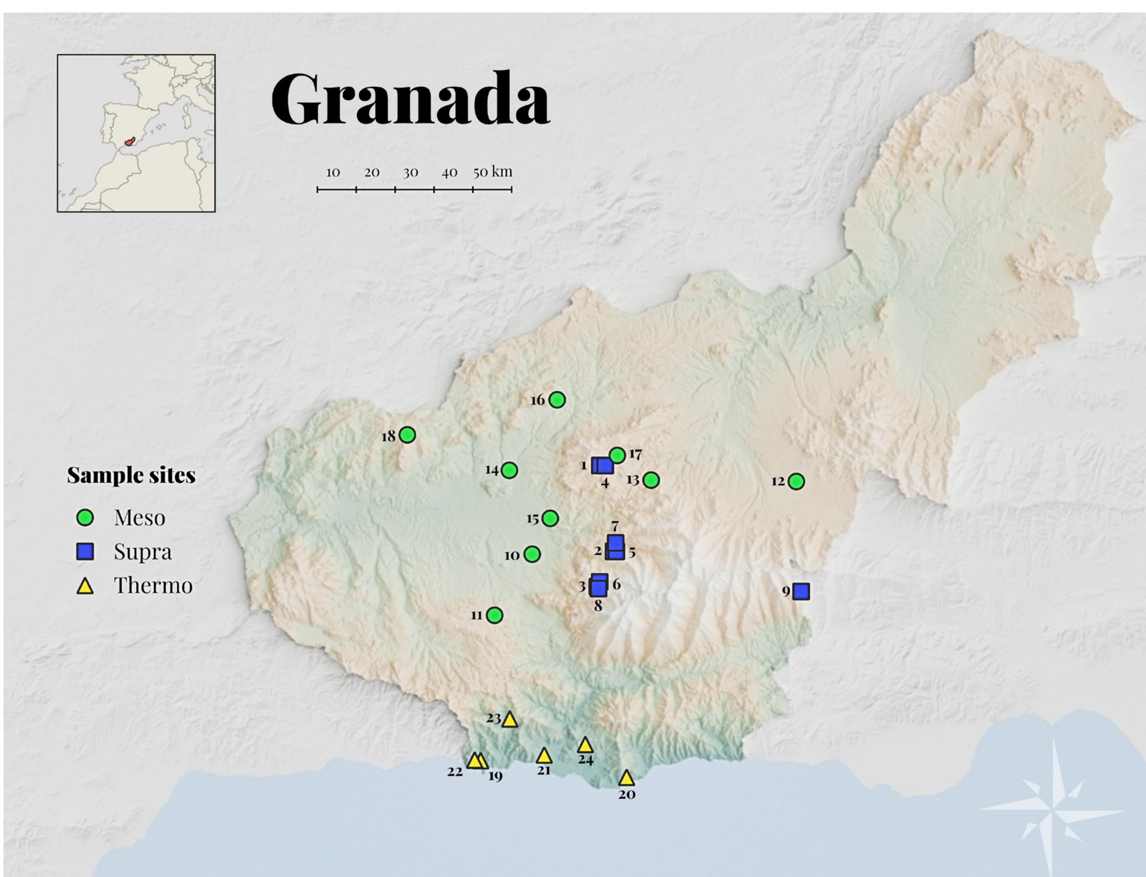

Fig 1. Map of sample sites. Numbers correspond to localities ID in Table 1.

forests (mainly *Quercus rotundifolia, Q. pyrenaica and Q. faginea* forests) – the most common biotopes in the province (Fig 1 and Table 1). However, the Granada coastal area lacks natural broadleaf forests, and this formation was therefore not sampled for the thermo-Mediterranean zone. The sampled localities were selected a priori using available information on the distribution of vegetal formations in each bioclimatic zone (Consejería de Medio Ambiente, 2015), satellite imagery (Google Earth), and our knowledge of forest conditions in the province of Granada. We chose localities that allowed straight linear transects within the desired homogeneous formation, staying at least 50 m from the formation limit, with transects of at least 200 m for grassland-shrubland and 1 km for forests. Localities of the same habitat and bioclimatic zone were selected for their distance (separated by a minimum of 15 km, and as far apart as possible given their availability in the central sector of the province). The sampling sites are scattered over 11000 km^2, include several formation types for each habitat category, and therefore represent the typical biotopes in the study area.

Table 1. The specific characteristics of each sampling locality.

BZ*	ID	Habitat type	Locality	Altitude (m a.s.l.)	Latitude	Longitude	Sampling date(s)	Nests examined	Description
Supra-	1	Grassland-shrubland	Huétor Santillán	1300	37.289142	-3.47148	May 6, 2025	66	Two grassland formations: grass-dominated and thyme-dominated
	2		El Dornajo	1750	37.130925	-3.439724	June 6, 2025	48	*Thymus* sp. scrubland
	3		Río Dílar	1750	37.065734	-3.476891	June 11, 2025	61	Steppe dominated by *Macrochloa tenacissima,* used for grazing
	4	Coniferous forest	Huétor Santillán	1300	37.288824	-3.458781	May 6, 2025	50	*Pinus pinaster* forest
	5		El Dornajo	1750	37.130717	-3.433135	June 6, 2025	30	*Pinus sylvestris* forest
	6		Cortijuela	1750	37.074551	-3.471752	June 11, 2025	61	*Pinus sylvestris* forest
	7	Broadleaf forest	Güéjar Sierra	1350	37.146526	-3.434695	May 10, 2025	51	*Quercus rotundifolia* forest
	8		Río Dílar	1750	37.062173	-3.474123	June 11, 2025	41	*Quercus pyrenaica* forest
	9		Sierra Nevada (Amería border)	1650	37.056898	-3.00574	June 14, 2025	46	*Quercus rotundifolia* forest
Meso-	10	Grassland-shrubland	Ogíjares	700	37.125698	-3.627639	April 14, 2024	20	Fallow grassland
	11		Padul	1000	37.012958	-3.714549	April 14, 2024	38	Sparse vegetation with *Macrochloa tenacissima* esparto grass and *Thymus* sp.
	12		Guadix	1100	37.259611	-3.016917	April 14, 2025	25	Semi-arid plain dominated by *Artemisia*
	13	Coniferous forest	La Peza	1200	37.262171	-3.352643	April 11, 2025	56	*Pinus pinaster* forest
	14		Cubillas Reservoir	650	37.280236	-3.680408	April 18, 2025	36	*Pinus halepensis* forest
	15		Cartuja	900	37.191727	-3.585971	April 26, 2025	31	*Pinus halepensis* forest
	16	Broadleaf forest	Hotel de la Nava (Iznalloz)	900	37.409846	-3.569879	May 12, 2025	34	*Quercus rotundifolia* forest
	17		Venta del Molinillo	1200	37.307549	-3.430815	May 20, 2025	41	*Quercus rotundifolia* forest
	18		Íllora	1050	37.345512	-3.916372	May 25, 2025	64	*Quercus rotundifolia* forest
Thermo-	19	Grassland-shrubland	La Herradura	50	36.744078	-3.746686	Feb 6, 2025	68	Grassland with *Retama* shrubs
	20		Los Gualchos	250	36.713932	-3.409852	February 10, 2025	73	Shrubland with *Thymus* sp., *Salvia* sp., *Rosmarinus* sp. and *Macrochloa tenacissima*
	21		Salobreña	400	36.754167	-3.6	February 16, 2025	45	Fallow grassland
	22	Coniferous forest	Cerro Gordo	130	36.745186	-3.76059	April 5, 2025	58	*Pinus halepensis* forest
	23		Otívar	450	36.821433	-3.679399	April 5, 2025	49	*Pinus halepensis* forest
	24		Motril	200	36.774191	-3.504742	April 13, 2025	64	*Pinus halepensis* forest

BZ* - bioclimatic zone: supra-Mediterranean, meso-Mediterranean and thermo-Mediterranean

Table 1 includes the specific characteristics and location of each sampling locality.

The maps showing the sampling points and cricket distribution (Figs 1, 3) were created using QGIS Geographic Information System ver. 4.2 (QGIS Development Team, 2026) and Blender ver. 5.2.0 (Blender Development Team, 2026).

Sampling methodology

Sampling involved walking in a straight line through each vegetation type, avoiding the formation border, and lifting stones along the transect to check whether they harbored ant colonies. Transects did not follow existing paths but crossed the formation, maintaining a fixed direction whenever vegetation density allowed progress. Each sampling was carried out by 1–3 people simultaneously, using different progress lines, with the participation of Matvey Logachev, Manuel Martín-Vivaldi, Nerea Megías-Valero, and Mathias Welz-Sol. All stones (of every size) found in the progress line (in a band of about five meters per side), were examined if they appeared suitable as potential ant nesting sites, such as stones partially embedded in the soil, in direct contact with the ground, or providing cavities underneath. Our sampling method is therefore similar to the "Hand Collection Method" (HCM) in transects used in some studies on ant communities (Salata et al., 2020), but our collection was centered on nests below stones instead of ant individuals, and the effort is standardized by researcher/sampled localities by considering the number of nests found. Given that our data of interest are not densities or population sizes, but the proportion of nests parasitized by crickets, the sampling effort was set to get a minimum number of nests within each locality to obtain representative samples per site. Given that we have only accessed "within nest spaces" found below stones, we have a biased sample towards ant species with sublapidicolous habits and cannot discard the presence of myrmecophilous crickets using ant hosts breeding in other substrates.

All stones, whether they contained a nest or not, were carefully returned to their original position after recording the relevant information. When a nest was found under a stone, its contents were thoroughly inspected, starting with a search for crickets and followed by the documentation of colony characteristics. Typically, these crickets remain motionless or blend in with the brood that clings to the underside of the stone or the substrate beneath it (personal observation). To increase detection chances, the team first observed the portion of the colony that remained on the substrate before the ants had a chance to retreat into their tunnels. Then the lifted stone was examined for crickets. In both cases, observations continued for several minutes, during which worker ants often attempted to relocate the brood. Most crickets were found clinging to the underside of the stone. When crickets were detected, at least one individual was collected using an entomological aspirator for proper identification. Whenever possible, a male adult, a female adult, and a juvenile were captured if multiple individuals were present. The team counted any additional crickets found in the nest but left them in the colony.

In addition to recording the presence, number, and type of crickets (juvenile or adult, and sex in the case of adults), the team estimated the number of visible workers and noted the presence or absence of brood under the stone. The ant species was identified at least to genus level. To do this, a couple of workers were collected and either identified in the field using a hand lens or later in the laboratory by Matvey Logachev.

Sampling was conducted between two and four hours after sunrise, a time when the stones had already been warmed by the sun, creating a suitable microclimate to incubate the brood without overheating the nest. In forested areas, where stones receive less direct sunlight, sampling was occasionally extended to a broader time, always ensuring that a significant portion of the colonies still had brood under the stones.

To ensure that conditions were suitable for detecting crickets during the planned sampling dates, activity checks were performed in nests where *Myrmecophilus* presence had previously been confirmed. If cricket activity was observed in these reference nests, study sites were then visited. A reference nest used for these checks was a *Messor barbarus* colony located in Otura (37.089795 N, -3.624650 E).

The duration of each sampling session was determined in the field based on the persistence of favorable conditions and with the aim of inspecting a large number of nests of typical ant species for each biotope. The initial goal was to locate at least five colonies of *Tetramorium* sp., *Messor* sp., or *Monomorium subopacum* (in coastal areas), since these three ant species are the usual hosts of the cricket *Myrmecophilus ochraceus*, the only ant cricket species recorded so far in southern Spain (Espadaler & Olmo-Vidal, 2011; Logachev, 2024). In all grassland-shrubland samplings, this minimum number (n = 5) of target nests was exceeded. In contrast, these ant species were generally absent or only present in the periphery and open areas of forests, so in forest habitats the decision to end the sampling session was based on the number of nests found in those areas (minimum 30 nests).

In total, 1,156 ant nests were examined, and 78 individuals of *Myrmecophilus* crickets were recorded across the province of Granada during the programmed surveys. In addition to the data collected during fieldwork, records and collections from the University of Granada (https://ccz.ugr.es/), gathered between 2018 and 2020 by Manuel Martín-Vivaldi and Víctor Escribano, were also analyzed. The total number of records was 263 crickets. Some *Myrmecophilus* specimens were preserved, while others existed only as database records of the authors without preserved material. Most of the crickets collected in this study are deposited in the collections of the Zoology Department at the University of Granada.

Identification of specimens

Adult crickets were identified to species level using available literature and by comparing photos and descriptions of other *Myrmecophilus* cricket species (Fischer, 1853; Stalling & Birrer, 2013; Stalling, 2013a, 2016, 2024). The main distinguishing features among the different European species include coloration, pubescence and hair density on the sternites and head, the morphology of the female subgenital plate, and the size of the spines on the hind legs.

Identifications were carried out under a stereomicroscope using both mounted specimens (n = 20) and unmounted ones (n > 50). However, since some morphological and coloration traits also differ clearly between the most common species (for example, *Myrmecophilus ochraceus* has “bushy” hairs on the head and only one pale band on the thorax; *M. acervorum* has two pale bands; *M. fuscus* shows one pale band per segment; while species like *M. hirticaudus* lack them at all), the remaining specimens found in association with the same type of ants were assigned to the same species without microscopic examination, based on color patterns.

Identifying juveniles in this group is more challenging, as no guides or studies describe the characteristics of juvenile *Myrmecophilus* specimens, though Stalling & Birrer (2013) considered that the body-surface diagnostic criteria of adults are also valid for nymphs. To properly identify juveniles, it was first assumed that those present in nests where adults were also found would belong to the same species if they shared certain morphological traits typical of the adults. In cases where only juveniles were found in the colony, their morphology was compared with that of these “reference juveniles” in order to assign them to a certain cricket species. The photos used to describe the features of the examined crickets were taken using a Sony A6000 camera equipped with Plan APO 10X and Nikon Mplan 40X ELWD microscope objectives. For the focus stacking technique, an electronic macro rail with a resolution of less than 1 µm per photo was used. The scale was obtained by photographing a calibrated slide with 0.01 mm divisions at the same magnification as the specimen photos. The photo of the mandible was taken using an OPPO A74 phone attached to an Olympus BX51 fluorescence microscope. The scale for that image was obtained using an Olympus DP72 camera (Olympus, Shinjuku, Tokyo, Japan) installed on the same microscope.

To identify the ants based on morphological criteria, the key by Arcos & Garcia (2023) was used.

Statistical methods

Statistical analyses were conducted in R (ver. 4.5.2) (Posit team, 2026). Only data collected during programmed samplings were used in the analysis.

We performed one programmed sampling per locality, and only two sites were sampled in 2024 (Table 1), while most sampling occurred in 2025. Because habitat types were not balanced between 2024 and 2025, including year as a factor to control for possible year effects in our analyses was not appropriate. To check whether there were differences between years in the probability of detecting crickets, we used five localities with known presence of them that were visited in 2024-2025 (Ogíjares, La Herradura, Cartuja, Otura) or 2025-2026 (Salobreña) either as reference sites for cricket activity or for catching specimens for other research objectives. In all visits to these five localities in spring in both years, we detected crickets below their stones. Moreover, comparing between consecutive years the proportion of nests found with crickets for the three confirmed host genera (*Messor, Tetramorium* and *Monomorium*) paired by locality, we found no significant difference between years (Wilcoxon Matched-pair test, n = 5, z = 0.405, p = 0.686; proportions for the same locality averaged for the available visits each year). These results show that year of sampling does not explain the probability of detecting crickets in the localities and, therefore, that year effects did not confound our analyses of the factors of interest.

To evaluate the effect of the bioclimatic zone on cricket presence in nests, a generalized linear model (GLZ) with a binomial distribution was fitted using the full dataset obtained from programmed sampling. The null model (no predictors) was compared with a model that included the bioclimatic zone as an explanatory variable with fixed effects, using ANOVA with a Chi-square test to assess model improvement. The response variable was binary (“yes” = cricket present, “no” = cricket absent). Additionally, the significance of each model coefficient was examined to determine whether any bioclimatic zone significantly influenced the probability of cricket presence. The meso-Mediterranean zone served as the reference level because it does not exhibit extreme conditions in terms of altitude, temperature, pressure, or other ecological factors, unlike the thermo- and supra-Mediterranean zones. The effects of the supra-Mediterranean and thermo-Mediterranean zones were evaluated in relation to cricket presence.

The same dataset was used to analyze the effect of habitat type (grassland-shrub, coniferous and broadleaf forest) on cricket presence by fitting additional generalized linear models (GLZs) with a binomial error distribution, testing whether habitat type significantly influenced the probability of cricket presence. A null model was compared with a model including habitat type as a predictor, using deviance analysis through ANOVA with a Chi-square test. Furthermore, the statistical influence of each habitat type was assessed relative to the reference category (grassland-shrub) through model coefficient estimation, standard errors, and associated significance levels. Positive coefficient values indicate a higher probability of cricket presence compared to the intercept factor, whereas negative values indicate a lower probability.

To determine whether the ant host genus significantly affected the presence of myrmecophilous crickets, a GLZ with binomial distribution was fitted using “genus” as the explanatory variable. The genus factor included the categories *Messor*, *Tetramorium*, *Monomorium*, and “other”, and was represented only by the genera detected during sampling in areas where the cricket was observed. This model was compared to a null model via deviance analysis using ANOVA with a Chi-square test.

To assess whether the number of workers and the presence of brood under the stone influenced the presence of myrmecophilous crickets, an analysis was conducted restricted to areas where *M. ochraceus* was observed and considering only the ant genera in which crickets were detected. From these data, a GLZ with a binomial distribution was fitted. A null model was compared to a model that included the ant host genus, worker number (log-transformed to approximate a normal distribution), and brood presence (yes/no) as explanatory variables. The comparison was performed using deviance analysis (ANOVA with a Chi-square test).

Results

In the programmed surveys conducted between 2024 and 2025, myrmecophilous crickets were found exclusively in the thermo-Mediterranean and meso-Mediterranean bioclimatic zones, at altitudes ranging from 50 to 950 meters (the maximum altitude for localities with crickets out of surveys was 1050 m) above sea level (Fig 2). In the thermo-Mediterranean zone, their presence was recorded in grasslands in La Herradura and Salobreña, as well as in a shrubland area of Los Gualchos. In the meso-Mediterranean zone, crickets were found exclusively in a grassland in Ogíjares. In both zones (resuming all data, not only the surveys), crickets were detected only in nests of the ant genera *Tetramorium* (only juveniles): *T.* gr. *caespitum* (2 nests), *T. biskrense* (3 nests), *T. forte* (4), *T. semilaeve* (5); *Messor* (both adults and juveniles): *M. barbarus* (39), *M. bouvieri* (14), *M. erwini* (1), *M. ibericus* (1), and, in coastal areas, in *Monomorium subopacum* (only juveniles, 15 nests) (Fig 2). During the surveys, no crickets were detected in association with the following ant genera found (number of nests inspected shown in parentheses): *Aphaenogaster* (74), *Bothriomyrmex* (5), *Camponotus* (168), *Cataglyphis* (12), *Crematogaster* (60), *Formica* (93), *Goniomma* (1), *Iberoformica* (7), *Lasius* (97), *Oxyopomyrmex* (3), *Pheidole* (106), *Plagiolepis* (212), *Proformica* (1), *Solenopsis* (5), *Tapinoma* (59), and *Temnothorax* (42). See Annex I for details.

Although the crickets were also observed in grasslands of Guadix, Cartuja, and Otura, as well as on the outskirts of the pine forest in Motril (always in *Messor* and *Tetramorium* nests), these localities were not part of the planned sampling design. Therefore, they are excluded from the analyses, and their presence is shown only on the general map displaying all detection points recorded in the province (Fig 3), and in Fig 7 showing the phenology of cricket detection. This map (Fig 3) also includes data from previous surveys conducted between 2018 and 2020, as well as from the programmed surveys carried out in 2024–2025. Detailed data for each observation can be found in Annex II.

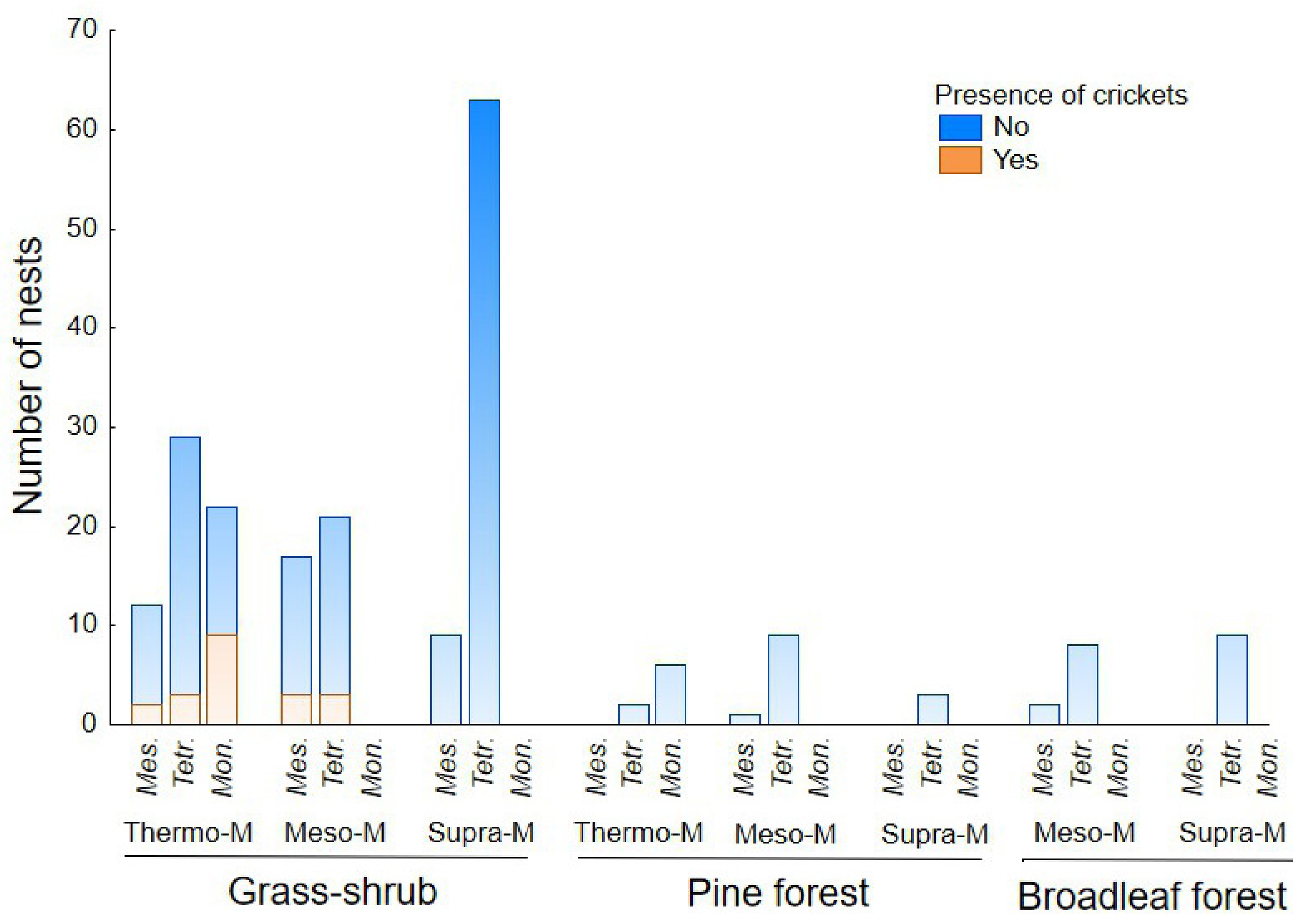

Fig 2. Number of nests found in the different types of habitats and bioclimatic zones sampled, for the three ant genera parasitized by *Myrmecophilus* crickets in the Granada province (southern Spain): *Messor* (*Mes.*), *Tetramorium* (*Tetr.*), *Monomorium* (*Mon.*).

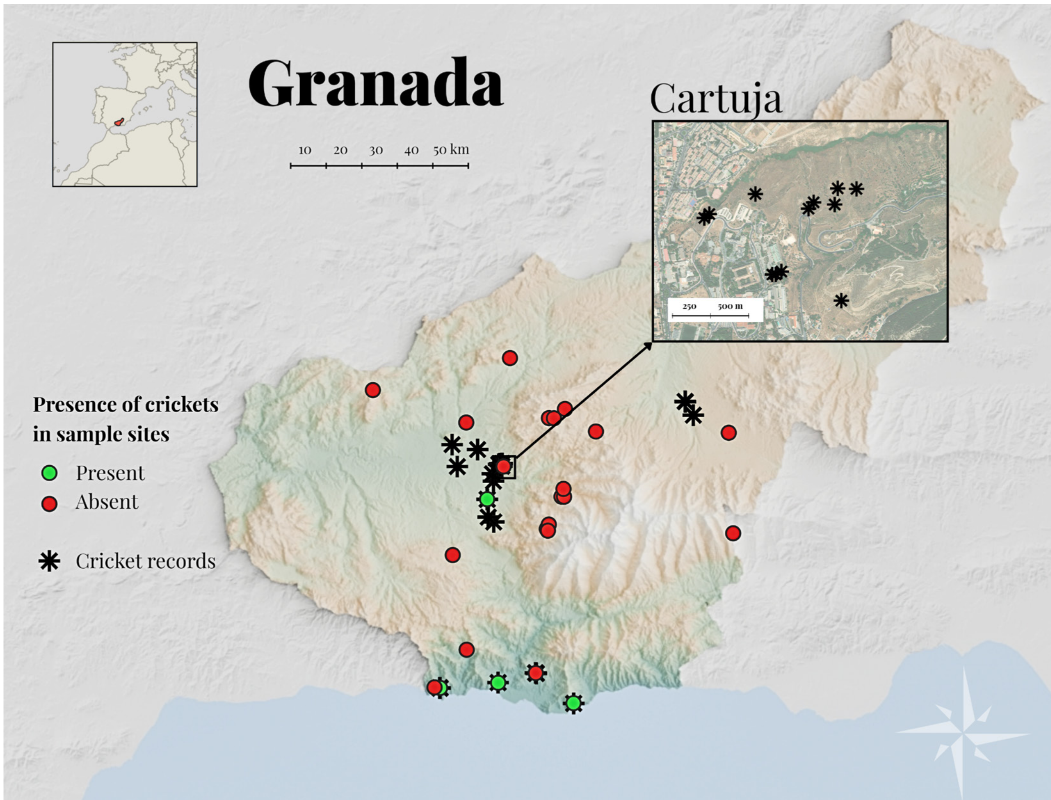

Fig 3. Map of localities with observations of the cricket *M. ochraceus* in Granada, 2018–2025. The aerial picture shows the distribution of occupied nests in a particular meso-Mediterranean grassland close to the city of Granada.

All the adult crickets belong to the species *Myrmecophilus ochraceus*. *M. ochraceus* is a small cricket, typically less than 5 mm in length. The adult's body is generally ochre-colored and features a characteristic pale band on the thoracic region, along with dense and well-developed pubescence (Fig 4B). Erect hairs are rare, except on the frontal region of the head, where they are noticeably longer and more abundant (Fig 4C). The female's subgenital plate is straight and slightly rounded at its distal end (Fig 5A).

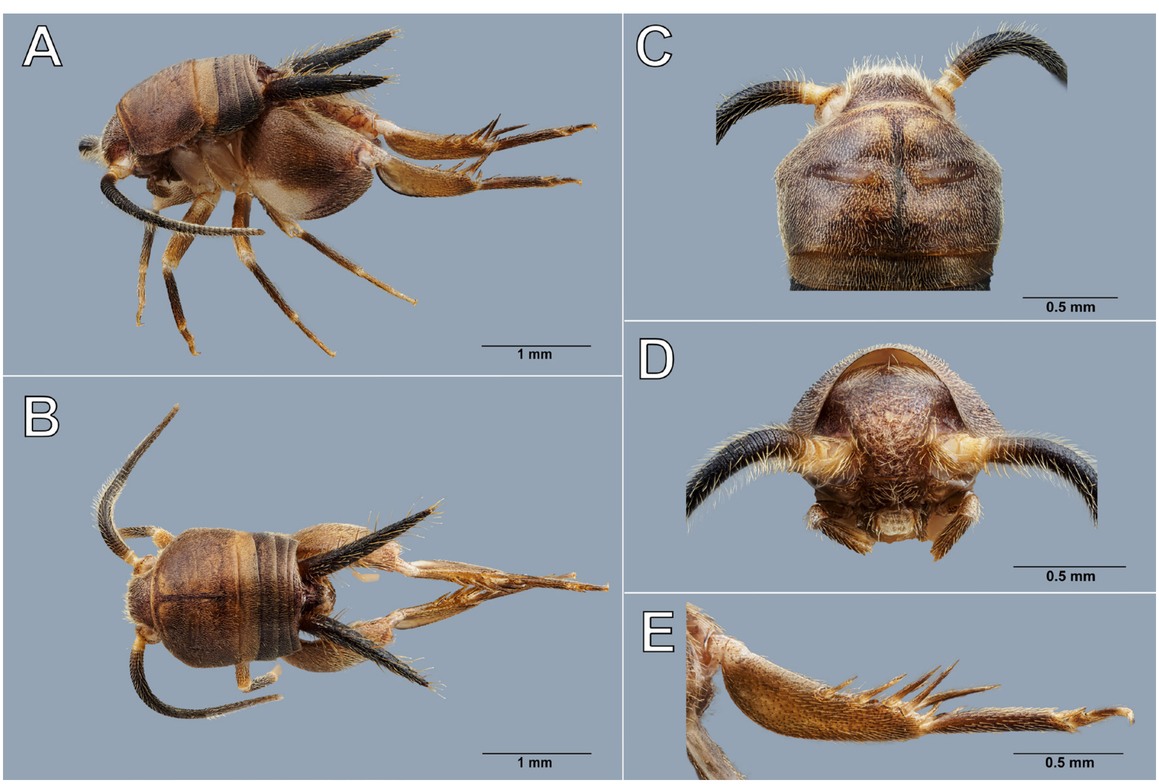

Fig 4. Aspect of *Myrmecophilus ochraceus* adult male from Otura. A. lateral view; B. dorsal view; C. hair density on the body and dense hairs on the head; D. frontal view; E. hind leg. Photos made by Paco Alarcón. Collection ID: 23407-CG.

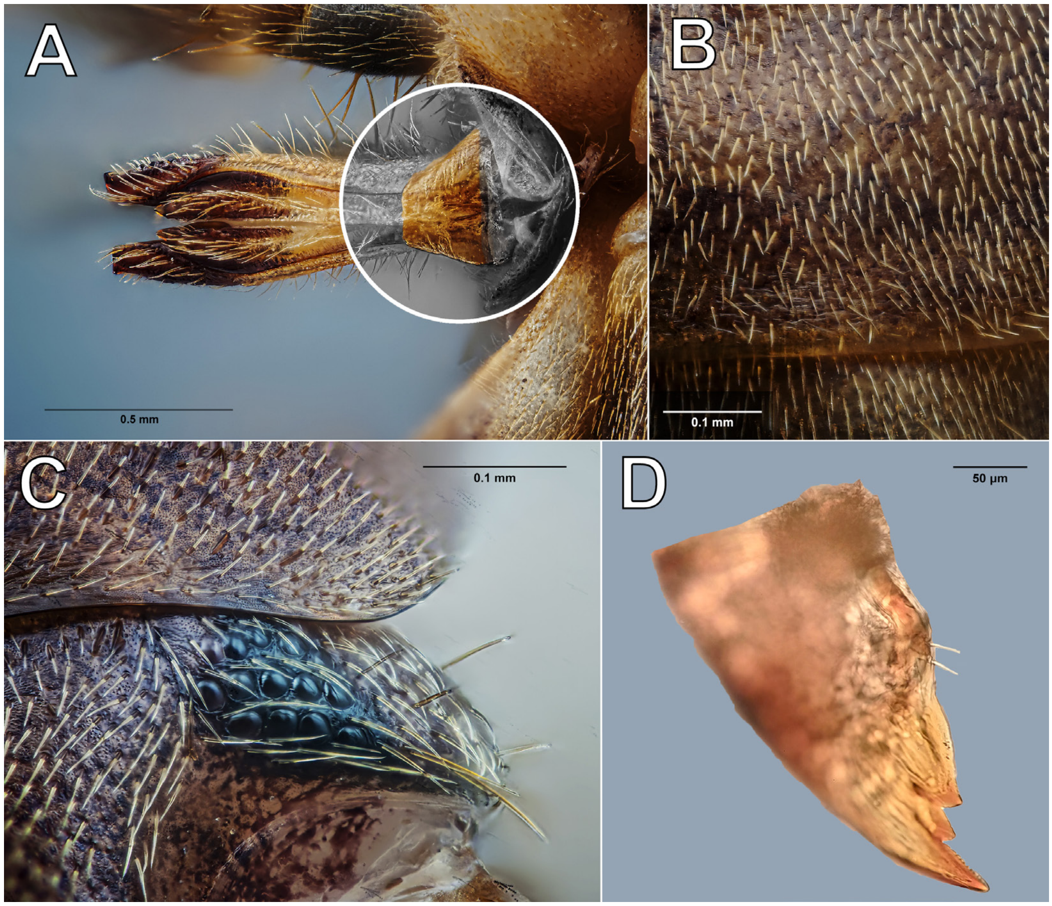

Fig 5. Aspect of *Myrmecophilus ochraceus* adult female from Otura. A. Subgenital plate; B. Body surface of the sternites showing hair density; C. Eye; D. Mandible. Photos A, B, and C made by Paco Alarcón; Photo D made by Matvey Logachev. Collection ID: 23405-CG.

All the juvenile specimens collected showed a morphology similar to those examined in nests where adult *M. ochraceus* were present. These reference juveniles shared the typical morphological characteristics of the adults of this species. Therefore, all the juveniles analyzed are considered to belong to this same species. Juveniles in the so-called "phase 2" retain the same general morphology as the adults, although they have a darker color and a distinctive white band on the second thoracic segment (Fig 6B). On the other hand, individuals in "phase 1" are noticeably paler, also with developed pubescence, although the dense hairs on the head are difficult to distinguish (Fig 6A). This is because, in this phase, their length is similar to that of other body hairs and their density on the head does not stand out, unlike in more advanced phases where

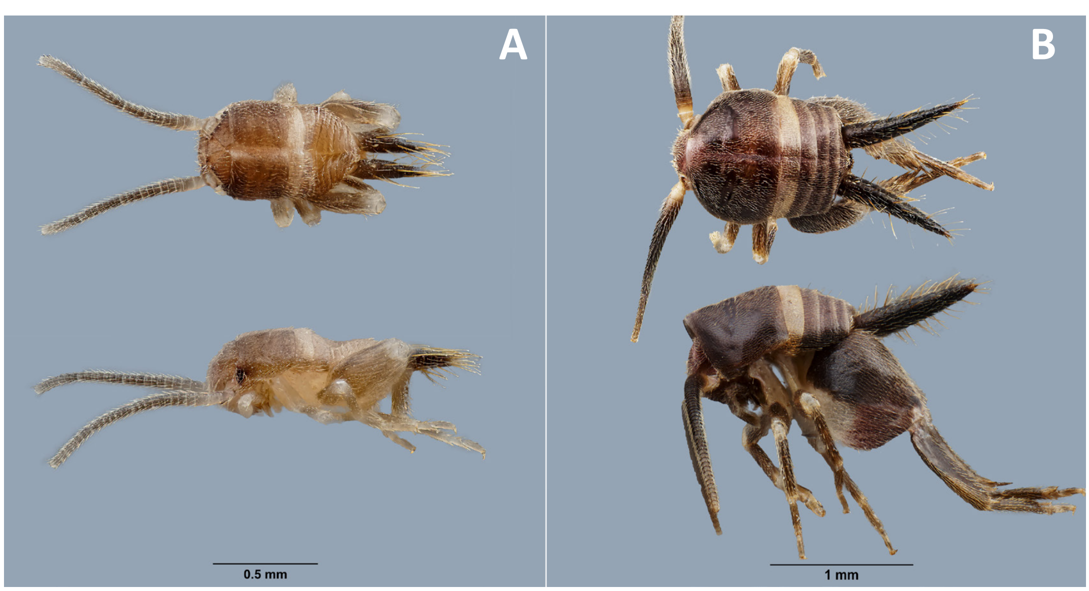

Fig 6. Juvenile stages of *Myrmecophilus* crickets found in nests with adults of the species *Myrmecophilus ochraceus,* Cartuja, Granada city: A. Juvenile "phase 1"; B. Juvenile "phase 2." Photos made by Paco Alarcón. Collection ID: 23404-CG and 23406-CG.

the frontal hairs are clearly denser and longer. In all phases, the ventral region of the body is lighter than the dorsal side. It is also worth noting that both juveniles in "phase 2" and adults have a characteristic white spot on the femur (Fig 4A, 6B). The teeth of the mandibles, both in adult crickets and in "phase 2" juveniles, are well developed (Fig 5D).

According to records from 2018–2025, crickets can be found below stones in the meso-Mediterranean and thermo-Mediterranean zones throughout the year, although most captures were concentrated in late autumn, late winter, and spring (Fig 7). In the supra-Mediterranean zone, crickets have never been observed.

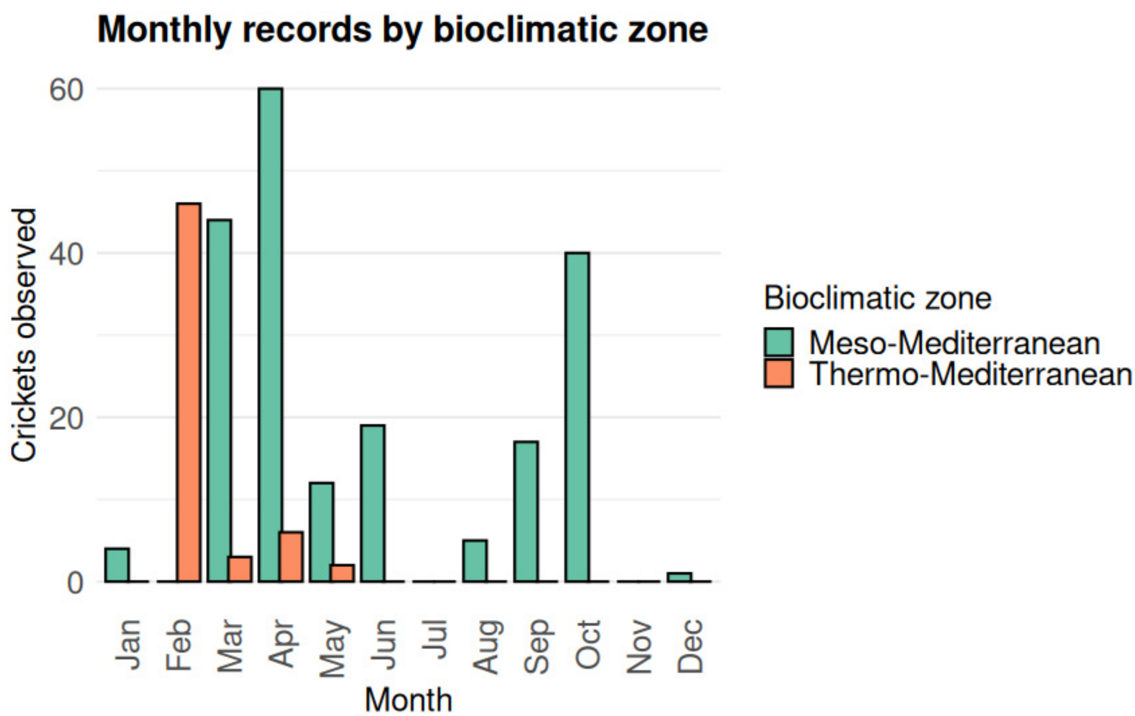

Fig 7. Monthly records of *Myrmecophilus ochraceus* by bioclimatic zones. Information includes all our records since 2018. Sampling effort was not consistent across different months.

Factors explaining the presence of Myrmecophilus ochraceus

The bioclimatic zone in which the sampling was conducted had a significant effect on the probability of detecting *Myrmecophilus ochraceus* in ant nests (GLZ with binomial distribution, deviance = 23.228, df = 2, $p < 0.00001$). The probability of detection was higher in the thermo-Mediterranean zone (coefficient = 0.8356, p = 0.0907, 3.92% of nests, N=357) than in the meso-Mediterranean zone, where cricket presence was lower (coefficient = –4.0342, $p < 0.00001$, 1.74% of nests, N=345). In contrast, in the supra-Mediterranean zone (N=454 nests), the cricket was not detected at any sampled site (coefficient = –17.5318, p = 0.9898, Fig 2).

The deviance analysis showed that habitat type also had a significant influence on the presence of the cricket (deviance = 38.843, df = 2, $p < 0.00001$, Fig 2). In the fitted model, the reference habitat was shrubland-grassland (coefficient = −3.054, standard error = 0.2288, $p < 0.0001$), where all cricket observations were recorded. The coefficients for the habitats "coniferous forest" and "broadleaf forest" were −18.51, with extremely high standard errors (1401.59 and 1756.4, respectively), and p = 0.99 in both cases. These results indicate that the most favorable habitat for *M. ochraceus* was shrubland-grassland.

The analysis of the importance of the ant genus showed a significant effect on the presence of the myrmecophilous cricket (deviance = 47.573, df = 3, $p < 0.001$). This indicates that the variable "genus" significantly improves the model fit compared to the null model, suggesting a statistically significant association between the ant genus and the probability of finding the cricket. As observed in field data, the cricket was recorded only in nests of the genera *Messor*, *Tetramorium*, and *Monomorium*.

Considering only the nests of the three parasitized genera in the localities with crickets, there were significant effects of ant genus, number of workers, and the presence of brood on the probability of cricket presence (GLZ with binomial distribution, deviance = 30.418, df = 4, $p < 0.0001$). Both the number of workers and presence of brood showed a significant positive association with cricket presence (Colony size: coefficient = 1.11, standard error = 0.339, p =0.001; presence of brood: coefficient = 3.126, standard error = 1.403, p = 0.0259, N=75, Fig 8). In contrast, compared with *Messor* nests, the probability of cricket occurrence was lower in *Monomorium* and *Tetramorium* nests (both coefficient ~ -3.5, standard error ~ 1.5, p = 0.02 in *Tetramorium* and 0.018 in *Monomorium*).

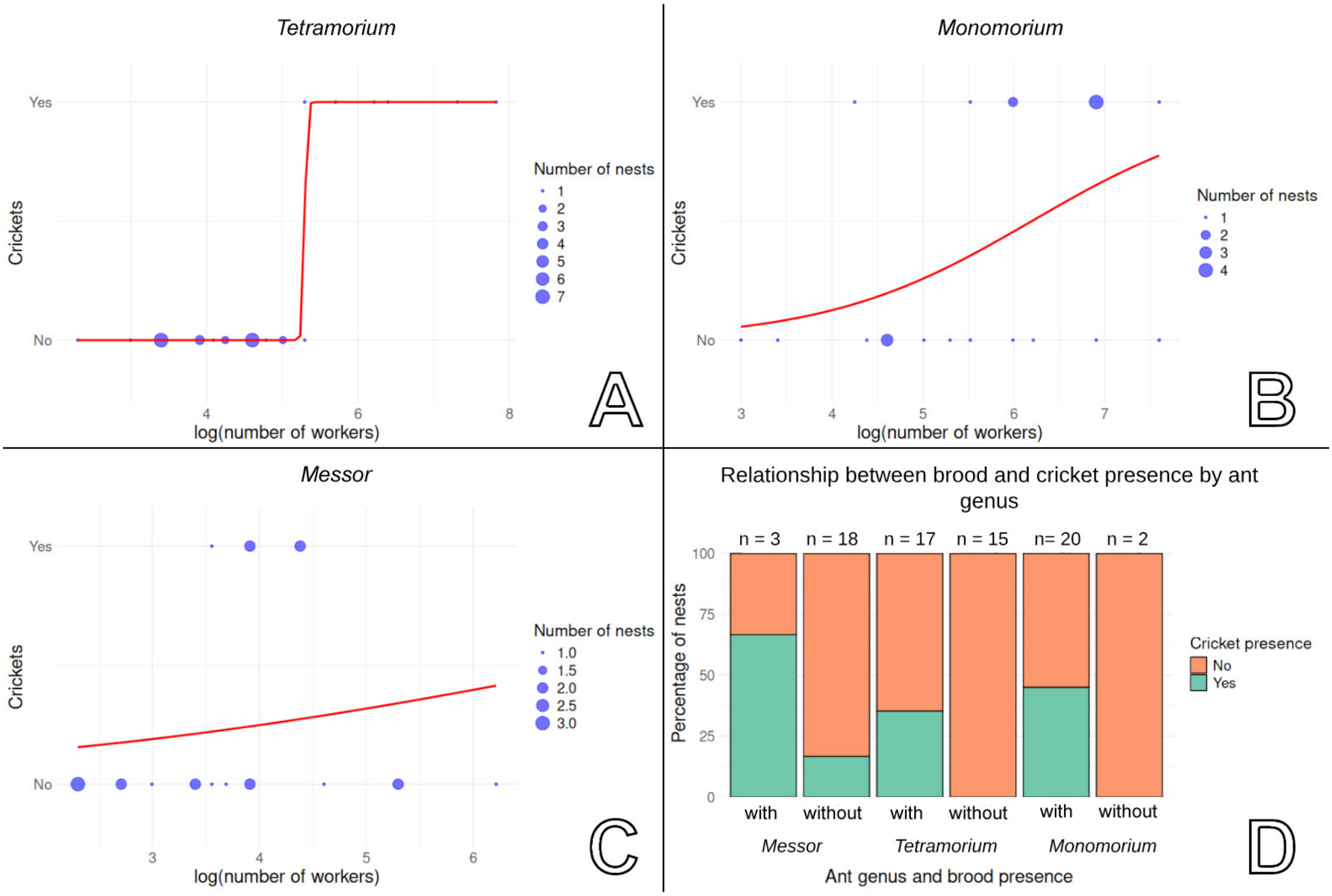

Fig 8. Factors explaining presence of *Myrmecophilus ochraceus* in ant nests for the genera used by this species in Granada. Relationship between the logarithm of number of workers under the stone and the presence of the cricket for *Tetramorium* (A), *Monomorium* (B), and *Messor* (C). D – Relationship between the presence of brood in the nest and the presence of crickets.

Discussion

After programmed sampling of ant nests in a variety of habitats and three bioclimatic zones, the diversity of crickets of the genus *Myrmecophilus* in the province of Granada (Southeastern Spain), so far, contrary to our expectations (prediction 1), seems to be restricted to a single species: *M. ochraceus*. Despite other European species being distributed in central and northeastern Spain (*M. fuscus*) and in northeastern Spain (*M. acervorum*) (Espadaler & Olmo Vidal, 2011; Stalling et al., 2015), the available information from the southern half of the Iberian Peninsula (this study and previous information reviewed in Espadaler & Olmo Vidal (2011)) suggests a segregation in the areas occupied by these two species and *M. ochraceus*. Such segregation may suggest a paleo-biogeographical origin of the distribution of these crickets associated with the north-south division of the distribution of ants in Iberia (Tinaut & Ruano, 2021). The known hosts of *M. fuscus* in Spain are mainly *Lasius* (several nests of each of four *Lasius* species as hosts in Mallorca, Barcelona and Madrid) with three additional sites in *Formica cunicularia, Crematogaster scutellaris,* and *Camponotus lateralis* (one parasitized nest for each species in Tarragona) (Stalling 2013; Stalling et al., 2015). The genera *Lasius* and *Formica* are preferentially distributed in the northern Iberian Peninsula and belong to the same ant group (N + T chorological categories), which is widely distributed across the northern half of Iberia (Tinaut & Ruano, 2021). This group includes species shared with the Western Palaearctic northern fauna and reflects the biogeographic connection between the Iberian ant fauna and the northern Palaearctic region (Tinaut & Ruano, 2021). On the other hand, *M. ochraceus* crickets were frequent within nests of *Tetramorium, Monomorium* and *Messor*; however, adults were exclusively found in species of the genus *Messor*. This result suggests (see also Hölldobler & Kwapich, 2022) that *M. ochraceus* depends mainly on *Messor* hosts to close its breeding cycle. *Messor* are typical inhabitants of grasslands in arid environments, which mainly colonized Iberia from North Africa (Juvé et al., 2025) and which are included among the species characterizing the connection with the southern Palaearctic ant fauna (Tinaut & Ruano, 2021). A similar geographic trajectory associated with the history of its host has been shown for another specialized myrmecophile – the beetle *Paussus favieri* Fairmaire, 1851 (Carabidae, Paussinae) and its host ant *Pheidole pallidula* (Bergamaschi et al., 2025). Given that *M. fuscus* is considered very closely related to *M. acervorum* (Stalling, 2013a) and this last species is the one with the largest distribution range across northern European countries, after expansion from a Balcanic refuge (Kaczmarczyk-Ziemba et al., 2024), the apparent segregated distribution of *Myrmecophilus* species in Spain could be related to the historical geographical origins of the hosts with which these parasites have co-evolved. Further studies completing the information about the geographic range of *Myrmecophilus* species/hosts in Spain, as well the position of *M. ochraceus* in the phylogenetic tree of the species of the genus, are needed to contrast this possibility.

Myrmecophilus ochraceus was common in the province of Granada but restricted to nests of ants from the genera *Messor*, *Tetramorium*, and *Monomorium* found in grasslands-shrublands in the thermo and mesomediterranean zones, in accordance with our prediction of ecological specialization of *Myrmecophilus* species (prediction 2). In several of the localities (both in those studied during programmed surveys or in others intensely searched between 2018 and 2025), the prevalence of the cricket was very high with 50-75% of available *Messor* and *Tetramorium* nests infested (Otura, Ogíjares, Cartuja, Guadix for example). The absence of the species in forested environments can be explained by the preference of its typical host species for open habitats (Lapeva-Gjonova et al., 2022; Arcos & Garcia, 2023). Although these ants are also abundant in open shrubland areas, not all such habitats hosted cricket specimens. For example, in several sampled shrublands with scattered vegetation, such as those in Guadix, or Padul, *Messor* and *Tetramorium* were common, but *Myrmecophilus ochraceus* was not detected. Interestingly, in Guadix, the cricket was later observed but only in areas with herbaceous grasslands, again indicating a preference for this type of habitat.

It was also clear that altitude limited the presence of the cricket, since it was absent from grasslands in the Supra-Mediterranean zone, despite *Messor* and *Tetramorium* nests being common there. Most known records of crickets of the genus *Myrmecophilus* in the Iberian Peninsula and Europe come from low-altitude areas (up to 400 meters above sea level) (Schembri, 1984; Aguirre-Segura et al., 1995; Stalling, 2010, 2016; Espadaler & Olmo-Vidal, 2011; Stalling & Birrer, 2013; Moyano Ayala, 2014; Logachev, 2024). *Myrmecophilus ochraceus* is not an exception, as it has been most frequently found in low-altitude zones. However, during the surveys in Granada, this myrmecophile was also observed at mid-altitudes, between 700 and 950 m above sea level (with a record at 1050 m, although not during the survey), in localities such as Otura, Ogíjares, Cartuja, and Guadix, the latter representing the highest recorded altitude for this species. If some ecological conditions, related to altitude, limit the viability of *Myrmecophilus* populations, this could explain the absence of other species using *Lasius* and *Formica* hosts in the arid Southeastern Spain, since these groups are common mostly at high altitudes (84.5% and 83.9 % of their 97 and 93 nests respectively, were in the Supra-Mediterranean zone in our samplings).

Among the ant genera found to host *Myrmecophilus* in Granada including all records between 2018 and 2025 (*Messor*, *Tetramorium*, and *Monomorium*), four species are cited, as host, for the first time: *Messor ibericus*, *M. erwini, Tetramorium forte*, and *T. biskrense*. It is worth noting that *Messor ibericus* may have been previously recorded under the name *Messor structor* or generally referred to as part of the *structor* group (Schembri, 1984; Cassar et al., 2023; Logachev, 2024), since its morphological distinction from other members of the group is relatively recent (Steiner et al., 2018; Schifani et al., 2021). It is also noteworthy that, after examination of 109 nests of *Pheidole* in Granada, no crickets were detected, not even in open habitats such as grasslands, despite several references indicating this ant genus as a host (Schembri, 1984; Stalling, 2016; Cassar et al., 2023). *M. ochraceus* was also cited once in a nest of *Camponotus amaurus* (Espadaler & Olmo-Vidal, 2011; Logachev, 2024), but this observation requires confirmation. Doubts arise because this species of cricket has not currently been found living with *Camponotus*, so there is a possibility that it might be another species. Moreover, two years after that study, *M. fuscus* was described, which has indeed been found associated with *Camponotus* (Stalling, 2013a; Stalling et al., 2015).

An interesting question related to the range of hosts used by *M. ochraceus* in Spain is the difference in the diet of some of their hosts and, therefore, the obtention of food by the crickets inside ant nests. *Tetramorium* and *Messor* are predominantly granivorous (Collingwood, 1979; Schöning et al., 2004), while *Monomorium* rarely exhibits this type of feeding behavior (Bolton, 1987). Although *Myrmecophilus* species are considered kleptoparasites that steal food from ants (Sanno et al., 2021), the exact diet of *M. ochraceus* has not been studied. According to Hölldobler & Kwapich (2022), mandibular morphology may offer clues about the diet of these insects. For example, *Myrmecophilus albicinctus*, which feeds exclusively via trophallaxis of liquids and cannot ingest food autonomously, has very reduced mandibular teeth. In contrast, *M. formosanus*, which does not participate in trophallaxis and consumes solid food (dead insects, ant eggs, and larvae), possesses more robust teeth (Komatsu et al., 2017; Hölldobler & Kwapich, 2022). The well-developed teeth and apical tooth with a finely denticulate inner edge in the mandibles of *M. ochraceus*, as shown in this study, suggest a possible adaptation for grinding solid materials. Additionally, the cricket has been observed frequently strigillating ant workers (pers. obs.), which may represent a feeding interaction, as proposed for other myrmecophilous species (Komatsu et al., 2013; Hölldobler & Kwapich, 2022). Our results also showed, in accordance with our hypothesis 2, that *M. ochraceus* was more frequently found when ant larvae, pupae, or eggs were present under stones, indicating that access to brood may play an important role in its relationship with hosts. This association could relate both to the presence of brood indicating optimal microclimatic conditions for the cricket under the stone and to the potential availability of food resources derived from the larvae. Further studies testing the ability of *M. ochraceus* individuals to feed on different food sources are needed to understand the nature of its relationship with the different host species used.

Conclusion

Myrmecophilus ochraceus is the only representative of the genus *Myrmecophilus* recorded in the province of Granada, where it inhabits nests of ants from the genera *Messor*, *Tetramorium*, and *Monomorium*, located in low and mid-altitude grasslands (50–1050 m.a.s.l.). Our results, based on programmed surveys of all available species in a variety of habitats in three bioclimatic zones, together with previous records in southern Spain, support the view that climatic conditions and the paleo-biogeographic history of hosts have resulted in a segregated distribution of *Myrmecophilus* species in Iberia. The new information on the distribution and ecology of *M. ochraceus* not only expands current knowledge about its biology but also provides a solid foundation for future studies on interactions between Iberian myrmecophilous crickets and their hosts.

Data availability

The dataset used in this study, as well as UGR (Universidad de Granada) collection data, are available from the repository https://doi.org/10.5281/zenodo.22165530.

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Authors' Contributions

M.L.: conceptualization, methodology, software, formal analysis, investigation, resources, data curation, writing-original draft, visualization.
N.M.V.: conceptualization, methodology, investigation, resources, writing-review & editing.
M.W.S.: Investigation, resources, writing-review & editing.
P.A.: Writing-review & editing, resources, visualization.
M.M.V.: conceptualization, methodology, investigation, resources, writing-review & editing, visualization, supervision, validation.

References

Aguirre-Segura, A., Barranco, P. & Pascual, F. (1995). La colección de ortópteros de la Estación Experimental de Zonas Áridas (C.S.I.C.) de Almería. (Insecta, Orthoptera). Boletín de la Asociación Española de Entomología, 19: 133-155. https://doi.org/10.70186/baeehocv4751

Akino, T., Mochizuki, R., Morimoto, M. & Yamaoka, R. (1996). Chemical camouflage of *Myrmecophilous* cricket *Myrmecophilus* sp. to be integrated with several ant species. Japanese Journal of Applied Entomology and Zoology, 40: 39-46. https://doi.org/10.1303/jjaez.40.39

Alexiou, S., Gavalas, I. & Papapavlou, K. (2017). Orthoptera (Saltatoria) of Iraklia Island, Cyclades, Greece: An annotated and illustrated catalogue. Israel Journal of Entomology, 47: 35-53.

Arcos, J. & García, F. (2023). Hormigas de la península Ibérica y de las Islas Baleares. Independently published, 491 p.

Arcos, M. A., Edo-Botella, R., Balaguer-Beser, Á. & Ruiz, L. Á. (2023). Analyzing independent LFMC empirical models in the mid-Mediterranean region of Spain attending to vegetation types and bioclimatic zones. Forests, 14: Article 7. https://doi.org/10.3390/f14071299

Azevedo, L., Emberson, R., Esteca, F. & Moraes, G. (2015). Macrochelid mites (Mesostigmata: Macrochelidae) as biological control agents. Prospects for Biological Control of Plant Feeding Mites and Other Harmful Organisms, 19: 13-132. https://doi.org/10.1007/978-3-319-15042-0_4

Bergamaschi, D., Moore, W. & Giulio, A.D. (2025). Co-phylogeny and biogeography of the myrmecophilous beetle *Paussus favieri* (Carabidae, Paussinae) and its host ant *Pheidole pallidula* (Hymenoptera, Myrmicinae). Insect Science 0: 1-17. https://doi.org/10.1111/1744-7917.70139

Blender Development Team (2026) Blender (Version 5.2.0 LTS) [Computer software]. Blender Foundation. Available from: https://www.blender.org/download/releases/5-2/ (accessed 30 July 2026). https://doi.org/10.1007/978-1-4302-1977-4_3

Bolton, B. (1987). A review of the *Solenopsis* genus-group and revision of Afrotropical *Monomorium* Mayr (Hymenoptera: Formicidae). Bulletin of the British Museum (Natural History). Entomology, 54: 263-452. https://doi.org/10.1017/s0968045402000019

Cassar, L., Bartolo, A., Stalling, T., Schembri, S. & Massa, B. (2025). *Myrmecophilus baronii* Baccetti, 1966: Biogeography and genetics (Orthoptera: Myrmecophilidae). Fragmenta Entomologica, 57: 9-20. https://doi.org/10.4081/fe.2016.164

Cassar, T., Lapeva-Gjonova, A. & Mifsud, D. (2023). The intranidal myrmecophiles of the Maltese Islands with notes on *Messor* nests as repositories of biodiversity. Insects, 14: 45. https://doi.org/10.3390/insects14010045

Cigliano, M. M., Braun, H., Eades, D. C. & Otte, D. (2025). Orthoptera Species File. Version 5.0/5.0. (Accessed: 18 March 2026). http://Orthoptera.SpeciesFile.org (Accessed: 1 Dec 2025).

Collingwood, C. A. (1979). The Formicidae (Hymenoptera) of Fennoscandia and Denmark (Vol. 8). Scandinavian Science Press, 174 p.

Consejería de Medio Ambiente. (2015). 3ª Adecuación del Plan Forestal Andaluz, Horizonte 2015 [Acuerdo de 7 de septiembre de 2010, del Consejo de Gobierno]. Junta de Andalucía.

De Almeida, T., Blight, O., Mesléard, F., Bulot, A., Provost, E. & Thierry, D. (2020). Harvester ants as ecological engineers for Mediterranean grassland restoration: Impacts on soil and vegetation. Biological Conservation, 245: 1-8. https://doi.org/10.1016/j.biocon.2020.108547

Dean, W. R. J. & Turner, J. S. (1991). Ants nesting under stones in the semi-arid Karoo, South Africa: Predator avoidance or temperature benefits? Journal of Arid Environments, 21: 59-69. https://doi.org/10.1016/s0140-1963(18)30728-6

Dekoninck, W., Lock, K. & Janssens, F. (2007). Acceptance of two native myrmecophilous species, *Platyarthrus hoffmannseggii* (Isopoda: Oniscidea) and *Cyphoderus albinus* (Collembola: Cyphoderidae) by the introduced invasive garden ant *Lasius neglectus* (Hymenoptera: Formicidae) in Belgium. European Journal of Entomology, 104: 159-161. https://doi.org/10.14411/eje.2007.023

Del Río Sánchez, J., Peñas, J., Lorite, J. & Muñoz, J. M. (2019). Itinerario botánico por Sierra Nevada. 9º Congreso de Biología de la Conservación de Plantas, 50 p.

Elmes, G. W. (1996). Biological diversity of ants and their role in ecosystem function. Biodiversity Research and Its Perspectives in East Asia, Chonbuk National University, Jeonju-Si, Korea, 33-48.

Espadaler, X. & Olmo-Vidal, J. (2011). The myrmecophilic cricket *Myrmecophilus* in Spain (Orthoptera, Myrmecophilidae). Sociobiology, 57: 321-328. https://doi.org/10.13102/sociobiology.v62i4.910

Fischer, L. H. (1853). Orthoptera Europaea: Accedunt tabulae lapidibus incisae XVIII quarum ultima coloribus partim illustrata. Wilhelm Engelmann, 500 p.

Franc, V., Majzlan, O., Krištín, A. & Wiezik, M. (2015). On the distribution and ecology of the ant cricket (*Myrmecophilus acervorum*) (Orthoptera: Myrmecophilidae) in Slovakia. Matthias Belivs University Proceedings, 5: 40-50.

Geiselhardt, S., Peschke, K. & Nagel, P. (2007). A review of myrmecophily in ant nest beetles (Coleoptera: Carabidae: Paussinae): Linking early observations with recent findings. Die Naturwissenschaften, 94: 871-894. https://doi.org/10.1007/s00114-007-0271-x

Henderson, G. & Akre, R. D. (1986). Biology of the myrmecophilous cricket, *Myrmecophila manni* (Orthoptera: Gryllidae). Journal of the Kansas Entomological Society, 59: 454-467.

Hsu, P.-W., Hugel, S., Wetterer, J. K., Tseng, S.-P., Ooi, C.-S. M., Lee, C.-Y. & Yang, C.-C. S. (2020). Ant crickets (Orthoptera: Myrmecophilidae) associated with the invasive yellow crazy ant *Anoplolepis gracilipes* (Hymenoptera: Formicidae): Evidence for cryptic species and potential co-introduction with hosts. Myrmecological News, 30: 103-129. https://doi.org/10.26686/wgtn.16999318

Hölldobler, B. & Kwapich, C. L. (2022). The Guests of Ants: How Myrmecophiles Interact with Their Hosts. Cambridge: Harvard University Press, 576 p. https://doi.org/10.2307/j.ctv2n4w5m5

Iorgu, I. Ștefan, Iorgu, E., Stalling, T., Puskás, G., Chobanov, D., Szövényi, G., Moscaliuc, L., Motoc, R., Tăușan, I. & Fusu, L. (2021). Ant crickets and their secrets: *Myrmecophilus acervorum* is not always parthenogenetic (Insecta: Orthoptera: Myrmecophilidae). Zoological Journal of the Linnean Society, 20: 1-18. https://doi.org/10.1093/zoolinnean/zlab084

Jiménez, J. & Tinaut, A. (1992). Mirmecofauna de la Sierra de Loja (Granada) (Hymenoptera, Formicidae). Orsis: Organismes i Sistemes, 7: 97-111.

Junker, E. (1997). Untersuchungen zur Lebensweise und Entwicklung von *Myrmecophilus acervorum* (Panzer, 1799) (Saltatoria: Myrmecophilidae). Articulata, 12: 93-106.

Juvé, Y., Weyna, A., Lauroua, E., Nidelet, S., Khaldi, M., Barech, G., Lebas, C., Rasplus, J.Y., Cruaud, A., Condamine, F.L. & Romiguier, J. (2025). Phylogenomics of *Messor* harvester ants (Hymenoptera: Formicidae: Stenammini) unravels their biogeographical origin and diversification patterns. Systematic Entomology, 50: 1025-1040. https://doi.org/10.1101/2025.02.13.638115

Kaczmarczyk-Ziemba, A., Wagner, G., Staniec, B., Zagaja, M., Pietrykowska-Tudruj, E., Iorgu, E. & Iorgu, I. Ștefan. (2024). Intraspecific diversity of *Myrmecophilus acervorum* (Orthoptera: Myrmecophilidae) indicating an ongoing cryptic speciation. Scientific Reports, 14: 1-18. https://doi.org/10.1038/s41598-024-75335-y

Komatsu, T., Maruyama, M. & Itino, T. (2010). Differences in host specificity and behavior of two ant cricket species (Orthoptera: Myrmecophilidae) in Honshu, Japan. Journal of Entomological Science, 45: 227-238. https://doi.org/10.18474/0749-8004-45.3.227

Komatsu, T., Munetoshi, M., Hattori, M. & Itino, T. (2017). Morphological characteristics reflect food sources and degree of host ant specificity in four *Myrmecophilus* crickets. Insectes Sociaux, 65: 47-57. https://doi.org/10.1007/s00040-017-0586-3

Komatsu, T., Munetoshi, M. & Itino, T. (2013). Nonintegrated host association of *Myrmecophilus tetramorii*, a specialist myrmecophilous ant cricket (Orthoptera: Myrmecophilidae). Psyche: A Journal of Entomology, 2013: 1-5. https://doi.org/10.1155/2013/568536

Kovář, P., Vojtíšek, P. & Zentsova, I. (2013). Ants as ecosystem engineers in natural restoration of human made habitats.

Journal of Landscape Ecology, 6: 18-31. https://doi.org/10.2478/v10285-012-0061-9

Lapeva-Gjonova, A., Csősz, S. & Báthori, F. (2022). Fungi associated with *Messor* ants on the Balkan Peninsula: first biogeographical data. Diversity, 14: 1–8. https://doi.org/10.3390/d14121132

Logachev, M. (2024). Ant-associated crickets of the genus *Myrmecophilus* Berthold, 1827 in the Iberian Peninsula and Balearic Islands. Iberomyrmex, 13: 30-42.

Loidi, J. (2017). The Vegetation of the Iberian Peninsula. Cham: Springer Nature, 676.

Maggenti, M. A. B., Maggenti, A. R. & Gardner, S. L. (2017). Dictionary of Invertebrate Zoology. Zea E-Books Collection, 61 p. https://doi.org/10.13014/k2dr2sn5

Mérel, V., Vogel, S., Lavanchy, G., Dumas, Z., Labédan, M., Stalling, T. & Schwander, T. (2025). Recent neo-X and Y sex chromosomes in an ant cricket. Journal of Evolutionary Biology, 38: 1000-1007. https://doi.org/10.1101/2024.06.21.599884

Moyano Ayala, L. (2014). Estudio y seguimiento de la fauna de Orthoptera de un entorno natural sometido a un programa de restauración ecológica en el sur de la Península Ibérica (Doctoral Dissertation). University of Cordoba, 284 p.

Offenberg, J. (2001). Balancing between mutualism and exploitation: The symbiotic interaction between *Lasius* ants and aphids. Behavioral Ecology and Sociobiology, 49: 304-310. https://doi.org/10.1007/s002650000303

Ortiz, F. J. & Tinaut, J. A. (1988). Formícidos del litoral granadino. Orsis: Organismes i Sistemes, 3: 145-163.

Pardo, G., Del Prado, A., Martínez-Mena, M., Bustamante, M., Rodriguez Martin, J. A., Álvaro-Fuentes, J. & Moral, R. (2016). Orchard and horticulture systems in Spanish Mediterranean coastal areas: Is there a real possibility to contribute to C sequestration? Agriculture, Ecosystems & Environment, 238: 153-167. https://doi.org/10.1016/j.agee.2016.09.034

Pierce, N., Braby, M., Heath, A., Lohman, D., Mathew, J., Rand, D. & Travassos, M. (2002). The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annual Review of Entomology, 47: 733-771. https://doi.org/10.1146/annurev.ento.47.091201.145257

Posit team. (2026). RStudio: Integrated Development Environment for R (Version 4.5.2) [Computer software]. Posit Software, PBC. http://www.posit.co/

QGIS Development Team. (2026). QGIS Geographic Information System (Version 4.2) [Computer software]. QGIS Association. http://qgis.org

Reznikova, Z. (2001). Interaction of the ant *Myrmica rubra* L. as a predator with springtails (Collembola) as a mass prey. Doklady Biological Sciences: Proceedings of the Academy of Sciences of the USSR, Biological Sciences Sections/ Translated from Russian, 380: 475-477. https://doi.org/10.1023/a:1012383607521

Rodríguez-Castilla, G. & Stalling, T. (2025). The Mediterranean ant cricket *Myrmecophilus myrmecophilus* (Savi, 1819), new species for Portugal (Orthoptera: Myrmecophilidae). Heteropterus Revista de Entomología, 25: 303-306. https://doi.org/10.13102/sociobiology.v62i4.910

Salata, S., Kalarus, K., Borowiec, L., Trichas, A. & Kujawa, K. (2020). How estimated ant diversity is biased by the sampling method? A case study of Crete: a Mediterranean biodiversity hotspot. Biodiversity and Conservation, 29: 3031-3050. https://doi.org/10.1007/s10531-020-02014-5

Sandoval Cortés, P. J., Aguayo Becerra, D., Tinaut, A. & Ruano Díaz, F. (2024). Dataset of the arthropodofauna of Sierra Nevada from the zoological collections of the University of Granada. Version 1.8. Dept. Of Zoology, Faculty of Science, University of Granada. Occurrence dataset. [Dataset]. https://doi.org/10.7818/ecos.2356

Sanno, R., Kataoka, K., Hayakawa, S., Ide, K., Chuong, N., Nguyen, T., Le, B., Kim, O., Mineta, K., Takeyama, H., Takeda, M., Sato, T., Suzuki, T., Yura, K. & Asahi, T. (2021). Comparative analysis of mitochondrial genomes in Gryllidea (Insecta: Orthoptera): Implications for adaptive evolution in ant-loving crickets. Genome Biology and Evolution, 13: 1-8. https://doi.org/10.1093/gbe/evab222

Schembri, S. P. (1984). Notes on the Orthoptera of the Maltese Islands: The genus *Myrmecophilus* (Orthoptera: Gryllidae). The Central Mediterranean Naturalist, 1: 57-59.

Schifani, E., Nalini, E., Gentile, V., Alamanni, F. M., Ancona, C., Caria, M., Cillo, D. & Bazzato, E. (2021). Ants of Sardinia: An updated checklist based on new faunistic, morphological and biogeographical notes. Journal of Zoology, 104: 2135. https://doi.org/10.19263/redia-104.21.03

Schöning, C., Espadaler, X., Hensen, I. & Roces, F. (2004). Seed predation of the tussock-grass *Stipa tenacissima* L. by ants (*Messor* spp.) in southeastern Spain: The adaptive value of trypanocarpy. Journal of Arid Environments, 56: 43-61. https://doi.org/10.1016/s0140-1963(03)00024-7

Stalling, T. (2010). First record of the ant-loving cricket *Myrmecophilus ochraceus* for Zakynthos (Greece) with notes on the synonymy of *Myrmecophilus salomonis* (Orthoptera: Myrmecophilidae). Entomologia Hellenica, 19: 1. https://doi.org/10.12681/eh.11592

Stalling, T. (2013a). A new species of ant-loving cricket from Mallorca, Balearic Islands, Spain (Orthoptera, Myrmecophilidae). Graellsia, 69: 153-156. https://doi.org/10.3989/graellsia.2013.v69.073

Stalling, T. (2013b). *Myrmecophilus balcanicus*, a new species of ant-loving cricket from the Former Yugoslav Republic of

Macedonia, with notes on the synonymy of *Myrmecophilus zorae*. Entomologia Hellenica, 22: 29-34. https://doi.org/10.12681/eh.11526

Stalling, T. (2015). New records of the ant-loving cricket *Myrmecophilus fuscus* Stalling, 2013 from the Mediterranean Basin (Orthoptera: Myrmecophilidae). Articulata, 30: 105-108. https://doi.org/10.13102/sociobiology.v62i4.910

Stalling, T. (2016). The presence of the ant-loving cricket *Myrmecophilus ochraceus* in Sardinia, Italy (Orthoptera: Myrmecophilidae). Fragmenta Entomologica, 48: 17. https://doi.org/10.4081/fe.2016.164

Stalling, T. (2017). *Myrmecophilus gallicus*, a new species of ant cricket from France (Orthoptera: Myrmecophilidae). Articulata, 32: 1-7. https://doi.org/10.1080/09397140.2017.1290764

Stalling, T. (2024). *Myrmecophilus jordanicus*, a new species of ant cricket from Jordan and Israel, with notes on the synonymy of *Myrmecophilus nigricornis* (Orthoptera: Myrmecophilidae). Israel Journal of Entomology, 53: 25-32. https://doi.org/10.12681/eh.11592

Stalling, T. & Birrer, S. (2013). Identification of the ant-loving crickets, *Myrmecophilus* Berthold, 1827 (Orthoptera: Myrmecophilidae), in Central Europe and the northern Mediterranean Basin. Articulata, 28: 1-11. https://doi.org/10.1080/09397140.2017.1290764

Stalling, T., Espadaler, X. & Carron, N. (2015). First record of the ant-loving cricket *Myrmecophilus fuscus* Stalling, 2013 (Orthoptera: Myrmecophilidae) in mainland Spain. Sociobiology 62: 481-483. https://doi.org/10.13102/sociobiology.v62i4.910

Stalling, T., Iorgu, I. Ștefan & Chobanov, D. (2020). The ant cricket *Myrmecophilus orientalis* on the Dodecanese Islands, Greece (Orthoptera: Myrmecophilidae). Travaux Du Muséum National d'Histoire Naturelle "Grigore Antipa"Antipa", 63: 63-67. https://doi.org/10.3897/travaux.63.e49546

Stalling, T., Sjödahl, M. & Ulrik, P. (2017). Records of the ant cricket *Myrmecophilus acervorum* from the northern border of the distribution range (Orthoptera: Myrmecophilidae). Entomologisk Tidskrift, 138: 97-101. https://doi.org/10.3897/caucasiana.1.e87210

Steiner, F., Csősz, S., Markó, B., Gamisch, A., Rinnhofer, L., Folterbauer, C., Hammerle, S., Stauffer, C., Arthofer, W., & Schlick-Steiner, B. (2018). Turning one into five: Integrative taxonomy uncovers complex evolution of cryptic species in the harvester ant *Messor* "structor". Molecular Phylogenetics and Evolution, 127: 387-404. https://doi.org/10.1016/j.ympev.2018.04.005

Temreshev, I. (2020). First record of the ant-loving cricket *Myrmecophilus crenatus* Gorochov, 1986 (Orthoptera, Myrmecophilidae) in Kazakhstan. Acta Biologica Sibirica, 6: 407-412. https://doi.org/10.3897/abs.6.e54135

Tinaut, A., Jiménez Rojas, J. & Pascual, R. (1994). Estudio de la mirmecofauna de los bosques de *Quercus* Linneo, 1753 de la provincia de Granada (Hymenoptera; Formicidae). Ecología, 8: 429-438. https://doi.org/10.35537/10915/4507

Tinaut, A., Martínez-Ibáñez M. D. & Ruano, F. (2007). Inventario de las especies de formícidos de Sierra Nevada, Granada (España) (Hymenoptera, Formicidae). Zool. Baetica, 18: 49-68.

Tinaut, A., Ruano, F. (2021). Biogeography of Iberian ants (Hymenoptera: Formicidae). Diversity, 13: 88. https://doi.org/10.3390/d13020088

Valle, F. (1985). Mapa de las series de vegetacion de Sierra-Nevada (España). https://doi.org/10.3406/ecmed.1985.1105

Wetterer, J. & Hugel, S. (2008). Worldwide spread of the ant cricket *Myrmecophilus americanus*, a symbiont of the longhorn crazy ant, *Paratrechina longicornis*. Sociobiology, 52: 157-165. https://doi.org/10.1603/ice.2016.94406

ANNEX I

Ant nests revised during the programmed surveys 2024–2025

Aphaenogaster

Aphaenogaster sardoa Complex (15 nests revised). No crickets;

Aphaenogaster gibbosa (Latreille, 1798) (14 nests revised). No crickets;

Aphaenogaster iberica Emery, 1908 (40 nests revised). No crickets;

Aphaenogaster senillis (5 nests revised). No crickets;

Bothriomyrmex

Bothriomyrmex sp. (4 nests revised). No crickets;

Bothriomyrmex atlantis Forel, 1894 (1 nests revised). No crickets;

Camponotus

Camponotus sp. (12 nests revised). No crickets;

Camponotus aethiops (Latreille, 1798) (2 nests revised). No crickets;

Camponotus cruentatus (Latreille, 1802) (22 nests revised). No crickets;

Camponotus foreli Emery, 1881 (4 nests revised). No crickets;

Camponotus lateralis (Olivier, 1792) (9 nests revised). No crickets;

Camponotus micans (Nylander, 1856) (4 nests revised). No crickets;

Camponotus piceus (Leach, 1825) (3 nests revised). No crickets;

Camponotus pilicornis (Roger, 1859) (35 nests revised). No crickets;

Camponotus sylvaticus (Olivier, 1792) (77 nests revised). No crickets;

Cataglyphis

Cataglyphis iberica (3 nests revised). No crickets;

Cataglyphis velox Santschi, 1929 (9 nests revised). No crickets;

Crematogaster

Crematogaster sp. (5 nests revised). No crickets;

Crematogaster auberti Emery, 1869 (33 nests revised). No crickets;

Crematogaster laestrygon Emery, 1869 (1 nests revised). No crickets;

Crematogaster scutellaris (Olivier, 1792) (1 nests built in a log revised). No crickets;

Crematogaster sordidula (Nylander, 1849) (20 nests revised). No crickets;

Formica

Formica sp. (80 nests revised). No crickets;

Formica cunicularia Latreille, 1798 (1 nests revised). No crickets;

Formica tombeuri Bondroit, 1917 (1 nests revised). No crickets;

Formica fusca Linnaeus, 1758 (10 nests revised). No crickets;

Formica gerardi Bondroit, 1917 (1 nests revised). No crickets;

Goniomma

Goniomma baeticum Reyes, Espadaler & Rodriguez, 1987 (1 nests revised). No crickets;

Iberoformica

Iberoformica subrufa (Roger, 1859) (7 nests revised). No crickets;

Lasius

Lasius sp. (81 nests revised). No crickets;

Lasius cinereus Seifert, 1992 (3 nests revised). No crickets;

Lasius flavus (Fabricius, 1782) (3 nests revised). No crickets;

Lasius grandis Forel, 1909 (2 nests revised). No crickets;

Lasius lasioides (Emery, 1869) (1 nests revised). No crickets;

Lasius myops Forel, 1894 (5 nests revised). No crickets;

Lasius piliferus Seifert, 1992 (2 nests revised). No crickets;

Messor

Messor sp. (1 nests revised). No crickets;

Messor barbarus (Linnaeus, 1767) (25 nests revised). Cricket found in 6;

Messor bouvieri Bondroit, 1918 (4 nests revised). No crickets;

Messor erwini Orou et al., 2023 (10 nests revised). No crickets;

Monomorium

Monomorium algiricum (Bernard, 1955) (3 nests revised). No crickets;

Monomorium subopacum (Smith, 1858) (24 nests revised). Cricket found in 10;

Oxyopomyrmex

Oxyopomyrmex magnus Salata & Borowiec, 2015 (3 nests revised). No crickets;

Pheidole

Pheidole pallidula (Nylander, 1849) (106 nests revised). No crickets;

Plagiolepis

Plagiolepis sp. (196 nests revised). No crickets;

Plagiolepis pygmaea (Latreille, 1798) (3 nests revised). No crickets;

Plagiolepis schmitzii Forel, 1895 (13 nests revised). No crickets;

Proformica

Proformica sp. (1 nests revised). No crickets;

Solenopsis

Solenopsis sp. (5 nests revised). No crickets;

Tapinoma

Tapinoma sp. (23 nests revised). No crickets;

Tapinoma erraticum (Latreille, 1798) (1 nests revised). No crickets;

Tapinoma gr. *nigerrimum* (35 nests revised). No crickets;

Temnothorax

Temnothorax sp. (2 nests revised). No crickets;

Temnothorax cristinae (Espadaler, 1997) (1 nests revised). No crickets;

Temnothorax fuentei (Santschi 1919) (2 nests revised). No crickets;

Temnothorax gr. *luteus* (16 nests revised). No crickets;

Temnothorax exilis group (2 nests revised). No crickets;

Temnothorax recedens (Nylander, 1856) (2 nests revised). No crickets;

Temnothorax tyndalei (Forel, 1909) (14 nests revised). No crickets;

Temnothorax unifasciatus (Latreille, 1798) (3 nests revised). No crickets;

Tetramorium

Tetramorium sp. (46 nests revised). No crickets;

Tetramorium biskrense Forel, 1904 (3 nests revised). Cricket found in 3;

Tetramorium forte Forel, 1904 (74 nests revised). Cricket found in 1;

Tetramorium gr. *caespitum* (5 nests revised). No crickets;

Tetramorium semilaeve André, 1883 (16 nests revised). Cricket found in 2.

ANNEX II

List of *Myrmecophilus ochraceus* crickets recorded during the years 2018–2025 in Granada.

Granada and surrounding areas

Albolote (37.22583, -3.65161); 15.X.2018; *M. ochraceus* (1 adult); leg. Óscar; nest of *Messor* sp. (without brood)

Atarfe (37.2358, -3.7161); 29.IX.2019; *M. ochraceus*; leg. Ana María Bergillos y David Fernández; nest of *Messor* sp. (~20 workers without brood)

Cartuja (37.19636, -3.59822); 5.V.2025; *M. ochraceus* (1♀, 1♂); leg. Matvey Logachev; nest of *Messor barbarus* (~200 workers with brood). Collection ID: 23357-CG

Cartuja (37.19617, -3.59852); 5.IV.2025; *M. ochraceus* (1 juv.); leg. Matvey Logachev; nest of *Tetramorium semilaeve* (with brood)

Cartuja (37.1973, -3.5955); 5.IV.2025; *M. ochraceus* (1 juv.); leg. Matvey Logachev; nest of *Tetramorium semilaeve* (with brood)

Cartuja (37.19754, -3.58953); 24.X.2024; *M. ochraceus* (1♂); leg. Matvey Logachev; nest of *Messor barbarus* (with brood). Collection ID: 23392-CG

Cartuja (37.19227, -3.59042); 30.IX.2024; *M. ochraceus* (1♀); leg. Matvey Logachev; nest of *Messor barbarus* (~1000 workers with brood). Collection ID: 23401-CG

Cartuja (37.19227, -3.59042); 21.IX.2024; *M. ochraceus* (4 juv.); leg. Matvey Logachev; nest of *Messor barbarus* (~1000 workers with brood). Collection ID: 23389-CG, 23390-CG, 23391-CG

Cartuja (37.12546, -3.62778); 14.IV.2024; *M. ochraceus* (1♀); leg. Matvey Logachev; nest of *Messor barbarus* (~100 workers with brood). Collection ID: 23370-CG

Cartuja (37.19364, -3.59397); 23.X.2020; *M. ochraceus* (1♀); leg. Manuel Martín-Vivaldi y Víctor Escribano; nest of *Messor barbarus* (without brood)

Cartuja (37.19364, -3.59397); 23.X.2020; *M. ochraceus* (1♀); leg. Manuel Martín-Vivaldi y Víctor Escribano; without ant nest

Cartuja (37.19364, -3.59397); 23.X.2020; *M. ochraceus* (3♀, 6♂, 2 juv.); leg. Manuel Martín-Vivaldi y Víctor Escribano; nest of *Messor bouvieri* (with brood)

Cartuja (37.19364, -3.59397); 16.VI.2020; *M. ochraceus* (1 juv.); leg. Manuel Martín-Vivaldi y Víctor Escribano; nest of *Messor barbarus* (without brood)

Cartuja (37.19364, -3.59397); 16.VI.2020; *M. ochraceus* (1 juv.); leg. Manuel Martín-Vivaldi y Víctor Escribano; nest of *Messor ibericus* (with brood)

Cartuja (37.19364, -3.59397); 16.VI.2020; *M. ochraceus* (1♀, 1♂, 1 juv.); leg. Manuel Martín-Vivaldi y Víctor Escribano; nest of *Messor bouvieri* (with brood)

Cartuja (37.19364, -3.59397); 16.VI.2020; *M. ochraceus* (1♀, 1♂, 4 juv.); leg. Manuel Martín-Vivaldi y Víctor Escribano; nest of *Messor barbarus* (with brood)

Cartuja (37.19364, -3.59397); 16.VI.2020; *M. ochraceus* (2♂, 4 juv.); leg. Manuel Martín-Vivaldi y Víctor Escribano; nest of *Messor barbarus* (without brood)

Cartuja (37.19364, -3.59397); 11.VI.2020; *M. ochraceus* (1 juv., 1 adult); leg. Manuel Martín-Vivaldi; nest of *Messor bouvieri* (without brood)

Cartuja (37.19364, -3.59397); 28.V.2020; *M. ochraceus* (3 juv.); leg. Manuel Martín-Vivaldi; nest of *Tetramorium* sp. (without brood)

Cartuja (37.19364, -3.59397); 28.V.2020; *M. ochraceus* (3♀, 1 juv.); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (without brood)

Cartuja (37.1935, -3.5943); 28.X.2019; *M. ochraceus* (1♂); leg. Víctor Escribano y Manuel Fernández Pernía; nest of *Messor barbarus* (~100 workers without brood)

Cartuja (37.19364, -3.59397); 25.X.2019; *M. ochraceus* (5♀, 1♂); leg. Víctor Escribano; nest of *Messor barbarus* (without brood)

Cartuja (37.19364, -3.59397); 25.X.2019; *M. ochraceus* (1♀, 1♂); leg. Víctor Escribano y Manuel Fernández Pernía; nest of *Messor bouvieri* (~200 workers without brood)

Cartuja (37.1935, -3.5945); 25.X.2019; *M. ochraceus* (2♀, 1♂); leg. Víctor Escribano y Manuel Fernández Pernía; nest of *Messor barbarus* (~150 workers without brood)

Cartuja (37.19364, -3.59397); 17.X.2019; *M. ochraceus*; leg. Manuel Martín-Vivaldi y Víctor Escribano; nest of *Messor barbarus* (without brood)

Cartuja (37.19364, -3.59397); 17.X.2019; *M. ochraceus* (1♀); leg. Manuel Martín-Vivaldi y Víctor Escribano; nest of *Messor barbarus* (~100 workers without brood)

Cartuja (37.19364, -3.59397); 17.X.2019; *M. ochraceus* (1♀); leg. Manuel Martín-Vivaldi y Víctor Escribano; nest of *Messor bouvieri* (without brood)

Cartuja (37.19364, -3.59397); 15.X.2019; *M. ochraceus* (1♀); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (without brood)

Cartuja (37.19364, -3.59397); 15.X.2019; *M. ochraceus* (1♂); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (without brood)

Cartuja (37.1935, -3.5943); 23.IX.2019; *M. ochraceus* (3♂); leg. Víctor Escribano y Manuel Fernández Pernía; nest of *Messor barbarus* (~300 workers with brood)

Cartuja (37.1935, -3.5945); 23.IX.2019; *M. ochraceus* (1♀, 2♂); leg. Víctor Escribano y Manuel Fernández Pernía; nest of *Messor bouvieri* (~250 workers with brood)

Cartuja (37.19364, -3.59397); 15.VIII.2019; *M. ochraceus* (2♀); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (without brood)

Cartuja (37.19364, -3.59397); 11.VIII.2019; *M. ochraceus* (2♀); leg. Manuel Martín-Vivaldi; nest of *Messor bouvieri* (without brood)

Cartuja (37.19364, -3.59397); 10.VIII.2019; *M. ochraceus*; leg. Manuel Martín-Vivaldi; nest of *Messor bouvieri* (without brood)

Cartuja (37.19364, -3.59397); 22.X.2018; *M. ochraceus* (1♀, 1♂); leg. Manuel Martín-Vivaldi; nest of *Messor bouvieri* (without brood)

Cartuja (37.19364, -3.59397); 20.X.2018; *M. ochraceus*; leg. Manuel Martín-Vivaldi; nest of *Messor bouvieri* (without brood)

Cartuja (37.19364, -3.59397); 17.X.2018; *M. ochraceus* (1♀); leg. Manuel Martín-Vivaldi y Víctor Escribano; under a stone without any ant colony, there was only an *Aphaenogaster dulcineae* founder queen, but there was no apparent interaction of the cricket with the queen.

Cartuja (37.19364, -3.59397); 17.X.2018; *M. ochraceus* (1♂); leg. Manuel Martín-Vivaldi y Víctor Escribano; nest of *Messor bouvieri* (without brood)

Cartuja (37.19364, -3.59397); 15.X.2018; *M. ochraceus*; leg. Víctor Escribano; nest of *Messor* sp. (without brood)

Cartuja (37.19364, -3.59397); 15.X.2018; *M. ochraceus*; leg. Víctor Escribano; nest of *Tetramorium* sp. (without brood)

Granada (37.12546, -3.62778); 24.IX.2024; *M. ochraceus* (1♀, 1♂); leg. Matvey Logachev; nest of *Messor barbarus* (without brood)

Granada (37.19757, -3.59064); 8.IX.2024; *M. ochraceus* (1♂, 1 juv.); leg. Matvey Logachev; nest of *Messor barbarus* (without brood). Collection ID: 23404-CG (Figure 6A)

Granada (37.19227, -3.59042); 14.IV.2024; *M. ochraceus* (1 juv.); leg. Matvey Logachev; nest of *Messor barbarus* (without brood)

Granada (37.1968, -3.59082); 6.IV.2024; *M. ochraceus* (1 juv.); leg. Matvey Logachev; nest of *Tetramorium forte* (without brood)

Granada (37.19661, -3.59236); 28.I.2024; *M. ochraceus* (2♀, 1♂); leg. Matvey Logachev; nest of *Messor barbarus* (without brood)

Granada (37.19691, -3.59206); 28.I.2024; *M. ochraceus* (1♂); leg. Matvey Logachev; nest of *Messor barbarus* (without brood)

Granada (37.1769, -3.6141); 7.X.2019; *M. ochraceus*; leg. Carlos Olmedo y Laura Valenzuela; nest of *Messor barbarus* (~20 workers without brood)

Granada (37.1769, -3.6141); 29.IX.2019; *M. ochraceus*; leg. Carlos Olmedo y Laura Valenzuela; nest of *Messor barbarus* (~20 workers without brood)

Granada (37.1769, -3.6141); 25.IX.2019; *M. ochraceus*; leg. Carlos Olmedo y Laura Valenzuela; nest of *Messor barbarus* (~20 workers without brood)

Granada (37.16196, -3.61153); 2018; *M. ochraceus* (2 juv.); leg. Víctor Escribano; nest of *Tetramorium* sp. (without brood)

Guadix (37.32201, -3.12645); 31.V.2025; *M. ochraceus* (1♀); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (without brood)

Guadix (37.29488, -3.10652); 29.IV.2025; *M. ochraceus* (3 juv.); leg. Manuel Martín-Vivaldi; nest of *Tetramorium forte* (~500 workers with brood). Collection ID: 23398-CG

Guadix (37.32273, -3.12727); 4.IV.2025; *M. ochraceus* (1 juv.); leg. Manuel Martín-Vivaldi; nest of *Tetramorium forte* (without brood)

Guadix (37.32273, -3.12727); 4.IV.2025; *M. ochraceus* (2♂); leg. Manuel Martín-Vivaldi; nest of *Messor erwini* (without brood). Collection ID: 23395-CG

Ogíjares (37.12526, -3.62722); 14.IV.2024; *M. ochraceus* (1 juv.); leg. Manuel Martín-Vivaldi; nest of *Tetramorium biskrense* (~200 workers with brood)

Ogíjares (37.12544, -3.62695); 14.IV.2024; *M. ochraceus* (1 adult); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (~80 workers with brood)

Ogíjares (37.12546, -3.62778); 14.IV.2024; *M. ochraceus* (1♀); leg. Nerea Megías-Valero; nest of *Messor barbarus* (without brood). Collection ID: 23368-CG

Ogíjares (37.12546, -3.62778); 14.IV.2024; *M. ochraceus* (>20 juv.); leg. Matvey Logachev; nest of *Tetramorium forte* (~2500 workers with brood). Collection ID: 23367-CG

Ogíjares (37.12546, -3.62778); 14.IV.2024; *M. ochraceus* (2♀, 2♂, 2 adults); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (~80 workers without brood). Collection ID: 23369-CG

Ogíjares (37.12554, -3.62756); 14.IV.2024; *M. ochraceus* (1 juv.); leg. Matvey Logachev; nest of *Tetramorium semilaeve* (~1500 workers with brood)

Otura (37.19754, -3.58953); 13.XII.2024; *M. ochraceus* (1♂); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (without brood). Collection ID: 23393-CG

Otura (37.08956, -3.62487); 13.V.2024; *M. ochraceus* (1♀, 1 juv.); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (without brood). Collection ID: 23387-CG, 23388-CG

Otura (37.08956, -3.62487); 26.IV.2024; *M. ochraceus* (1 juv.); leg. Manuel Martín-Vivaldi; nest of *Tetramorium semilaeve* (without brood). Preserved with its molt. Collection ID: 23380-CG

Otura (37.08956, -3.62487); 26.IV.2024; *M. ochraceus* (1♀, 2♂, 1 juv.); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (with brood). Collection ID: 23377-CG, 23381-CG, 23382-CG, 23384-CG

Otura (37.08956, -3.62487); 11.IV.2024; *M. ochraceus* (7♀, 3♂, 3 juv.); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (with brood). Collection ID: 23365-CG, 23366-CG, 23371-CG, 23372-CG, 23373-CG, 23375-CG, 23376-CG, 23378-CG, 23379-CG, 23383-CG, 23385-CG

Otura (37.07974, -3.6109); 11.IV.2024; *M. ochraceus*; leg. Manuel Martín-Vivaldi; nest of *Messor bouvieri* (without brood)

Otura (37.07974, -3.6109); 21.III.2024; *M. ochraceus* (10 juv.); leg. Manuel Martín-Vivaldi; nest of *Tetramorium* gr. *caespitum* (~800 workers with brood)

Otura (37.07974, -3.6109); 21.III.2024; *M. ochraceus* (2 juv., 12 adults); leg. Manuel Martín-Vivaldi; nest of *Messor bouvieri* (~15 workers without brood)

Otura (37.07974, -3.6109); 21.III.2024; *M. ochraceus* (2 juv.); leg. Manuel Martín-Vivaldi; nest of *Tetramorium* gr. *caespitum* (~30 workers without brood)

Otura (37.08956, -3.62487); 21.III.2024; *M. ochraceus* (12♀, 4♂, 2 juv.); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (with brood). Collection ID: 23351-CG, 23352-CG, 23353-CG, 23358-CG, 23359-CG, 23360-CG, 23361-CG, 23362-CG, 23363-CG. 23364-CG. 23405-CG (Fig 5A-C), 23406-CG (Fig 6B), 23407-CG (Fig 4)

Santa Fe (37.19151, -3.70293); 2019; *M. ochraceus* (1 adult); leg. Belén Arenas Pérez; nest of *Messor* sp. (without brood)

Los Gualchos

Los Gualchos (36.71236, -3.40896); 22.III.2025; *M. ochraceus* (3 juv.); leg. Matvey Logachev; nest of *Monomorium subopacum* (without brood)

Los Gualchos (36.71284, -3.40863); 10.II.2025; *M. ochraceus* (2 juv.); leg. Manuel Martín-Vivaldi; nest of *Monomorium subopacum* (~1000 workers with brood). Collection ID: 23402-CG

La Herradura

La Herradura (36.74339, -3.74642); 6.II.2025; *M. ochraceus* (1 juv.); leg. Manuel Martín-Vivaldi; nest of *Monomorium subopacum* (~70 workers with brood). Collection ID: 23348-CG

La Herradura (36.74339, -3.74642); 6.II.2025; *M. ochraceus* (1♀, 1♂); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (~50 workers with brood). Collection ID: 23350-CG.

La Herradura (36.74344, -3.74715); 6.II.2025; *M. ochraceus* (1 juv.); leg. Mathias Welz-Sol; nest of *Tetramorium semilaeve* (~500 workers with brood)

La Herradura (36.74394, -3.7471); 6.II.2025; *M. ochraceus* (2 juv.); leg. Matvey Logachev; nest of *Monomorium subopacum* (without brood)

La Herradura (36.74394, -3.7471); 6.II.2025; *M. ochraceus* (3 juv.); leg. Mathias Welz-Sol; nest of *Monomorium subopacum* (~400 workers with brood). Collection ID: 23367-CG

La Herradura (36.74402, -3.74697); 6.II.2025; *M. ochraceus* (3 juv.); leg. Matvey Logachev; nest of *Monomorium subopacum* (~1000 workers with brood). Collection ID: 23349-CG

La Herradura (36.7445, -3.74716); 6.II.2025; *M. ochraceus* (6 juv.); leg. Mathias Welz-Sol; nest of *Monomorium subopacum* (~400 workers with brood). Collection ID: 23403-CG

La Herradura (36.74391, -3.74756); 18.V.2024; *M. ochraceus* (1 juv.); leg. Nerea Megías-Valero; nest of *Messor barbarus* (~100 workers with brood). Collection ID: 23386-CG

La Herradura (36.74415, -3.74645); 5.V.2024; *M. ochraceus* (1 juv.); leg. Manuel Martín-Vivaldi; nest of *Monomorium subopacum* (~150 workers with brood)

Motril

Motril (36.77307, -3.50322); 13.IV.2025; *M. ochraceus* (1 juv.); leg. Matvey Logachev; nest of *Monomorium subopacum* (~200 workers with brood). Collection ID: 23356-CG

Motril (36.77427, -3.50373); 13.IV.2025; *M. ochraceus* (1 juv., 1 adult); leg. Manuel Martín-Vivaldi; nest of *Messor bouvieri* (~300 workers with brood)

Motril (36.77427, -3.50373); 13.IV.2025; *M. ochraceus* (2 juv.); leg. Manuel Martín-Vivaldi; nest of *Monomorium subopacum* (~200 workers with brood). Collection ID: 23400-CG

Motril (36.77462, -3.50539); 13.IV.2025; *M. ochraceus* (1 juv.); leg. Mathias Welz-Sol; nest of *Monomorium subopacum* (~50 workers with brood). Collection ID: 23355-CG

Salobreña

Salobreña (36.75471, -3.60003); 16.II.2025; *M. ochraceus* (4 juv.); leg. Matvey Logachev; nest of *Monomorium subopacum* (~2000 workers with brood). Collection ID: 23354-CG

Salobreña (36.75493, -3.59975); 16.II.2025; *M. ochraceus* (1 juv.); leg. Manuel Martín-Vivaldi; nest of *Monomorium subopacum* (~250 workers with brood)

Salobreña (36.75493, -3.59975); 16.II.2025; *M. ochraceus* (1 juv.); leg. Manuel Martín-Vivaldi; nest of *Tetramorium biskrense* (~300 workers with brood). Collection ID: 23394-CG

Salobreña (36.75493, -3.59975); 16.II.2025; *M. ochraceus* (3 juv.); leg. Manuel Martín-Vivaldi; nest of *Tetramorium biskrense* (~600 workers with brood). Collection ID: 23396-CG

Salobreña (36.75493, -3.59975); 16.II.2025; *M. ochraceus* (4 juv.); leg. Manuel Martín-Vivaldi; nest of *Monomorium subopacum* (~1000 workers with brood). Collection ID: 23399-CG

Salobreña (36.75493, -3.59975); 16.II.2025; *M. ochraceus* (6 juv.); leg. Manuel Martín-Vivaldi; nest of *Monomorium subopacum* (~1000 workers with brood). Collection ID: 23374-CG

Salobreña (36.75494, -3.59988); 16.II.2025; *M. ochraceus* (1♀, 1♂, 5 juv.); leg. Manuel Martín-Vivaldi; nest of *Messor barbarus* (~35 workers without brood). Collection ID: 23397-CG